

The dental evidence on the differentiation of the ctenomyine rodents (Caviomorpha, Octodontidae, Ctenomyinae)

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Primitive species in the differentiation of the subfamily Ctenomyinae are revisited, and, on molar evidence, a new interpretation of the evolutionary pattern of these earliest members of the group is proposed. The octodontid *Phloramys* is rejected as possible ancestor, whereas the genus *Chasichimys* (including *Pattersonmys*), previously included in the family Echimyidae, is transferred to the Octodontidae as a primitive member of the ctenomyine radiation. During the Chasicoan and Huayquerian Ages (Late Miocene), an anagenetic event represented by an increase of hypsodonty in *Chasichimys*, may have led to the differentiation of the primitive euhypsodont ctenomyines of the genus *Xenodontomys*. Coeval cladogenetic processes, occurring during the protohypsodont evolutionary stage of the group, would have resulted in the separation of the genus *Palaeoctodon* from the lineage *Chasichimys-Xenodontomys*. These ancient representatives of the subfamily would have differentiated in central Argentine pampas. The recognition of such evolutionary events and concordant evidence from other octodontoid rodents suggest temporal differences among the outcroppings of the Cerro Azul Formation in central Argentina.

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Introduction

Living members of the family Octodontidae are small to middle-sized caviomorph rodents with derived euhypsodont molars (*sensu* Mones 1982), terrestrial to subterranean habits, and are endemic to southern South America (Mares and Ojeda 1982, Woods 1984).

In accordance with the evidence of the most ancient extinct species (*Platypitamyas brachyodon* Wood, 1949, *Migraveramus beatus* Patterson and Wood, 1982), this family has been considered the most primitive among the New World Hystricognathi, probably ancestral to the remaining families except for the peculiar Erethizontidae (Wood 1949, Wood 1955, Wood and Patterson 1959, Patterson and Pascual 1972, Patterson and Wood 1982). However, those taxa of Deseadan to Friasian Age (Middle Oligocene–Middle Miocene) have doubtful taxonomic relationships (Reig 1986, 1989, Vucetich and Verzi 1991). Only since the Chasicoan Age (Late Miocene), can undisputed Octodontidae, with hypsodont molars and increasingly simplified occlusal designs, be recognized.

Ctenomyinae was scarcely diversified in the Latest Miocene; one genus (*Palaeoctodon*) or two (*Palaeoctodon* and *Xenodontomys*) were described for the Huayquerian Age (Montalvo and Casadio 1988, Verzi *et al.* 1991). In the Pliocene, Ctenomyinae was characterized by low species richness, although it reached its highest diversity of adaptive types; four genera (*Xenodontomys*, *Actenomys*, *Eucelophorus*, and *Praectenomys*) were recognized, whose differentiation involved varied strategies of adaptation to the subterranean life (Reig and Quintana 1992, Quintana 1994b, Verzi 1994). In the Pleistocene, long-biochron genera disappeared (Tonni *et al.* 1995, Vucetich and Verzi 1995) and the explosive speciation of *Ctenomys* began, leading to the present state (Reig 1989, Reig *et al.* 1990, Reig and Quintana 1992, Verzi 1994). In the living fauna, the highly polytypic genus *Ctenomys* includes nearly 56 species (*vide* Reig *et al.* 1990) of subterranean rodents (approximately 30 % of the total species of South American caviomorphs).

The cohesion of the subfamily Ctenomyinae and its identity as an independent group is mainly supported by its dental morphology. Thus, among caviomorphs, ctenomyines have highly derived molar morphology without flexi/ids. But this dental pattern is only present in the euhypsodont representatives (crown-group). Consequently, the primitive species (stem-group) related to the origin of the subfamily had not been recognized. In this paper, the affinities of those taxa related to the differentiation of the Ctenomyinae are reviewed. Though only mandibles are known from these primitive species, the preserved characters permit a significant restatement about the origin and differentiation of the ctenomyine rodents.

Material and methods

The specimens of living and extinct Octodontoidea studied in this work belong to the mammalogical and/or paleontological collections of the following institutions: Geología Histórica, Universidad Nacional de La Pampa, Argentina (GHUNLPam); Instituto de Ecología y Evolución, Universidad Austral de Chile; Museo Argentino de Ciencias Naturales "B. Rivadavia" (MACN); Museo de La Plata, Argentina (MLP); Museo de Ciencias Naturales de Mar del Plata, Argentina (MMP); Museum of Vertebrate Zoology, Berkeley, California. In addition, unpublished illustrations of materials belonging to the Natural History Museum, London, and Smithsonian Institution collections were reviewed.

The masseteric configuration of the jaw (see text) was analyzed in specimens or illustrations of the following octodontoid species: *Myocastor coypus* (Molina, 1872), *Capromys pilorides* (Say, 1822), *Thrichomys apereoides* (Lund, 1839), *Olallamys albicauda* (Günther, 1879), *Echimyus* sp., *Clyomys bishopi* Avila-Pires and Wutke, 1981, *Diplomys labilis* (Bangs, 1901), *Euryzygomatomys spinosus* (Fischer, 1814), *Mesomys hispidus* (Desmarest, 1817), *Isothrix bistrata* Wagner, 1845, *Dactylomys dactylinus* (Desmarest, 1817), *Makalata armata* (I. Geoffroy, 1830), *Proechimys brevicauda* (Günther, 1877), *Proechimys canicollis* (Allen, 1899), *Proechimys guyannensis* E. Geoffroy, 1803, *Proechimys quadruplicatus* Hershkovitz, 1948, +*Eumysops* spp., *Ctenomys* spp. and all the extant species of the subfamily Octodontinae.

Jaws were measured with a dial caliper nearest 0.01 mm. Tooth measurements were taken through the reticule eyepiece of a Zeiss stereomicroscope. Hypsodonty indices (H/L) were determined as m1 height divided by m1 anterolabial-posterolingual length. Drawings were made with the aid of a drawing tube of a Wild M5 stereomicroscope. Nomenclature of tooth morphology follows Vucetich and Verzi (1996).

Origin of the Ctenomyinae

According to dental evidence, *Ctenomys* and its related fossil genera are generally believed to have evolved from the Octodontinae (or Octodontidae) (Wood 1955, Pascual *et al.* 1965, Patterson and Pascual 1972, Contreras *et al.* 1987, Pascual *et al.* 1988, Reig and Quintana 1990), so that the Octodontinae ought to be accepted as a paraphyletic taxon. Nevertheless, this hypothesis has different connotations for different authors, mainly because of the lack of consensus in the intensional and extensional meaning (*sensu* Reig 1987a) of the Octodontinae (or Octodontidae).

Wood (1955: 181) proposed that the family Ctenomyidae "...apparently is a late-Tertiary derivative of the octodontids". In this case, the Octodontidae taxon-concept (*sensu* Reig 1987a) is broad and comprises such genera as *Platypittamys* of the Deseadan Age, which was later tentatively transferred to the Echimyidae (Reig 1989, Vucetich and Verzi 1991). In any case, the specification of the Late Tertiary representatives presupposes an origin from some protohypsodont or euhypsodont species.

Reig and Quintana (1990) pointed out that the subfamily Ctenomyinae would have "...diferenciado de los Octodontinae a principios o mediados tempranos del Mioceno...", probably influenced by the supposed Chasicohan age (Late Miocene; Fig. 1) of a mandibular fragment of the ctenomyine *Xenodontomys* found in Chascó, Buenos Aires province (Reig *et al.* 1990). Upon the basis of the same empirical evidence, Quintana (1994a) proposed an age no older than Chasicohan for the Octodontinae-Ctenomyinae dichotomy.

Pascual *et al.* (1988) suggested two morphogenetic sequences illustrating the probable origin of the Ctenomyinae. In one of them, the genus *Phthoramys* is the ancestor of the subfamily. This idea was proposed earlier by Pascual *et al.* (1965), Patterson and Pascual (1972) and partly by Ameghino (1889). In the alternative pathway, ctenomyines would have evolved from "modern" octodontines with euhypsodont molars.

The case of the genus *Phthoramys*

The genus *Phthoramys* (Fig. 2 H-J) was described by Ameghino (1887) on the basis of a mandibular fragment found in Farola Monte Hermoso, Buenos Aires province (central Argentina; Montehermosan Age, Early Pliocene; Tonni *et al.* 1992). Besides the type species *Phthoramys homogenidens* Ameghino, 1887, two other species are known: *Phthoramys pulcher* Rovereto, 1914 and *Phthoramys hidalguense* Pascual, Pisano and Ortega, 1965. *P. pulcher* comes from the Araucanian beds and the Corral Quemado Formation (Huayquerian-Early? Montehermosan Ages; Fig. 1), northwestern Argentina; *P. hidalguense* was found in deposits of similar age, in central Argentina (Rovereto 1914, Pascual *et al.* 1965, Marshall and Patterson 1981, Verzi *et al.* 1991). As previously mentioned, this genus has been proposed as the ancestor of the Ctenomyinae by Pascual *et al.* (1965) and partly by Ameghino (1889). Later, Spencer (1987) placed *Phthoramys* in its own subfamily:

M.a.	EPOCHS	LITHOSTRATIGRAPHIC UNITS	AGE
0.01	PLEISTOCENE	Luján Fm. Guerrero Mb. Santa Isabel Fm. Arroyo Seco Fm.	Lujanian
0.7			
1.6		Miramar Fm.	Ensenadan
2.47		San Andrés Fm. Vorohué Fm.	Marplatan
3.4		Barranca de Los Lobos Fm.	
5.00	PLIOCENE	Chapadmalal Fm. (Limolitas claras Mb. included)	Chapadmalalan
		Monte Hermoso Fm. (Limolitas claras Mb. excluded)	Montehermosan
9.00	MIOCENE	Los Salitrales Fm.	Huayquerian
		Cerro Azul Fm.	
		Cerro Azul Fm.	Chasicoan
		Arroyo Chasicó Fm. Vivero Mb.	
10.5			

Fig. 1. Stratigraphic scheme of the Argentine Upper Cenozoic.

Phthoramyinae, and supporting the prior ideas, he considered this subfamily as the sister group of the Ctenomyinae.

Phthoramyia has been accepted as a ctenomyine ancestor because its dental morphology tends ontogenetically towards a simplification as indicated by the formation of fossettids. Particularly, the dp4 acquires an occlusal design similar to that of the ctenomyines, especially when the hypofossettid disappears. However, the formation of fossettids during ontogeny is a common character in both brachyodont and protohypsodont cheek teeth. Moreover, *Pseudoplateaomys innominatus* Rovereto 1914, an undoubted Octodontinae from the Araucanian beds of

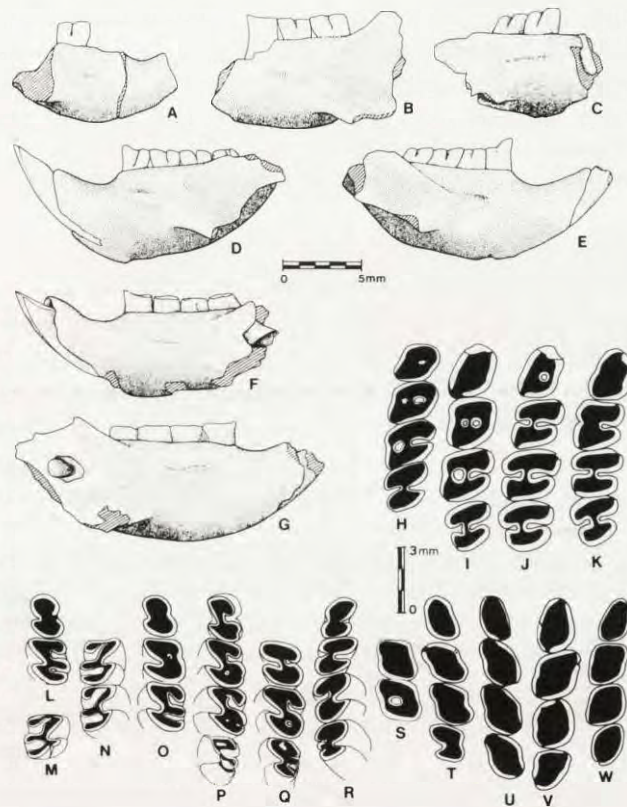


Fig. 2. Octodontidae mentioned in the text. *Chasichimys bonaerense*: A - right mandible MLP 60-VI-18-108 (holotype), B - left mandible MLP 55-IV-28-4, C - right mandible GHUNLPam 5068, L - left dp4-m1 MLP 55-IV-28-99, M - right m1 MLP 60-VI-18-108, N - right m1-2 GHUNLPam 5068, O - left dp4-m2 MLP 55-IV-28-4; *Chasichimys scagliai*: D - left mandible MMP 481-M (holotype), E - right mandible MLP 87-XI-20-30, P - left dp4-m3 MMP 481-M, Q - left m1-3 GHUNLPam 2011, R - right dp4-m3 MLP 87-XI-20-30; *Chasichimys* sp.: S - left m1-2 GHUNLPam 2217; *Xenodontomys simpsoni*: F - left mandible MMP 553-M (holotype), T - left dp4-m3 MMP 553-M, U - left dp4-m3 GHUNLPam 442; *Palaeoctodon simplicidens*: G - right mandible MACN 8576 (holotype), V - right dp4-m3 MACN 8576; *Phthoramyia homogenidens*: H - right dp4-m3 MACN A-1643; *Phthoramyia pulcher*: I - right dp4-m3 MACN 8370 (holotype), J - right dp4-m3 MACN 8363; *Pseudoplateaomys innominatus*: K - right dp4-m3 MACN 8364; *Palaeoctodon* aff. *P. simplicidens*: W - right dp4-m3 GHUNLPam 78.

Catamarca province (northwestern Argentina), also has a simple dp4 (Fig. 2 K). In contrast with the morphology of the dp4, on the other end of the molar row, *Phthoramys* has a clearly octodontiform m3. In fact, such octodontiform morphology occurs in every molar, though in m1-2 it vanishes earlier with the closure of the flexids.

Phthoramys' molars have transverse lobes and opposing flexids, two derived characters that it shares with the euhypsodont Octodontinae. Moreover, the metaflexid is absent even in the youngest specimens known; the mesoflexid closes slightly earlier than the hypoflexid, suggesting a similar response of both flexids to hypsodonty. Young specimens are quite similar to those of the euhypsodont octodontine *Pseudoplataeomys* (cf Fig. 2 J and K). This fact was noted by Spencer (1987), but he did not consider its systematic consequences.

Phthoramys is here considered an Octodontinae, probably the sister group of the euhypsodont genera. This assignment is supported by: (a) the transverse lobes of its molars, (b) the absence of a metaflexid in the known specimens, (c) the ontogenetic persistence of the mesoflexid similar to that of the hypoflexid, and (d) the opposing arrangement of both flexids (Pascual *et al.* 1965).

The genus *Chasichimys* as ancestor

A consequence of considering an Octodontinae as ancestor to the Ctenomyinae (Pascual *et al.* 1965) is that it should be accepted that the occlusal morphology of the cheek teeth must have changed from two transverse lobes to an oblique subrombic figure, longer than broad. However, the transverse disposition is derived in octodontids and would have evolved in the octodontines with the attainment of propalinal mastication (Verzi 1994).

The phylogenetic ideas of Pascual *et al.* (1965) were based on criteria previously established by Wood and Patterson (1959) to distinguish the Octodontidae from the Echimyidae and accepted until now (Patterson and Wood 1982, Vucetich and Verzi 1991). By these criteria, a pre-Huayquerian (and post-Deseadan) octodontoid whose molars have oblique lophs/ids and crowns slightly longer than broad, must be considered an Echimyidae (Wood and Patterson 1959). In other words, the possible ancestor of the Ctenomyinae with the above mentioned dental characteristics should be expected to occur among the Echimyidae and not among the Octodontidae.

Chasichimys (including *Pattersomys*) (Fig. 2 A-E and L-S) has the characteristics mentioned above. This genus was first found in the Arroyo Chasicó Formation, southeastern Buenos Aires province (central Argentina; Fig. 3). Pascual (1967) linked *Chasichimys* with the Santacruzian octodontoid *Acarechimys* on one hand, and with the living echimyid "*Cercomys*" (= *Thrichomys*) on the other. The latter was mentioned by Reig (1989) as a possible senior synonym of *Chasichimys*. Reviewing the materials from Chasicó we could verify that the only described species of this genus, *Chasichimys bonaerense* Pascual, 1967, is a composite taxon. Its holotype is very close to that of *Pattersomys scagliai* Pascual, 1967 and it is

indistinguishable from the paratypes of the latter (see below), while its paratype MLP 55-IV-28-3 represents a different genus.

P. scagliai was originally considered a Heteropsomyine echimyid, linked with the "Proechimys group" (see the extension of this group in Pascual 1967). Afterwards, Reig (1989) proposed *Chasichimys* and *Pattersomys* as the most ancient Eumysopinae (Rusconi 1935). This subfamily of Echimyidae was revalidated by Patton and Reig (1989) to separate these genera, and others previously included within the Heteropsomyinae, from the Antillean genera *Heteropsomys*, *Boromys* and *Brotomys*.

Though Pascual (1967) did not explain why he included *Chasichimys* and *Pattersomys* among the Echimyidae, the decision was probably influenced by their occlusal morphology and the presence of a dp4 in the latter.

Among the Hystricognathi, the retention of the DP4/4 is known in post-Deseadan Echimyidae (but see Vucetich and Bond 1984, Vucetich and Verzi 1991), Myocastoridae, Capromyidae and post-Fayum Thryonomyoidea in the Old World (Woods 1982, Wood 1985). A normal dental replacement was assumed for the Octodontidae, fossil and Recent, without any justification (eg Hartenberger 1985, Woods and Hermanson 1985). However, extant octodontids also retain the DP4/4 throughout life (Spencer 1987, Verzi 1994). Moreover, such retention of the DP4/4 seems to have occurred in the Octodontidae at least since the Chasicuan Age. In every protohypsodont representative known of this Age (*Chasicomys* and *Chasichimys*) and the following Huayquerian (*Chasichimys* and *Phthoramys*) and Montehermosan Ages (*Phthoramys*), the first molariform of the dental series is always more worn than the following ones (Fig. 2 H-J, L, O, P, and R). These results support the hypothesis stated by Woods (1982) that the retention of the deciduous premolars could have been achieved several times independently among the Hystricognathi. Its usefulness as a diagnostic character at the familial level, separating Octodontidae from Echimyidae, is doubtful.

The recognition of these two families (particularly in the comparison of the Octodontidae with the most primitive Echimyidae of the subfamily Eumysopinae) in the living fauna is clear enough because octodontids have euhypsodont molars and therefore a derived crown morphology (eg diagnosis in Woods 1984). Likewise, the acquisition of hypsodonty in some Huayquerian and extant Eumysopinae allowed the recognition of a different evolutionary pathway for their molars (Verzi *et al.* 1994). Though the two groups can be recognized as independent lineages, it is difficult to separate their primitive, less hypsodont representatives.

Verzi *et al.* (1994) recently proposed two characters to differentiate the Octodontidae from eumysopine Echimyidae: the masseteric configuration of the mandible and the closure sequence of the molar flexids. Though we have not reviewed all the Octodontoidea, the extensive sample studied (see Material and methods) suggests that the first character would separate the octodontids from the remaining Octodontoidea. In the mandible examined of Capromyidae, Myocastoridae and Echimyidae, the point of origin of the angular process involves the area of the notch

for the tendon of the *M. masseter medialis* (infraorbital part, *sensu* Woods and Howland 1979). The ventral edge of this notch and the convexity produced by the masseteric crest are either continuous or separated by a slight interruption. In contrast, in octodontids, the point of origin of the angular process is further back with respect to the masseteric notch, and it does not involve the notch. There is no continuity between the notch and the masseteric crest. In dorsal view, a concavity can be observed between them, because the inflexion point where the crest becomes convex is placed further backward in respect to the notch than in the remaining Octodontoidea (see Verzi *et al.* 1994). This latter condition represents a synapomorphic character of Octodontidae (Verzi 1994), and is present in *Chasichimys* (Fig. 2 A-E).

With regard to the closure sequence of flexids, *Chasichimys* is like other protohypodont octodontids (eg *Chasicomys*, *Phthoramys*): the mesoflexid is more persistent than the metaflexid, so that the mesofossettid is formed later than the metafossettid (Fig. 2 O-R). In Eumysopinae, in contrast, meso- and metafossettids are formed simultaneously (eg *Eumysops*) or the former is formed before the latter (eg *Thrichomys apereoides*, *Clyomys*, *Euryzygomatomys*, *Reigechimys*) (see Petter 1973, Verzi *et al.* 1994, 1995).

In short, *Chasichimys* must be considered as a primitive representative of the Octodontidae, with more hypodont molars and more oblique lophids than *Phthoramys*.

Recently, new materials of *Chasichimys* were recovered from the Cerro Azul Formation (*sensu* Linares *et al.* 1980) in La Pampa Province (central Argentina, Fig. 3), as well as almost five thousands remains of other micromammals. The new materials together with the sample of *Chasichimys* from Chasicó allow a new interpretation of the systematics, age and evolutionary history of the genus.

Systematics

Order Rodentia Bowdich, 1821

Suborder Hystricognathi Tullberg, 1899

Infraorder Caviomorpha Wood and Patterson in Wood, 1955

Family Octodontidae Waterhouse, 1839

Subfamily Ctenomyinae Tate, 1935

Genus *Chasichimys* Pascual, 1967

(Fig. 2 A-E, L-S; Fig. 4 A-C; Table 1)

Pattersomys Pascual, 1967

Type species: *Chasichimys bonaerense* Pascual, 1967

Emended diagnosis: Small octodontids with protohypodont molars higher than those of *Chasicomys* and *Neophanomys*. Lophids and flexids moderately oblique. Hypoflexid and mesoflexid not opposing; the former ontogenetically more persistent. dp4 eight-like. m1-2 trilophodont, bilobed to subrombic, without mesolophid, and

Table 1. Mandibular and dental measurements (in mm) of *Chasichimys* and *Xenodontomys simpsoni*. The measurements denoted with asterisk were taken on X-ray plates. Abbreviations: a – alveolar, al-pl – anterolabial-posterolingual, ant – anterior, c – coronal, H/L – hypsodonty index (see Material and methods), M – mandible, post – posterior. MLP, GHUNLPam, MMP – explanations are given in Material and methods.

	<i>Chasichimys bonaerense</i>			<i>Chasichimys scagliai</i>			<i>Chasichimys</i> sp.			<i>Xenodontomys simpsoni</i>							
	MLP	GHUNLPam	MMP	MLP	GHUNLPam	MMP	GHUNLPam	MMP	MMP	GHUNLPam	MMP	GHUNLPam					
60-VI-18-108	55-IV-28-4	55-IV-28-99	5068	8035	M-481 type	87-XI-20-30	311	2011	2217	M-553 type	342	441	442	2005	2134	5016	5935
M depth at dp4					6.04	6.34					6.42					7.96	6.92
Diastema length					4.42	5.10			4.74		4.56		5.04				
dp4-m3 (c) length					7.70	7.82					7.82		9.00				8.36
dp4-m3 (a) length					8.46	8.66					8.62		9.10				
dp4 al-pl length	1.98	2.05			2.18	2.21	2.21				2.12	2.13	2.01	2.13	2.21	2.13	1.97
dp4 ant. width	1.26	1.26			1.20	1.18	1.38				1.40	1.50	1.26	1.42	1.34	1.26	1.11
dp4 post. width	1.46	1.42			1.42	1.34	1.50				1.53	1.54	1.42	1.26	1.50	1.46	1.26
m1 al-pl length	2.37	2.45	2.45		2.51	2.37	2.53	2.37			2.40	2.45	2.53	2.48	2.37	2.57	2.61
m1 ant. width	1.62	1.74	1.58		1.53	1.66	1.86	1.82			1.75	1.74	1.50	1.61	1.66	1.70	1.50
m1 post. width	1.50	1.82	1.66		1.54	1.62	1.82	1.82			1.75	1.58	1.58	1.58	1.66	1.66	1.66
m2 al-pl length	2.53	2.53	2.76		2.51	2.53		2.69			2.48	2.53	2.60			2.69	2.45
m2 ant. width	1.82	1.58	1.90		1.64	1.70		1.98			1.75	1.66	1.61			1.66	1.74
m2 post. width	1.74	1.50	2.05		1.64	1.58		1.82			1.75	1.78	1.74			1.74	1.82
m3 al-pl length					1.86	2.05		1.98			2.10	2.29	2.29			2.05	2.05
m3 ant. width					1.20	1.50		1.58			1.58	1.56	1.56			1.34	1.34
m3 post. width	4.72*	4.70*	4.46	4.86*	0.98	1.18		1.11			1.31	1.34				1.34	1.34
m1 height						5.91*	5.92	5.77	6.56						8.28	8.16	
m1 H/L	1.99	1.92	1.73	1.98		2.49	2.34	2.43	2.86					3.49	3.18		
I1 depth	1.42				1.76	1.58					1.38	1.62				2.13	
I1 width	1.26				1.46	1.90					1.73	1.78				1.97	

with mesoflexid and anteroflexid coalescent. m3 (known only in *Chasichimys scagliai*) tetralophodont, with an anterofossettid in early stage of wear.

***Chasichimys bonaerense* Pascual, 1967**
(Fig. 2 A-C, L-O; Fig. 4 A; Table 1)

Chasichimys bonaerense Pascual, 1967, *partim*

Pattersonomys scagliai Pascual, 1967, *partim*

Holotype: MLP 60-VI-18-108, fragmentary right mandible with intra-alveolar portion of i1, m1 and base of dp4.

Referred material: MLP 55-IV-28-99, fragment of left mandible with dp4-m1 (paratype of *P. scagliai*); MLP 55-IV-28-4, partial left ramus with dp4-m2 (paratype of *P. scagliai*); GHUNLPam 5068, fragmentary right mandible with m1-2 and intra-alveolar portion of dp4; GHUNLPam 8035, fragmentary left mandible with m2.

Localities (Fig. 3): Chasicó, Buenos Aires province, Arroyo Chasicó Formation, Vivero Member (type locality)(MLP 60-VI-18-108, MLP 55-IV-28-4 and MLP 55-IV-28-99); Cerro La Bota, La Pampa province, Cerro Azul Formation (GHUNLPam 5068); Cerro Patagua, La Pampa province, Cerro Azul Formation (GHUNLPam 8035).



Fig. 3. Geographic distribution of the *Chasichimys-Xenodontomys* lineage in central Argentina, showing the localities mentioned in the text: 1 - Cerro Patagua, 2 - Cerro La Bota, 3 - El Guanaco, 4 - Barrancas Coloradas, 5 - Bajo Giuliani, 6 - Naicó, 7 - Laguna Chilluú, 8 - Chasicó; 9 - Salinas Chicas.

The Arroyo Chasicó Formation is composed of two members: the Vivero (lower) and Las Barrancas (upper) (Fidalgo *et al.* 1978, Bondesio *et al.* 1980). The fauna recorded in the Vivero Member is considered Early Chasicóan in age (Bondesio *et al.* 1980, Fidalgo *et al.* 1987) and is composed of "pan-araucanian" representatives, together with some "pan-santacrucean" survivors (Bondesio *et al.* 1980).

In Cerro La Bota, until now, only a lower molar (m1 or m2) of an Octodontidae other than *Chasichimys* has been found. It is very similar to the specimen MLP 55-IV-28-3 from the Arroyo Chasicó Formation, Vivero Member, described by Pascual (1967). No associated fauna is known from Cerro Patagua.

Emended diagnosis: The least hypsodont species of the genus. Molars with roots already formed when the metaflexid is still open.

Description: These specimens have the lowest-crowned molars of the examined sample (Fig. 4 A and Table 1). MLP 60-VI-18-108 and GUNLPam 5068 are the youngest specimens, the molars have narrow lophids and wide, deep flexids. In MLP 55-IV-28-99, the m1 has the metaflexid almost closed, while in MLP 55-IV-28-4 this molar, more worn, lacks a metaflexid and its mesoflexid is transformed into a mesofossettid (Pascual 1967). X-ray images of these materials demonstrate the presence of deep transverse inter-radicular spaces. In the dp4-m1 of MLP 55-IV-28-99 there are two anterior roots clearly separate and a posterior one with an incipient division (Fig. 4 A). The m2 of GHUNLPam 5068, whose base is partially exposed, has two anterior and one posterior roots, all of them well developed and with deep inter-radicular spaces.

Chasichimys scagliai (Pascual, 1967) *nov. comb.*
(Fig. 2 D-E, P-R; Fig. 4 B; Table 1)

Pattersomys scagliai Pascual, 1967, *partim*.

Holotype: MMP 481-M, left mandible with i1 and dp4-m3.

Referred material: GHUNLPam 311, fragmentary left mandible with dp4-m1; GHUNLPam 2011, fragmentary left mandible with m1-3; MLP 87-XI-20-30, right mandible with dp4-m3.

Localities (Fig. 3): Chasicó, Buenos Aires province, Arroyo Chasicó Formation (type locality) (MMP 481-M); Laguna Chillhué, La Pampa province, Cerro Azul Formation (GHUNLPam 311 and GHUNLPam 2011); Naicó, La Pampa province, Cerro Azul Formation (MLP 87-XI-20-30).

The Laguna Chillhué fauna was assigned to the Huayquerian Age by Pascual and Bondesio (1982: like "Valle de General Acha"), and Verzi *et al.* (1994, 1995). No associated fauna is known from Naicó.

Emended diagnosis: Species of *Chasichimys* with more hypsodont molars and the metaflexid more ephemeral than *C. bonaerense*. Roots develop later than the closure of the metafossettid.

Description: GHUNLPam 311, 2011 and MLP 87-XI-20-30 are more hypsodont than *C. bonaerense*, as indicated by the higher crowns, more ephemeral metaflexid and later formation of the roots (Figs 1 and 3, Table 1). This degree of hypsodonty is like that of MMP 481-M, judging by the worn sequence of the occlusal surfaces. GHUNLPam 311 maintains dp4-m1, the latter with hypoflexid, mesofossettid, and four well developed roots. GHUNLPam 2011 has m1-3 somewhat more worn than MMP 481-M, but congruent with it (cf Fig. 2 P and Q). The m1 shows a transverse inter-radicular space, while in its anterior face has only a slight constriction (Fig. 4 B). The X-ray image of both specimens from Laguna Chillhué demonstrates that the inter-radicular space of the m1 is proportionally less deep than in *C. bonaerense*. Moreover, the m2-3 of GHUNLPam 2011 had not yet developed roots. The molars of MLP 87-XI-20-30 show a stage of evolution similar to that of MMP 481-M and the specimens from Laguna Chillhué. They are more worn, however; there is no trace of the metaflexid in dp4-m2, nor of the anterofossettid in the m3. The

X-ray image of this material shows a shallow tranverse inter-radicular space in the dp4-m1, and no inter-radicular space in m2-3.

Remarks: The fauna recorded in both members of the Arroyo Chasicó Formation is hitherto conventionally of Chasicóan Age (Late Miocene; Fig. 1). But strong evidence suggests that the fauna from the Las Barrancas Member is younger, and could be interpreted as either transitional between the Chasicóan and Huayquerian Ages, or perhaps referable to the Huayquerian (Latest Miocene) (Fidalgo *et al.* 1978, Fidalgo *et al.* 1987, Bondesio *et al.* 1980, Marshall *et al.* 1983). Though the holotype of *P. scagliai* MMP 481-M has no precise stratigraphic references (see Pascual 1967, Bondesio *et al.* 1980), its degree of dental evolution indicates that very probably, it was found in younger levels than the Vivero Member where the sample of *C. bonaerense* was found. Moreover, in view of its morphology, this specimen may have been contemporary with those of *C. scagliai* from the Huayquerian levels of La Pampa province.

***Chasichimys* sp. morphotype a**
(Fig. 2 S; Fig. 4 C; Table 1)

Referred material: GHUNLPam 2217, fragmentary left mandible with m1-2.

Locality: Bajo Giuliani, La Pampa province, Cerro Azul Formation (Fig. 3). Fossil Octodontoidea from this locality were referred to the Huayquerian Age by Montalvo and Casadío (1988), and Verzi *et al.* (1995).

Diagnosis: A species with more hypsodont molars than *C. scagliai*. m1-2 with subrombic occlusal morphology and ephemeral flexids. Roots develop later than closure of the hypoflexid.

Description: This specimen is clearly more hypsodont than is *C. scagliai* (Fig. 4 and Table 1). Its crowns are higher and the occlusal shape of the m1 is completely simplified, while the m2 retains only one hypofossettid. Roots develop, but are more delayed in relation to the wear condition of the occlusal surface than in the two remaining species. There are two anterior and one posterior roots in the m1 and only a slight constriction in the anterior face of the m2.

***Xenodontomys simpsoni* Kraglievich, 1961**
(Fig. 2 F, T-U; Fig. 4 D; Table 1)

Proctenomys simpsoni Pascual *et al.*, 1965.

Holotype: MMP 553-M.

Referred material (Verzi *et al.* 1991): GHUNLPam 342, 441, 442, 2005, 2015, 2134, 2140, 2141, 2403, 5016, 5018, 5027, 5935, 5936.

Localities: Salinas Chicas basin, Buenos Aires province, Los Salitrales Formation (*sensu* Fidalgo *et al.* 1987) (type locality); Barrancas Coloradas and El Guanaco, La Pampa province (Cerro Azul Formation) (Fig. 3). Los Salitrales Formation was referred by Fidalgo *et al.* (1987) to the Late Miocene-Pliocene, while the fauna of El Guanaco and Barrancas Coloradas was assigned to the Huayquerian Age (Goin and Montalvo 1988, Verzi *et al.* 1991).

Description (Verzi *et al.* 1991): No remains assignable to *Chasichimys* have been found in these localities. However, the most primitive ctenomyine recorded, *X. simpsoni*, is here interpreted as an euhypsodont representative of this lineage. Its molars lack roots, are higher-crowned than in *Chasichimys*, and their occlusal pattern is more slender than that of GHUNLPam 2217, the immediately preceding member of the evolutionary series (Fig. 4 and Table 1).

Hypsodonty and age of *Chasichimys*

A biochronologic sequence (*sensu* Lindsay 1990) with four consecutive levels can be defined by dental changes in *Chasichimys-Xenodontomys*. These levels are represented by the deposits cropping out in the following localities (Figs 3 and 4): (A) Chasicó (Arroyo Chasicó Formation, Vivero Member) – Cerro La Bota – Cerro Patagua; (B) Laguna Chillhué – Naicó; (C) Bajo Giuliani; (D) Barrancas Coloradas – El Guanaco – Salinas Chicas (Los Salitrales Formation).

The evolutionary events between levels A and C are (a) increasing height of the molar crowns, (b) increasing simplification of the occlusal shape and (c) progressive delay of the development of roots. In level D, the dental roots are definitively lost.

This pattern of dental evolution suggests chronological differences among localities. The remaining rodent fauna also supports this claim. Increasing hypsodonty in the echimyid *Reigechimys* (Verzi *et al.* 1994) was detected between Laguna Chillhué and Bajo Giuliani localities (levels C and D); this pattern of change is similar to that observed in *Chasichimys*, reinforcing the interpretation that these localities are different in age. Moreover, the molar evolution of the lineage *Chasichimys-Xenodontomys*, as represented in the Cerro Azul Formation, was accompanied by a decrease in the abundance and diversity of the brachyodont to protohypsodont octodontoids

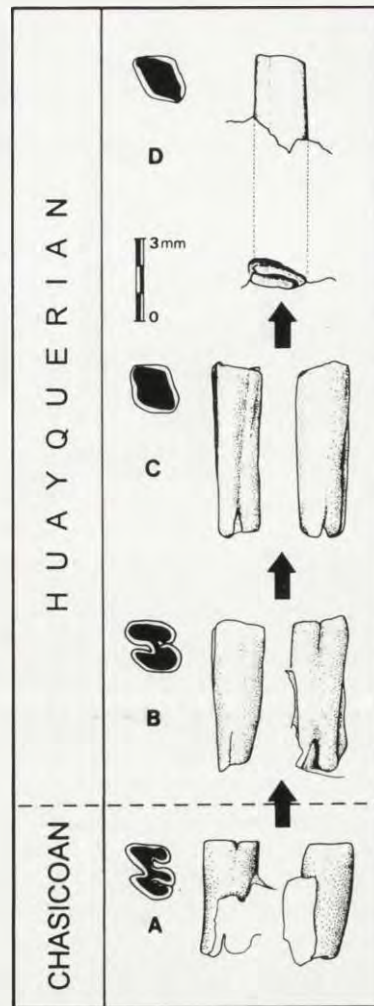


Fig. 4. Evolution of the hypsodonty in the *Chasichimys-Xenodontomys* lineage: A – left m1 of *Chasichimys bonaerense* MLP 55-IV-28-99, occlusal, lingual and posterior view; B – left m1 of *Chasichimys scagliai* GHUNLPam 2011, occlusal, anterior and lingual view; C – left m1 of *Chasichimys* sp. GHUNLPam 2217, occlusal, anterior and lingual view; D – right m1 (inverted) of *Xenodontomys simpsoni* GHUNLPam 2005, occlusal and labial view. A–D correspond to biostratigraphic levels (see text).

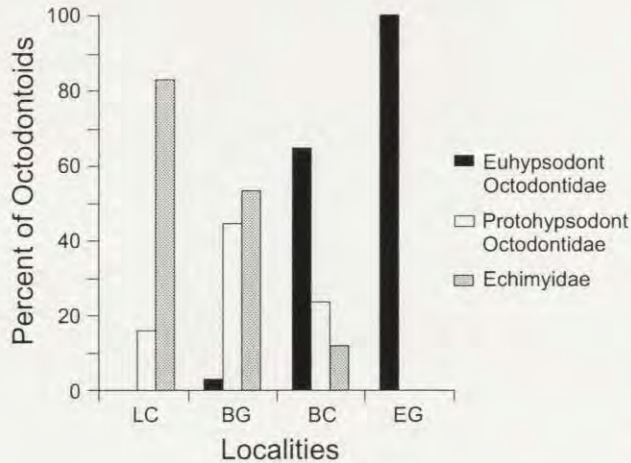


Fig. 5. Changes in the composition of the Octodontoid communities from the Cerro Azul Formation. The relative abundance of each group of Octodontoids is expressed as percent of the total of Octodontoid specimens. Protohypsodont Octodontoids are represented by Octodontidae and Echimyidae; euhypsodont Octodontoids are only Octodontidae. LC - Laguna Chillhué, BG - Bajo Giuliani, BC - Barrancas Coloradas, EG - El Guanaco.

and the differentiation of euhypsodont species (Fig. 5). This trend to a increasing hypsodonty was probably a response to increasing aridity, and consequent development of open environments such as steppes or savannas, during the late Miocene. Available data show the global character of the late Miocene cooling and drying trend, determining the differentiation of savanna-adapted mammals in different continents (eg Janis 1993, Leakey *et al.* 1996, MacFadden and Cerling 1996, Pascual and Ortiz Jaureguizar 1990).

According to previous information (Bondesio *et al.* 1980, Goin and Montalvo 1988, Verzi *et al.* 1991, 1995) and the new materials, we consider level A of Chasicoan Age (Late Miocene), and the rest as different stages of the Huayquerian Age (Latest Miocene) (Figs 1 and 4). Level D approximates the Miocene-Pliocene boundary (Fidalgo *et al.* 1987).

The beginning of the Chasicoan Age followed the withdrawal of a widespread marine transgression that extended from northern Patagonia, in Argentina, to western Uruguay and southern Paraguay ("Mar Paranense", see Pascual *et al.* 1985, Pascual and Ortiz Jaureguizar 1990, Pascual *et al.* 1996). The withdrawal of the Paranense sea could have been synchronous with the marked global sea level fall at 10.5 million years (Ma) (Haq *et al.* 1987). If this dating is accepted as the beginning of the Chasicoan Age (Cione 1987), and if the age of the Los Salitrales Formation is close to the Mio-Pliocene boundary, about 5 Ma would have been necessary for the *Chasichimys-Xenodontomys* lineage to attain euhypsodonty (Fig. 1). *Xenodontomys ellipticus* Kraglievich, 1927, a probable derivative of *X. simpsoni* (Pascual *et al.* 1965, Verzi 1994), is recorded later during the "Irenense" (Pliocene, see Goin *et al.* 1994).

Recently, Quintana (1994a) mentioned a specimen of *Xenodontomys* sp. in Chasicoan sediments. This mention would refute the evolutionary sequence

proposed here. Nevertheless, there are no secure collection data, so it is not possible to verify the specimen's provenance as Vivero Member.

Anagenesis and the attainment of the euhypsodont grade

According to the new evidence, the *Chasichimys-Xenodontomys* lineage can be interpreted as a temporally continuous succession of populations, whose pattern of dental evolution suggests anagenetic change (*sensu* Chaline and Mein 1979, Reig 1987b, 1990). Representatives with lower and more complex crowned molars underwent a progressive delay in the development of the dental roots, to the point of the euhypsodonty. As often occurs in small rodents, the increase of hypsodonty was linked to a simplification of the occlusal pattern (Schmidt-Kittler 1984); this led to the differentiation of the ctenomyine molar pattern, characterized by the lack of flexids. Though the sample size is small, the directionality and probable adaptiveness of the changes support this hypothesis. Phyletic gradualism in the development of euhypsodonty in rodents has been demonstrated in lineages as divergent as the Arvicolidae and Theridomyidae of the Old World (see Vianey-Liaud 1976, Chaline and Mein 1979, Chaline 1985, Schmidt-Kittler and Vianey-Liaud 1987, Chaline *et al.* 1993).

Although the recognition of discrete, named species, in continuous lineages facilitates biostratigraphic or systematic analyses (eg Chaline and Mein 1979, Schmidt-Kittler and Vianey-Liaud 1987), anagenetic change may represent adaptation, but not necessarily speciation (Chaline and Mein 1979, Wiley 1981). Despite this, we use the generic and specific names of the *Chasichimys-Xenodontomys* lineage to remain consistent with the literature and avoid confusion.

Differentiation of *Palaeoctodon* as evidence of cladogenesis

As mentioned above, another Ctenomyinae is recorded in the fauna of Bajo Giuliani: *Palaeoctodon* aff. *simplicidens* Montalvo and Casadío, 1988. *Palaeoctodon* is a small sized ctenomyine with completely simplified molars, similar to *X. simpsoni* (Fig. 2 G, V-W). *Palaeoctodon* was considered to be the only ctenomyine lineage present in the Late Miocene (Reig 1989, Reig *et al.* 1990, Reig and Quintana 1990, Reig *et al.* 1991, Reig and Quintana 1992), as a result of considering *X. simpsoni* to be a junior synonym of *P. simplicidens*. Accordingly, *Palaeoctodon* was interpreted as ancestral to the rest of the subfamily (Montalvo and Casadío 1988, Pascual *et al.* 1988).

Verzi *et al.* (1991), using dental and mandibular characters, recognized both taxa as genera, as did Kraglievich (1961). This is reinforced by the identification of the *Chasichimys-Xenodontomys* evolutionary succession. The presence of *Palaeoctodon* in Bajo Giuliani suggests an early cladogenetic event in an ancestral ctenomyine stock probably protohypsodont.

Biogeographic origin of the Ctenomyinae

If *Chasichimys* and *Phthoromys* are accepted as representatives of Ctenomyinae and Octodontinae, respectively, their morphological similarity suggests that the Ctenomyinae-Octodontinae split must have occurred during the Chasicoan or slightly earlier (Verzi 1994). Using different evidence, Quintana (1994a) proposed an age no older than the Chasicoan for the Octodontinae-Ctenomyinae split. However, assignment of *Xenodontomys* to the Chasicoan (Quintana 1994a) would imply a dichotomy prior to this Age (Reig and Quintana 1990).

Most fossil Octodontidae are from Argentina. This fact and the present distribution of the family (Contreras *et al.* 1987) suggest that the group has been mainly austral (Pascual 1967). Spotorno *et al.* (1995) recently suggested that the Octodontoidea (exclusive of the Echimyidae) might have originated in the central Andes. To support this hypothesis for the ctenomyine, Spotorno *et al.* (1995) cite the more primitive sperm morphology of the *Ctenomys* species of this area, in comparison to those living southward (see Feito and Gallardo 1982, Vitullo *et al.* 1988, Vitullo and Cook 1991, Gallardo 1991, Roldan *et al.* 1992). However, *Ctenomys* is the most recent genus in the subfamily (Verzi 1994), recorded only since the Upper Marplatán (Early Pleistocene, 2.4 Ma; Cione and Tonni 1995). Therefore, the Andean hypothesis does not account for about eight Ma of the group's prior history (Fig. 1). Evidence for the differentiation of the Ctenomyinae and their initial radiation comes mainly from central Argentina (Rovereto 1914, Kraglievich 1961, Montalvo and Casadio 1988, Verzi *et al.* 1991, Reig and Quintana 1992, Quintana 1994a, Verzi 1994). Only the derived *Praectenomys rhombidens* Villarroel, 1975 adapted to the increasing heights of the Bolivian altiplano during the Early Pliocene (see Villarroel 1975, Marshall and Sempere 1991, Quintana 1994b). The absence of differentiated ctenomyines from the Huayquerian-Montehermosan sediments of northwestern Argentina, where Octodontidae fossils are abundant (Rovereto 1914, Spencer 1987, D. Verzi, unpubl.), suggests that the colonization of the central Andes would have occurred after the differentiation of the group at higher latitudes, probably in the present pampasic region.

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