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Phylogenetic position of *Abalosia* and the evolution of the extant Octodontinae (Rodentia, Caviomorpha, Octodontidae)

Diego H. VERZI

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South American octodontid rodents of the subfamily Octodontinae currently show low species richness but great morphological and chromosomal diversity. This diversity is interpreted alternatively as the remnant of a wider past radiation or as the result of saltational evolution. These hypotheses are discussed in relation to a phylogenetic analysis of the Late Pliocene octodontine *Abalosia castellanosi*. My results suggest that *Abalosia*, together with *Tympanoctomys* and *Octomys*, is part of a clade of desert specialist propalinal octodontids, which would have differentiated east of the Andes in the emergent semi-deserts of western Argentina. The presence of *Abalosia* in the coastal region of central Argentina during the Upper Marplatan Age (Late Pliocene) suggests a pulse of expansion of such arid environments, probably coeval with the global climatic deterioration detected around the transition Gauss-Matuyama magnetic ages. The phylogenetic position of *A. castellanosi* suggests that extinction events affected the clade of the octodontine desert specialists. Accordingly, regardless of how rough or gradual the differentiation of the octodontine's diversity has been, the living representatives seem to be remnants of a wider radiation.

CONICET, Departamento Científico Zoología Vertebrados, Museo de La Plata, Paseo del Bosque s/Nş (1900) La Plata, Argentina, e-mail: dverzi@museo.fcnym.unlp.edu.ar

Key words: Octodontinae, rodents, morphology, phylogeny, biogeography

Introduction

In the extant fauna, the family Octodontidae includes an assemblage of middle to small-sized caviomorph rodents, endemic to southern South America (Reig 1981, Mares and Ojeda 1982). Within this family, two lineages with unstable taxonomic status can be recognized: Ctenomyinae (or Ctenomyidae) and Octodontinae (or Octodontidae *sensu stricto*; see Discussion).

According to current taxonomy, Octodontinae includes six genera, two of which are mainly surface dwellers (*Octodontomys* and *Octomys*), one semifossorial (*Octodon*), and the remaining, semisubterranean (*Aconaemys* and *Tympanoctomys*) or completely subterranean (*Spalacopus*) (Reig 1986, 1989, Ojeda *et al.* 1996). Their distribution is mainly Andean or restricted to adjacent lowlands, between 16° and 40°S latitude (Mares and Ojeda 1982, Pearson 1984, Justo *et al.* 1985, Contreras *et* *al*. 1987, Ojeda *et al*. 1989, 1996, Verzi and Alcover 1990, Gallardo and Reise 1992, Hutterer 1994).

None of the extant Octodontinae is known hitherto in the fossil record (but see Reig 1986), despite some mentioned in archeological sites (eg Massoia 1979, Pearson and Pearson 1982, Pearson 1987, Simonetti 1989, Gallardo 1992, Massoia and Silveira 1996). However, undoubted members of the subfamily are known in the fossil record of Argentina since the Late Miocene (Rovereto 1914, Reig 1989), but their phylogenetic relationships with the living species remain unknown.

In this paper the craneomandibular and dental morphology of *Abalosia castellanosi* is revisited and its phylogenetic relationships to the extant Octodontinae are analyzed. *Abalosia* is the extinct octodontine appearing latest in the fossil record (D. H. Verzi, unpubl.). It is known only from the Sanandresian (Late Marplatan, Late Pliocene; Cione and Tonni 1995), from the coastal cliffs of the Chapadmalal region between the cities of Mar del Plata and Miramar (southeastern Buenos Aires Province, Argentina). *A. castellanosi* was described by Rusconi (1933) and assigned to the genus *Plataeomys* (= *Pseudoplataeomys*). Reig and Quintana (1991) demonstrated that this octodontine belongs to a different genus. These authors considered *A. castellanosi* ancestral to the living *Octodon*. This hypothesis and alternatives are tested through a phylogenetic analysis of *Abalosia* in relation to the extant Octodontinae based upon craneomandibular and dental morphology. On the basis of the results, both the evolutionary and palaeoenvironmental significance of *Abalosia* are discussed.

Material and methods

The phylogenetic analysis was carried out using genera as terminal taxa. *Abalosia* and specimens of all extant species of Octodontinae were analyzed (Appendix I), except for *Octodon pacificus* which was examined only through the original illustrations (Hutterer 1994). The sister subfamily Ctenomyinae (Pascual *et al*. 1965, Reig 1989, Gallardo 1997) was included as an outgroup. In addition to the living *Ctenomys*, the Pliocene *Actenomys priscus*, known through complete skulls, was included. The Echimyidae *Thrichomys apereoides* was included as root, according to the assumption that Echimyidae is the sister taxon of Octodontidae (eg Winge 1941, George and Weir 1972, Reig 1986, Cook and Lessa 1998).

The program NONA 2.0 (Goloboff 1993) was used to find the most parsimonious trees, and for assessment of support for branches in the cladogram. Characters were considered equally weighted and multistate characters were coded as non-additive. In searching for the shortest tree, the option for exact solutions 'mswap+' was used. Branch support was evaluated by calculating Bremer support (Bremer 1988) and relative Bremer support (Goloboff 1993).

The specimens of Octodontoidea studied belong to the mammalogical or paleontological collections of the following institutions: Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa (LP); Instituto de Ecología y Evolución, Universidad Austral de Chile (IEEUACH); Instituto Miguel Lillo, Tucumán, Argentina (IML); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN); Museo de La Plata (MLP); Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia" (MMP); Museum of Vertebrate Zoology, Berkeley (MVZ). In addition, unpublished illustrations of specimens of the Natural History Museum, London; the National Museum of Natural History, Washington, and the Field Museum of Natural History, Chicago (FMNH), were examined. Cranial and dental schemes were drawn using a Wild M5 stereomicroscope with a drawing tube.

Results

Spatial-temporal distribution of *A. castellanosi*

The holotype of *A. castellanosi* was recovered from Cañadón Chapar, Partido de General Alvarado, Buenos Aires Province, Argentina (Rusconi 1933, Reig and Quintana 1991). However, materials with the most precise stratigraphic provenance were found in Punta San Andrés and Santa Isabel, Partido de General Pueyrredón, Buenos Aires Province. In both areas this species has been recorded exclusively in Kraglievich's (1952) San Andrés Formation. Reig (in Marshall *et al.* 1984), who proposed the Sanandresian as a Subage of the Uquian Land Mammal Age, already

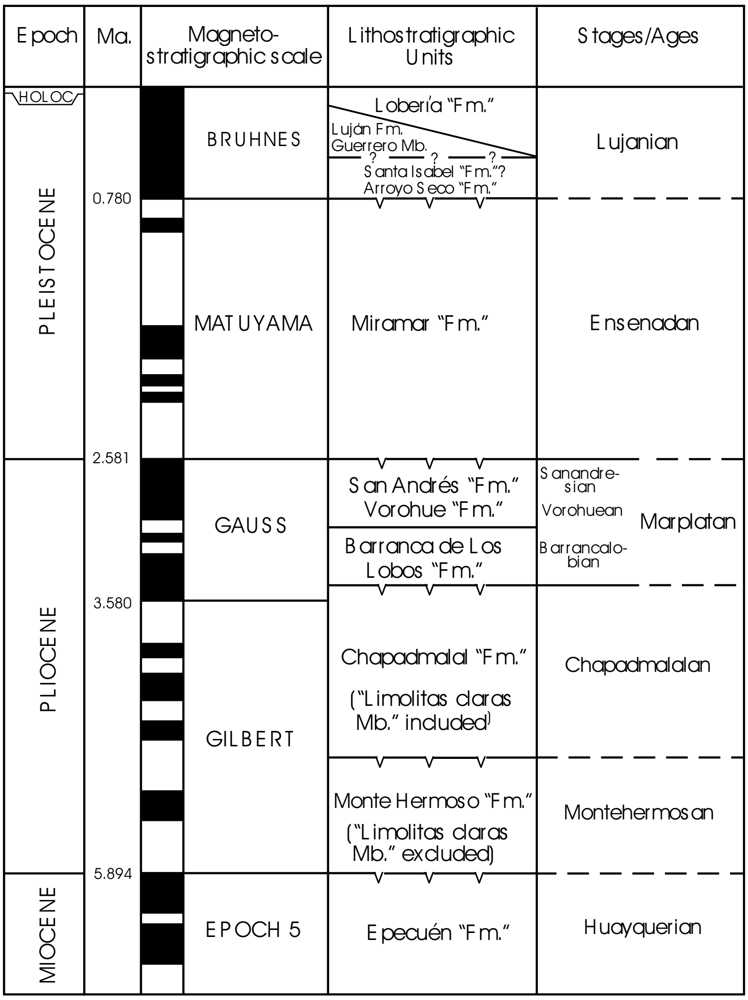

Fig. 1. Stratigraphic scheme of the Argentine Upper Cenozoic. Black strips – normal polarity and white strips – reverse polarity intervals, after the standard magnetostratigraphic scale. Abbreviations: Ma. – million years ago, Fm. – formation, Mb. – member.

recognized the identity of the fauna from this Formation. Cione and Tonni (1995) agreeing with Reig maintained the Sanandresian as an Upper Substage of the Marplatan local Stage (Fig. 1). A detailed revision of the lithological and stratigraphic aspects of the San Andrés Formation can be found in Teruggi *et al*. (1974), Zárate (1989), and Zárate and Fasano (1989); the biostratigraphy was analyzed by Cione and Tonni (1995) and magnetostratigraphic data were discussed by Orgeira (1991 and literature therein).

Cranial, mandibular and dental morphology of *A. castellanosi*

Skull

Reig and Quintana (1991: 296) pointed out that: "The skull of *Abalosia*... is much more similar to that of species of *Octodon* than to any other genus of living

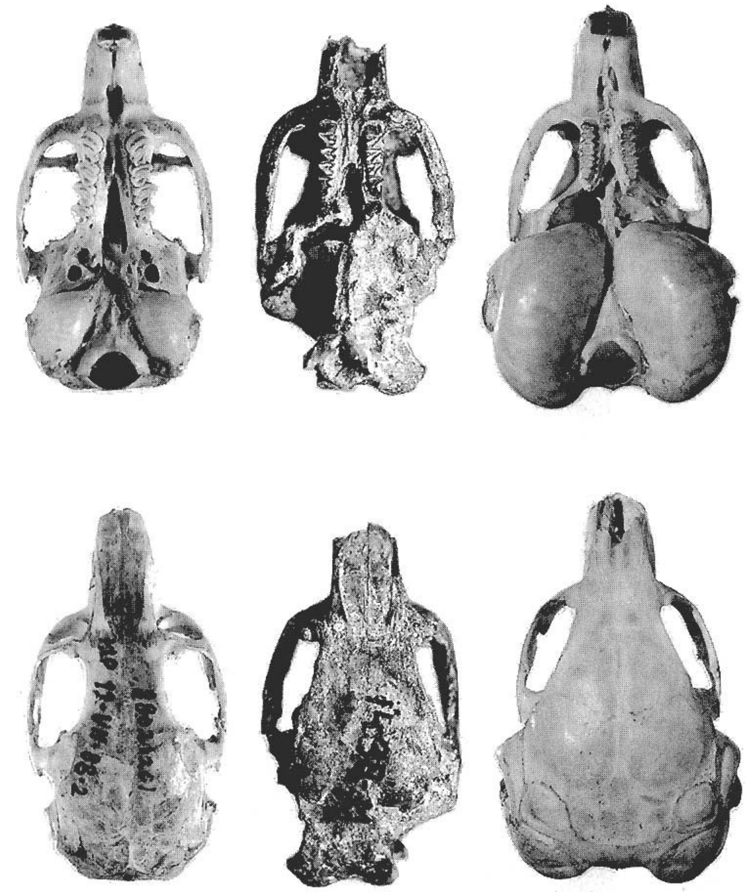

Fig. 2. Ventral (upper) and dorsal view (bottom) of the skull of (A) *Octodon* sp. MLP 12.VII.88.2 (1.1×), (B) *Abalosia castellanosi* MMP 1439-M (1.2×), (C) *Tympanoctomys barrerae* MACN 39949 (1.2×).

octodontines". The similarities recognized by these authors include both size and general shape of the skull and rostrum. I re-examined these characters and my results were somewhat different. Most of the available characters were revised in the most complete specimen MMP 1439-M (Fig. 2).

The rostrum of *Abalosia* is similar not only to that of *Octodon* (Reig and Quintana 1991), but also to that of *Octomys*, *Octodontomys* and *Tympanoctomys*. Behind the incisor foramina, medially, the maxillary extends at least up to the lateral premaxillary-maxillary suture. Though MMP 1439-M is rather damaged dorsally, frontals are clearly more similar to those of *Tympanoctomys* and *Octomys* than to those of *Octodon*. The frontal width increases markedly posteriorly and the

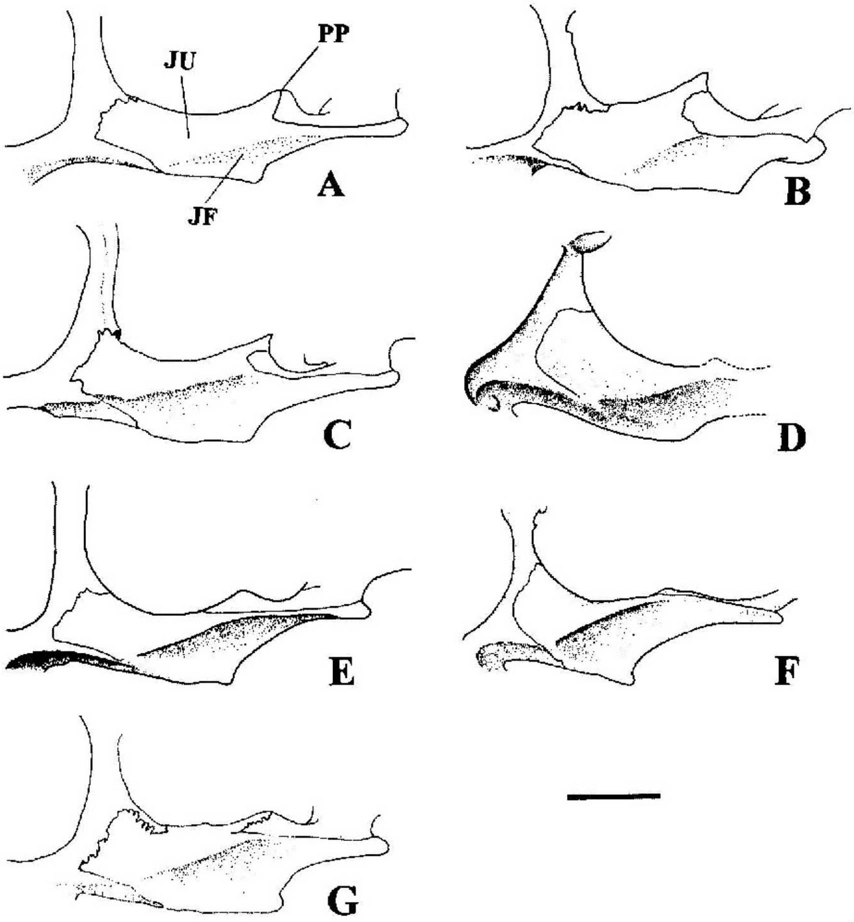

Fig. 3. Lateral view of the left zygomatic arch of (A) *Octodontomys gliroides* IML 00369, (B) *Spalacopus cyanus* IEEUACH 955, (C) *Octodon degus* IEEUACH 745, (D) *Abalosia castellanosi* MMP 1439-M (reversed right zygomatic arch), (E) *Octomys mimax* MACN 13770, (F) *Tympanoctomys barrerae* LP 213, (G) *Aconaemys fuscus* IEEUACH3. Abbreviations: JF – jugal fossa, JU – jugal, PP – Paraorbitary process. Scale: 5 mm.

borders are straight, not excavated in the orbital portions. Consequently, the distance between the frontal bone and the zygomatic arch is shorter than in *Octodon*, *Aconaemys*, *Spalacopus* and *Octodontomys*, as also occurs in *Octomys* and *Tympanoctomys*.

The zygomatic arches are deeper anteriorly than in *Octodon* and more similar to those of *Tympanoctomys* (Fig. 3). As in some specimens of the latter, the anteorbital zygomatic bar enlarges ventrally and the jugal encroaches upon the bar posteroventrally. The ventral border of the zygomatic arch is markedly descending posteriorly, but in *Octodon* is nearly horizontal. The jugal fossa (for the origin of the masseter posterior muscle, *sensu* Woods and Howland 1979) is deep and it faces more posteriorly than in *Octodon*. In the latter, the jugal fossa is more horizontal and practically continuous with the area for the origin of the anterior part of the masseter lateralis muscle (*sensu* Woods and Howland 1979). The lateral flange separating the canal for the infraorbital nerve is reduced, as in specimens of *Tympanoctomys* and *Spalacopus*, while *Octodon* has a large flange.

In the orbital region (Fig. 4) there is an elongated fissure-like sphenopalatine foramen (*sensu* Lavocat 1971, 1976). The posterior margin of the foramen continues with the posterior border of the alveolar sheath of the M^1. This alveolar capsule protrudes in the foramen and reaches its dorsal border. As in *Tympanoctomys*, it is more external than the dorsal border of the foramen. In *Octodon*, the foramen extends up to the alveolus of the M^2 and the dorsal portion of the alveolar sheath of the M^1 is hidden inside the foramen.

The posterior end of the maxilla, behind M^3, is slightly keeled and has an apophysis dorsal to the lateral plate of the palatine (Fig. 4). This apophysis is not seen in *Octodon*, and the alisphenoid extends anteriorly, dorsal to the palatine. The components of the basicranium (basioccipital, basisphenoid) are narrower than in *Octodon*, and the braincase, between the M^3 and the occipital condyle, is longer (Fig. 2). Both characters suggest that *Abalosia* had large auditory bullae.

The occipital region of MMP 1439-M, though damaged, preserves in the left side a fossa which is externally limited by the root of the paroccipital process (Fig. 5). As in *Tympanoctomys* and to a lesser extent *Octomys* and *Octodontomys*, this root paroccipital is perpendicular to the occiput. In the remaining genera, the root of this process is in the plane of the occiput. This character suggests that the mastoid bullae of *Abalosia* were large.

Mandible

Reig and Quintana (1991: 296) pointed out that the mandible "...is more massively built and deeper than in *Octodon* and resembles that of *Pithanotomys*". This is due to the greater development of the chin process under the dP4, and the more vertical disposition of the root of the masseteric crest (Fig. 6). In *Octodon* the chin process is smaller and more posterior, and the origin of the masseteric crest is more horizontal. In these characters, *Abalosia* is similar not only to *Pithanotomys* but also to *Aconaemys*, *Octomys*, and *Tympanoctomys*. The chin process of *Tympa-*

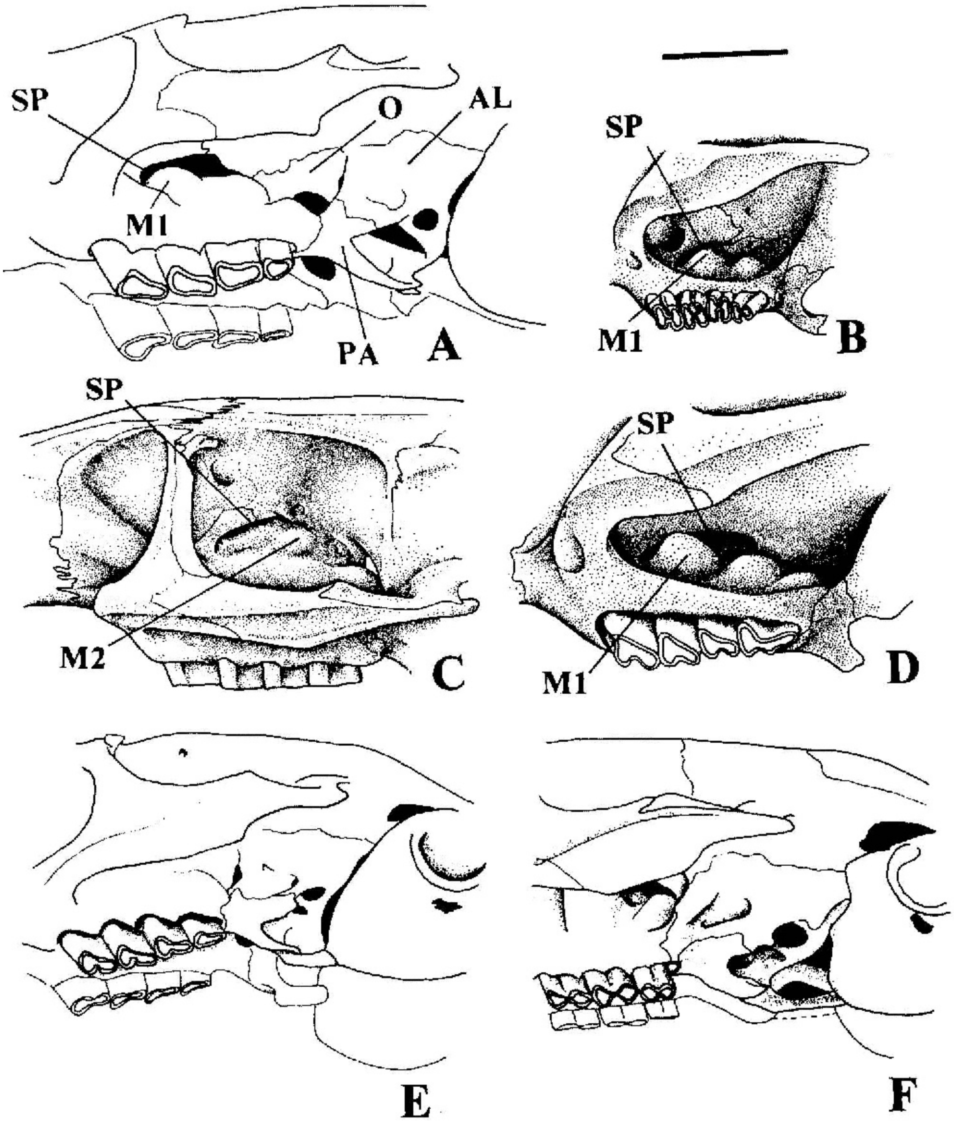

Fig. 4. Orbitotemporal region (A–D) and basitemporal region (E–F) of (A) *Octodontomys gliroides* IML 00369, (B) *Tympanoctomys barrerae* MMP 3199, (C) *Octodon* sp. MLP 12.VII.88.7, (D) *Abalosia castellanosi* MMP 1439-M, (E) *Octodon degus* IEEUACH 5216, (F) *Aconaemys porteri* MLP 17.II.92.5. Abbreviations: AL – alisphenoid, M1 – alveolar sheath of M^1, M2 – alveolar sheath of M^2, O – orbitosphenoid, PA – lateral palatine plate, SP – sphenopalatine foramen. Scale: 5 mm.

noctomys is more developed in fossil representatives (D. H. Verzi, unpubl.). In *Abalosia*, the anterior end of the diastema is level with the alveolar border of the cheek teeth in lateral view; in *Octodon*, and in most of the remaining genera, it is below this level.

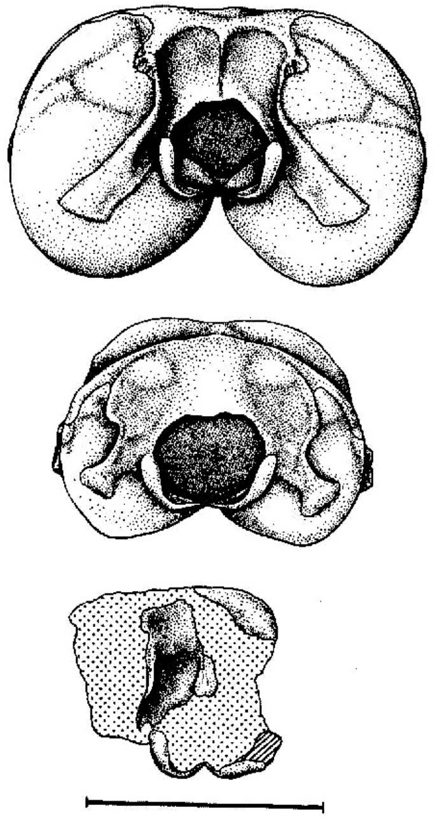

Fig. 5. Occipital region of *Tympanoctomys barrerae* LP 213 (upper), *Octodon* sp. MLP 12.VII.88.5 (center) and *Abalosia castellanosi* MMP 1439-M (bottom). Scale: 15 mm.

Molariforms

The upper molariforms of *Abalosia* (Fig. 7) are similar to those of *Octodon* (Reig and Quintana 1991). They lack a mesoflexus because the posterior lobe of the molars is not extended laterally (Reig and Quintana 1991). These molariforms of *Abalosia* are also partially similar to those of *Octodontomys* and the protohypsodont *aff. Neophanomys biplicatus* from the Pliocene of Farola Monte Hermoso, Argentina (Verzi and Carrin Iglesias 1999). But in these latter taxa, unlike *Abalosia*, there are relics of the mesoflexus (or mesofossette) during the ontogeny (Verzi and Carrin Iglesias 1999, Fig. 1).

The lower molariforms (Figs 6 and 7) are eight-like and clearly different from those of *Octodon* (Reig and Quintana 1991). The dP_4 has a secondary lingual fold in the anterior lobe (paraflexid in Reig and Quintana 1991) which is shared only with *Tympanoctomys*.

Dental wear and mastication

Dental morphology has always played a main role in systematic and evolutionary studies of mammals. In *Abalosia*, the morphology of molariforms was the main support for the hypothesis of its relation to *Octodon* (Reig and Quintana 1991).

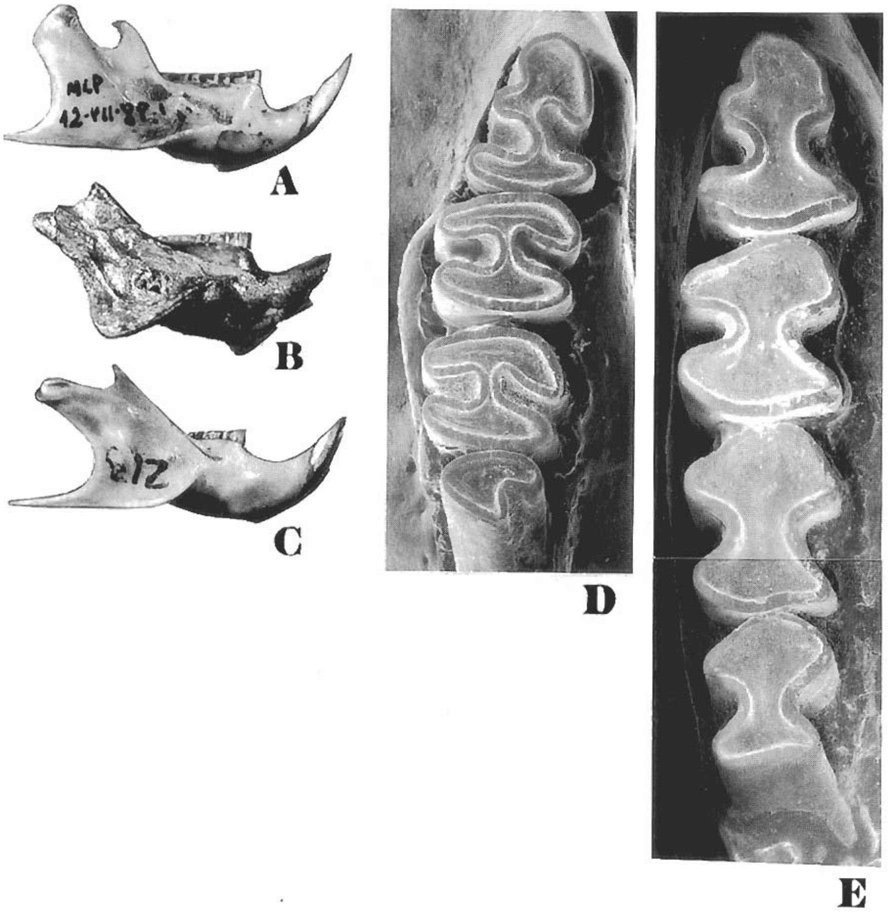

Fig. 6. External view of right mandible (A–C) and occlusal view of dP$_4$–M$_3$ (D–E) of (A) *Octodon* sp. MLP 12.VII.88.1 (1.3×), (B) *Abalosia castellanosi* MMP 1439-M (1.8×), (C) *Tympanoctomys barrerae* LP 213 (1.8×), (D) *T. barrerae* LP s/N§ (12×), and (E) *Abalosia castellanosi* MMP 1439-M (12×).

In order to better interpret the dental characters of *Abalosia*, the wear pattern of the molariforms was analyzed and compared with that of the other octodontids. Asymmetry in wear of the dentine was assessed between the leading edge (which is first exposed to the occlusion according to the sense of the masticatory movements) and the trailing edge (in the opposite side). In the former, the dentine is protected from food erosion by the preceding enamel. As a result, the leading enamel and dentine boundary is smooth and uninterrupted (Greaves 1973). In the trailing edge, the increase of abrasion due to accumulation of food particles causes an enamel step over the dentine (Greaves 1973, Rensberger 1973, Koenigswald *et al.* 1994). This asymmetrical wear of the dentine enables determination of the sense of masticatory

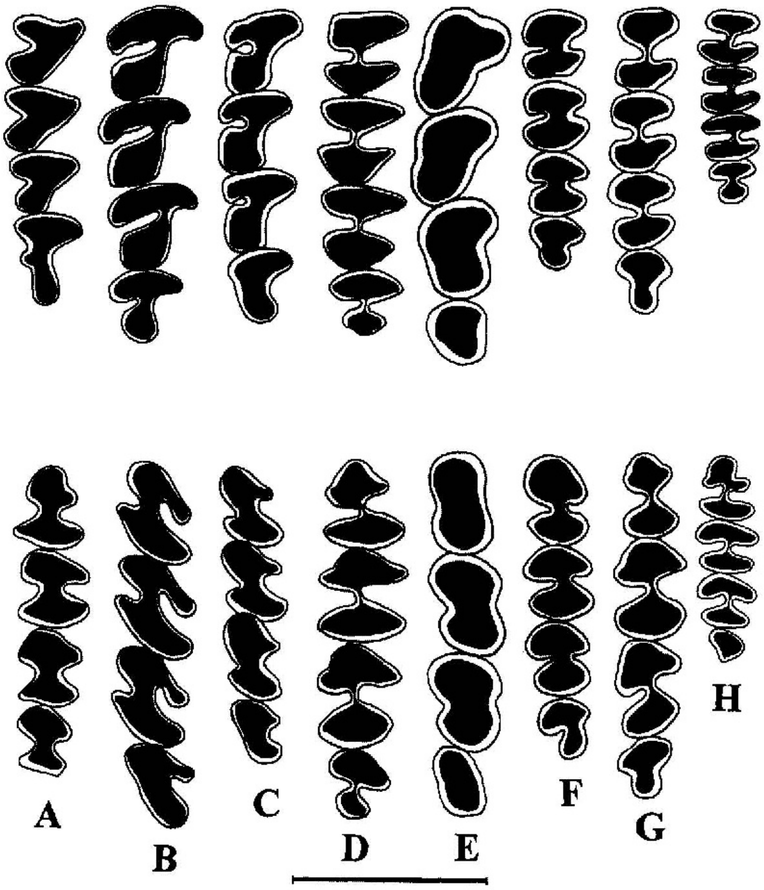

Fig. 7. Occlusal view of left dP^4–M^3 (upper) and dP_4–M_3 (bottom) of (A) *Abalosia castellanosi* MMP 1439-M, (B) *Octodon bridgesi* IEEUACH 3501, (C) *Octodon degus* IEEUACH 2737, (D) *Aconaemys porteri* MVZ 159436, (E) *Octodontomys gliroides* IML 00369, (F) *Spalacopus cyanus* IEEUACH 953, (G) *Octomys mimax* MACN 13765, and (H) *Tympanoctomys barrerae* MACN 39947. Scale: 7 mm.

movements. The tooth scars observed mainly on the enamel (though sometimes also on the dentine) permit interpretation of the direction of these movements.

In *Abalosia*, the anterior edge of the dP_4–M_3 and the posterior edge of the dP^4–M^3 represent the leading edge. In the dP_4–M_2 the enamel forms a step on the anterior and medial face of the hypoflexid and mesoflexid and the posterior edge of each molar (trailing edge). In the dP^4–M^2 such a step is placed on the posterior and medial face of the hypoflexus and on the anterior edge of each molar (trailing edge). The scars observed on the enamel are parallel to the sagittal axis of the skull or mandible. These features suggest that chewing in *Abalosia* was propalinal.

The tooth wear and masticatory movements in other octodontids have been analyzed by Wilkins and Cunningham (1993), Koenigswald *et al.* (1994) and Verzi

(1994), with similar results. In *Actenomys*, *Ctenomys*, *Octodontomys*, and *Octodon* the wear of the dentine and the scars show that in the examined species of these genera (Appendix I), the masticatory movement is oblique, posterolabial-anterolingual, and unilateral. In *Aconaemys*, *Octomys* and *Tympanoctomys* the leading edge of the molars is the posterior edge of each lobe of the dP^4–M^3 and the anterior edge of the dP_4–M_3. Tooth scars are parallel to the sagittal axis of the skull and mandible, suggesting a propalinal masticatory movements. Tooth scars could not be detected in specimens of *Spalacopus cyanus*, but the pattern of the dentine wear suggests propalinal mastication with a slight oblique component (Koenigswald *et al*. 1994, Verzi 1994).

Phylogeny

A matrix of 28 craneomandibular and dental characters was constructed from the comparative analysis of *Abalosia* and the living octodontines (Appendix II). A single cladogram was obtained (Fig. 8) 54 steps long, with a consistency index (taking into account only informative characters) CI = 0.82 and a retention index RI = 0.80. In this cladogram, the monophyly of Octodontinae (in its classical sense, ie excluding *Ctenomys* and *Actenomys*; Tate 1935, Reig 1958; Fig. 8, node 3) is only supported by the aspect of the premaxillary portion of the septum of the incisive foramen (character state 2^1). *Abalosia* clusters with *Octomys* and *Tympanoctomys*, (Fig. 8, node 7) and represents the sister genus of the latter. The clade (*Octomys*

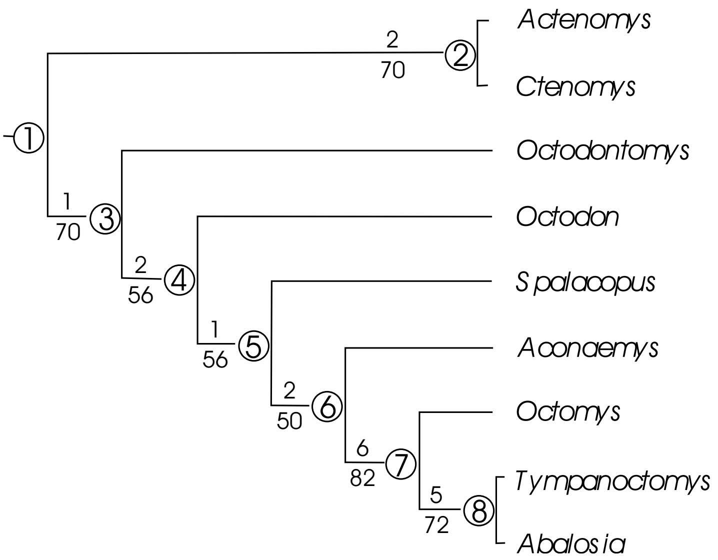

Fig. 8. Cladistic relationships of *Abalosia castellanosi* to the extant Octodontinae (see Appendix II). Node 1: 4^1, 14^1, 19^1, 21^1, 24^3; Node 2: 1^2, 12^1; Node 3: 2^1; Node 4: 1^1, 6^1; Node 5: 7^2; Node 6: 20^1, 24^1, 25^1, 26^1; Node 7: 5^0, 7^1, 11^1, 13^1, 17^1, 18^1; Node 8: 8^1, 9^4, 16^1, 24^2, 27^1. Only non-ambiguous synapomorphies are indicated. Bremer support and relative Bremer support values are shown above and below the nodes, respectively.

(*Tympanoctomys Abalosia*)) is supported by character states 5^0, 7^1 and 13^1. The other three character states shared by *Octomys* and *Tympanoctomys* are not preserved in *Abalosia* (11^1, 17^1 and 18^1). The clade *Tympanoctomys*-*Abalosia* (Fig. 8, node 8) is supported by 5 non-ambiguous synapomorphies in the lateral flange of the infraorbital canal, the zygomatic arch, the braincase length, and the anterior lobe of the dP_4 and M_1–M_2 (character states 8^1, 9^4, 16^1, 24^2 and 27^1, respectively); the character state 15^2 that appears as ambiguous could also be a synapomorphy of this clade (see Apendix II).

Discussion

Comments about the phylogeny of the living Octodontinae

Octodontinae is a taxon that has been poorly diagnosed (Spotorno 1979, Verzi 1999). Likewise, its membership and taxonomic rank have been unstable in the literature (see Pascual *et al*. 1965). In classificatory proposals prior to Tate (1935), *Ctenomys* was usually included in the taxon that was alternatively considered as family Octodontidae (eg Ameghino 1889, Rusconi 1931) or subfamily Octodontinae (eg Miller and Gidley 1918, Ellerman 1940, Landry 1957). First Tate (1935), and then Reig (1958; see justification in Pascual *et al*. 1965) removed *Ctenomys* from the octodontines. This proposal prevailed in later literature, but without agreement in relation to the taxonomic rank assigned to both lineages (familial – eg Tate 1935, Simpson 1945, Wood 1955, Cabrera 1961, Parent 1980, Gallardo 1992, Contreras *et al*. 1993, Woods 1993; subfamilial – eg Pascual *et al*. 1965, Woods 1972, Reig 1989, Gallardo 1997). Beyond the evident relationships of Octodontinae and Ctenomyinae as sister groups (Pascual *et al*. 1965, Gallardo 1997), to accept these latter either as a family or subfamily of Octodontidae is a decision supported by the importance of the gap between both groups. I assume here, as have Woods (1972: 190) and Gallardo (1997), that the inclusion of *Ctenomys* and allied genera in Octodontidae is the best representation of their linkage within the Octodontoidea.

The hypothesis of the octodontine's relationships of Fig. 8 is partially in agreement with that proposed by Hutterer (1994) who interpreted *Octodon* as a primitive genus, and *Aconaemys*, *Octomys*, *Tympanoctomys*, and *Spalacopus* as members of a more derived clade. This clade acquired a propalinal mastication, which in rodents is accepted as derived with respect to the oblique mastication (Vianey-Liaud 1976, Butler 1985, Woods and Hermanson 1985, Woods and Mckeen 1989).

Octodontomys is a monotypic genus (Appendix I) with uncertain affinities (cf George and Weir 1972, Rossi *et al*. 1990, Gallardo 1992, 1997). Hutterer (1994: 37) interpreted this genus "...perhaps as an offshoot of *Octodon*...". On the contrary, Verzi and Carrin Iglesias (1999) and Verzi *et al*. (1999) interpreted *Octodontomys* as probably related to the origin of the Ctenomyinae, according to dental characters. Whatever its affinities are, it is the most primitive living octodontid in its cranial and dental morphology. It shows similarities with some species from the Mio--Pliocene of Argentina (Verzi *et al.* 1999, Verzi and Carrin Iglesias 1999), suggesting that it may belong to an early offshoot which persisted with few changes.

Octodontidae is the most diverse family of mammals with respect to its chromosome numbers (Contreras *et al.* 1990, Gallardo 1997). Among the species with 2N = 56–58, Contreras *et al.* (1994) found more chromosome similarity between *Octomys mimax* and *Aconaemys fuscus*, than between the former and *Spalacopus cyanus* or *Octodon degus*. Differences were greater between *O. mimax* and *Octodontomys gliroides*. This interpretation agrees with cranial and dental data; but these authors, supporting eco-morphological gradients proposed for the octodontines, suggested that: "...the identical or similar diploid and autosomal arm numbers observed for *O. mimax*, *A. fuscus*, and some other species probably are a consequence of parallel evolution and not due to common ancestry".

Gallardo (1997: Fig. 21.1) presented an allozymic tree of Octodontidae with the following topology: (*Ctenomys*((*Spalacopus Abrocoma*)(*Octodontomys*((*Octomys Tympanoctomys*)(*Octodon Aconaemys*))))). It shows significant differences with the hypothesis proposed here, especially in the position of *Octodon* and *Spalacopus*. However, both hypotheses are consistent respect to the relationship of *Octomys* and *Tympanoctomys*.

Adaptive diversity of the octodontines and paleoenvironmental meaning of *Abalosia*

Contreras and collaborators (Contreras and Torres-Mura 1986, Contreras *et al.* 1993, Contreras *et al.* 1994) analyzed the adaptive diversity of the octodontines. They proposed three clusters which follow two eco-morphological gradients: from the generalist *Octodon*, one adaptive gradient to subterranean life represented by *Aconaemys* and *Spalacopus*, and another adapted to deserts through *Octodontomys*, *Octomys* and *Tympanoctomys*. Recently, Ojeda *et al.* (1996) reported that *Tympanoctomys* also builds complex subterranean galleries.

The adaptive gradients were thought to constitute phyletic lines (Contreras and Torres-Mura 1986, Contreras *et al.* 1993, Contreras *et al.* 1994). On the contrary, in the cladogram of Fig. 8, both subterranean habits and adaptation to arid biomes have been acquired independently more than once in Octodontinae. Likewise, the cladogram proposed by Gallardo (1997; Fig. 21.1) supports a multiple origin of both subterranean and desert adaptations.

However, the situation is different in the clade including *Octomys* and *Tympanoctomys*. These are the most cohesive genera of living octodontids (previously included in a single genus, eg Lawrence 1941, Woods 1982, Reig 1986), and also the caviomorphs most adapted to xeric conditions (Mares 1975, 1993, Bozinovic and Contreras 1990, Ojeda *et al.* 1996). They both inhabit arid environments of the Monte semi-desert in western Argentina (Fig. 9). *Tympanoctomys* also occupies the margins of the Patagonian steppe (Ojeda *et al.* 1996). As in other desert specialists, the most clear cranial evidence of adaptation to arid biomes is the strong development of the auditory bullae (eg Mares 1980, Randall 1994, Ojeda *et al.* 1996, 1999).

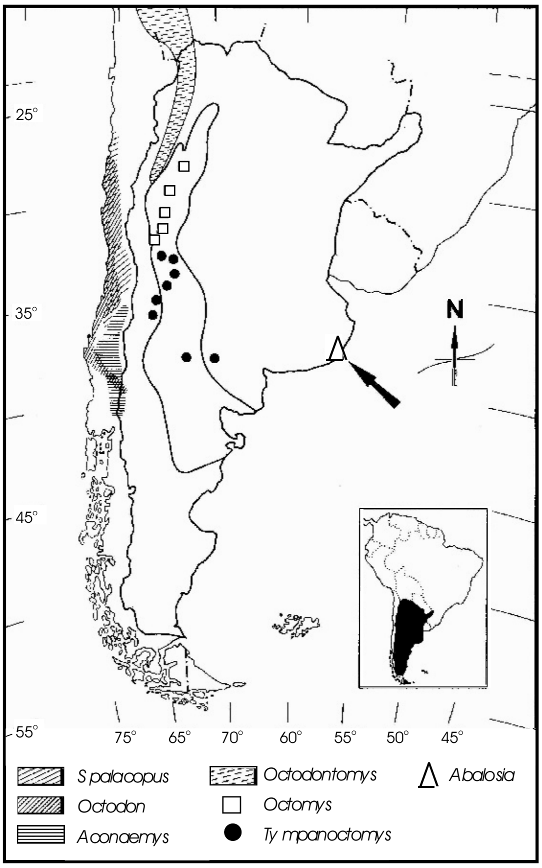

Fig. 9. Geographic distribution of *Abalosia castellanosi* (arrow) and the extant Octodontinae. The blank enclosed within the solid line indicates the Monte semi-desert (after Mares 1979).

If it is accepted, as Vrba (1992: 3) suggested, that habitat-specificities are inheritable from species to species, and for entire clades, it may be proposed that the adaptation to arid biomes has been inherited in the clade including *Octomys* and *Tympanoctomys* (Gallardo 1997). Consequently, the phylogenetic position of *A. castellanosi* suggests that it was also a desert specialist. The basicranial and occipital morphology of this species suggesting large bullae reinforces this claim.

The sudden appearance of *Abalosia* in the Sanandresian record is preceded by the absence of ancestors or sister-taxa presumably related to its origin, in the rich Plio-Pleistocenic coastal deposits of the Buenos Aires Province. Likewise, it is never recorded again after the Sanandresian. This fact suggests that *Abalosia* was an immigrant to the coastal region of central Argentina (Vucetich and Verzi 1999). According to the present distribution of related genera, it may have originated in the emergent semi-deserts of western Argentina (Fig. 9). These deserts probably began their development during the global climatic deterioration of the Late Miocene (eg Pascual and Ortiz Jaureguizar 1990, Janis 1993, Leakey *et al.* 1996, MacFadden and Cerling 1996). But they became differentiated especially during the Pliocene, due to the rain shadow effect produced by the uplift of the Sierras Pampeanas in the Diaguita phase of the Andean Orogeny (Mares *et al.* 1985, Pascual *et al.* 1985, Pascual and Ortiz Jaureguizar 1990).

Abalosia may have reached the coastal region of central Argentina during a pulse of expansion of such arid environments. Tonni and Cione (1995) propose an arid pulse for the Sanandresian. The episodic character of the Sanandresian caviomorph fauna reinforces this claim. Other caviomorphs indicating aridity, besides *A. castellanosi*, are suddenly recorded at this time: *Abrocoma* sp., *Ctenomys chapalmalensis* and *Pediolagus* sp. (Quintana 1994, Vucetich and Verzi 1995). This caviomorph assemblage, also integrated by the Pliocenic genera *Pithanotomys* and *Microcavia*, represents the fossil caviomorph fauna most clearly indicative of arid conditions. In accordance with palaeomagnetic data (Orgeira 1991 and literature cited therein, Berggren *et al.* 1995), the Sanandresian may be coetaneous with the global climatic deterioration detected around the limit Gauss-Matuyama magnetic ages (Vrba 1985, 1989, 1992, Bonadonna and Alberdi 1987, Tonni *et al.* 1992, Janis 1993, de Menocal 1995, Vrba *et al.* 1995, Willis *et al.* 1999).

Evolutionary meaning of *Abalosia*

Reig and Quintana (1991: 298) proposed *Abalosia* as the ancestor of *Octodon*, a "generalist" octodontine distributed almost exclusively in Chile (Contreras *et al.* 1987, Verzi and Alcover 1990, Hutterer 1994) but these authors offered no phylogenetic support for their hypothesis. Hutterer (1994) disagreed with the proposal of Reig and Quintana (1991) and considered *Abalosia* of uncertain phylogenetic position.

In the phylogenetic hypothesis proposed in the present study, *Abalosia* is part of a clade of desert specialist, propalinal octodontids, which would have evolved east of the Andes (Fig. 9). *Abalosia* groups with *Octomys* and *Tympanoctomys* and represents the sister genus of the latter. However, *Abalosia* is clearly divergent in its morphology both from *Octomys* and also *Tympanoctomys*. It seems to be the rule within the octodontines, that the low species richness (Appendix I) contrasts with a great morphological diversity; namely that the morphological gaps among the generic taxa are wide (Fig. 8). A similar situation is observed from a karyotypic approach, as the octodontines show the largest span for chromosomal variation observed in a mammal family together with extreme gaps between chromosome numbers (Contreras *et al.* 1990, Gallardo 1997). Both karyotypic and morphological evidence led to the interpretation of the living octodontines as the remnant of a wider past radiation (Gallardo 1992, Contreras *et al.* 1993, Verzi 1994), or as the result of saltational evolution (Gallardo 1997). Although this last interpretation was proposed as an alternative to the first one, both may not represent opposite hypotheses.

Unlike other groups of living rodents (Hafner and Hafner 1988, Hafner 1993), no hypothesis of the origin of the octodontine diversity is based on morphology. However, recently Gallardo (1997) proposed a saltational model to explain it on karyotypic evidences. This model involves at least one event of tetraploidy and it proposes *Tympanoctomys* as a tetraploid-descendant from the parental *Octomys*. Such a model was proposed as alternative to a gradualistic view which would require intermediate forms not found in the fossil record: “Since no fossil evidence exists for *Octomys*, *Tympanoctomys*, *Spalacopus* or *Octodontomys* (...), any model will have to deal with ‘missing karyotypic links’(...). The necessary assumption of these intermediate forms constitutes an *ad hoc* hypothesis of gradualism”. (Gallardo 1997: 357). In this case, the presumed absence of fossils, and not the possible gaps between them and with the living Octodontinae species, is interpreted as evidence of a particular evolutionary non-gradual dynamic. The situation of *Abalosia*, however, demonstrates that the existence of fossils related to the living species does not necessarily lead to a gradualistic view; it notices, instead, of a possible ontological problem if fossils are not considered in the evolutionary interpretation of the living species.

Evidences from DNA and sperm morphology suggest that *Tympanoctomys* is a noteworthy case of tetraploidy (Gallardo *et al.* 1999). However, the origin of this evolutionary innovation (process) would not be justified through the phylogeny of the living species if it is accepted that there is extinction affecting the octodontine clade. As Cracraft (1990: 23) pointed out, an ontological mistake arises when the analysis of evolutionary innovation is made in hierarchical levels well above that at which processes producing the innovation have operated: “Manifestations of pattern above the level of differentiating populations, or basal taxa, are epiphenomena, or effects, of lower level processes”.

The phylogenetic position of *A. castellanosi* suggests that extinction events affected the clade of the octodontine desert specialists. However, the information given by *A. castellanosi* does not favor a gradualistic view, as this species does not represent a morphological link between *O. mimax* and *T. barrerae*; on the contrary, it is clearly divergent.

According to magnetostratigraphy of the San Andrés Formation, the divergence of *Abalosia* and *Tympanoctomys* has a minimal age of 2.6 Ma – million years ago (Orgeira 1990, 1991, Berggren *et al.* 1995). The remaining dichotomies among the octodontine genera of the cladogram of Fig. 8 may have been even earlier. Although the modern genera are not known as fossils, unquestionable members of the subfamily are recorded since the Late Miocene in Argentina (Rovereto 1914, Reig 1989). According to this, it seems clear that, beyond how rough or gradual the differentiation of the octodontine’s diversity has been, the living representatives are the remnant of a wider radiation. Probably, the current scarce contribution of the fossil record to the knowledge of this history is not mainly due to its fragmentary nature, but to the poor knowledge of the relationships of the extinct species to the living ones. This study represents a case of clear relationships between them, which is expectable for a group that shows a rich fossil record in the same area of distribution of the living species.

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Appendix I. Taxa and specimens examined. The list of living species of Octodontinae represents all the known species but *Octodon pacificus*, of which only illustrations have been revisited.

Octodontinae. *Abalosia castellanosi*: Argentina, Buenos Aires, San Andrés Formation, Late Pliocene, Punta San Andrés (MMP 572-M, 1060-M, 1439-M); Playa Santa Isabel (MMP 1452-M, 1522-M–1524-M). *Aconaemys fuscus*: Argentina, Neuquén, Lago Ñorquinco (MLP 17.II.92.11); Chile, Malleco Province, Tolhuaca National Park (IEEUACH 1–3, 2524–2528, 3703); Ñuble Province, Pozo Arenas (IEEUACH 2254); Hacienda El Roble (IEEUACH 4179–4183). *Aconaemys porteri*: Argentina, Neuquén, Ruca Malén (MVZ, 159431, 159433, 159436); Lago Currhue (MLP 17.II.92.1–17.II.92.3, 17.II.92.5–17.II92.7); Volcán Huanquihue (MLP 17.II.92.4); Chile, Cautín Province, Termas de Palquín (IEEUACH 2255, 3704); Cautín Province, Quetropillán (IEEUACH 2256–2274, 3705–3723, 4184–4201, 4386–4398); Osorno Province, Puyehue (IEEUACH 3701, 3702). *Aconaemys sagei*: Argentina, Neuquén, Pampa de Hui-Hui (MVZ 163417, 163421, MLP 17.II.92.8–17.II.92.10, IEEUACH 4399, 4401); Chile, Malleco Province, Pedregoso (IEEUACH 2785). *Spalacopus cyanus*: Chile, El Chuisco Norte (MMP 3807); Aconcagua Province, Papudo (MMP 3583, 3585, 3590, 3591); Aconcagua Province, Zapallar (3619, 362, 3623–3625, 3628, lot from pellets of strigiform birds); Cordillera Province, Lagunillas (IEEUACH 953–955); Choapa Province, Los Vilos (IEEUACH 956, 957, 4017–4019, 4523–4551, 5326–5330); Choapa Province, Huentelauquén (IEEUACH 2510, 4020, 4552–4561); Choapa Province, Los Cristales (IEEUACH 4562–4568); San Antonio Province, Algarrobo (IEEUACH 958, 959); San Antonio Province, El Quisco (IEEUACH 960); San Antonio Province, El Tabo (IEEUACH 961); Valparaíso Province, Concón Bajo (IEEUACH 962–966); Valparaíso Province, Concón Alto (MLP 30.XI.93.1); Elqui Province, Parque Nacional Fray Jorge (IEEUACH 1844); Ñuble Province, Los Rematos (IEEUACH 1845–1850, 2511–2516, 4001–4016, 4358–4365, 4367–4379, 4381–4385, 4894; MLP 10.XI.95.5); Ñuble Province, Quirihue (IEEUACH 2517–2523). *Octodon degus*: Chile, Santiago Province (MLP 30.XI.93.2, IEEUACH 745); Elqui Province, Fray Jorge National Park (IEEUACH 1763, 2738–2745); Quillota Province, La Campana National Park (IEEUACH 5216–5225, 5433–5436). *Octodon bridgesi*: Chile, Malleco Province, Río Colorado (IEEUACH 1764, 2455, 3883–3885); Malleco Province, Malalcahuello (IEEUACH 2456–2461); Ñuble Province, Burca (IEEUACH 1066, 2736, 3144–3146, 3501–3503, 3887–3889); Ñuble Province, Las Eras (IEEUACH 3874–3880, 4485–4487); Ñuble Province, Los Remates (3881, 4328); Curico Province, Valle Teno (IEEUACH 3882); Unihue (IEEUACH 5211–5215). *Octodon lunatus*: Chile, Elqui Province, Fray Jorge National Park (IEEUACH 2747). *Octodon* sp.: Argentina, Neuquén, Lago Currhue Chico (MLP 12.VII.88.1–12.VII.88.7). O*ctodontomys gliroides*: Argentina, Jujuy, route between Uquía and Calpalá (MLP 25.XI.98.1, 25.XI.98.2); Jujuy, Tilcara (MLP 12.VII.88.10, MACN 17832–17837, MMP 755, 2200, 2532, 3057, 3557); Jujuy, Maimará (MACN 27.92–27.94, 27.96, 31.39); Jujuy, Sierra de Zenta (32.15, 32.16, 32.59); Jujuy, Pucapampa (MACN 49.101); Jujuy, Cochinoca (MLP 11.XII.35.19); Salta, San Antonio de Los Cobres (MACN 30.51, 30.52, 30.54, 30.55); Salta, Chorrillos (MACN 30.112); Chile, Parinacota Province, Lago Chungará (IEEUACH 2462–2464); Iquique Province, Chusmisa (IEEUACH 4329–4333); Iquique Province, Isluga (IEEUACH 4338); Parinacota Province, Murmutani (IEEUACH 4335–4337). *Octomys mimax*: Argentina, San Juan, Valle Fértil (MMP 388, MACN 13764, 13765, 13770, 13773, 13782). *Tympanoctomys barrerae*: Argentina, Mendoza, Malargüe (MACN 39944–39949); Mendoza, La Paz (MMP 3199); La Pampa, Lihuel, Calel and Casa de Piedra (lot from pellets of strigiform birds).

Ctenomyinae. *Ctenomys australis*: Argentina, Buenos Aires, Necochea (MLP 3.XI.95.5, 7.XI.95.1–-7.XI.95.7, 7.XI.95.9, 7.XI.95.11, 7.XI.95.12, 10.XI.95.2). *Ctenomys azarae*: Argentina, La Pampa, Gral. Acha (MLP 21.III.78.27). *Ctenomys talarum*: Argentina, Buenos Aires, Verónica (20.III.78.1–20.III.78.7, 21.III.78.19–21.III.78.22); Buenos Aires, Punta Indio (10.V.87.1–10.V.87.9, 1.XI.95.8, 1.XI.95.9–1.XI.95.15, 3.XI.95.1–3.XI.95.4, 10.XI.95.6, 10.XI.95.7). *Ctenomys tuconax*: Argentina, Tucumán, Infiernillo (MLP 12.VI.70.3, 12.VI.70.4, 12.VI.70.6, 27.III.78.2). *Ctenomys sp.*: Argentina, Catamarca, Antofagasta de La Sierra (MLP 7.X.92.1–7.X.92.3, 7.XI.95.8, 7.XI.95.10, 9.XI.95.2). *Ctenomys mendocinus*: Argentina, Mendoza, Divisadero Largo (MLP 7.X.92.4, 3.XI.95.7). *Ctenomys latro*: Argentina, Tucumán, Tapia (MLP 3.XI.95.6, 10.XI.95.1). *Ctenomys pearsoni*: Uruguay, San José, Ruta 1 km. 29 (MLP 30.XI.93.3). *Actenomys priscus*: Argentina, Buenos Aires, Chapadmalal Formation, Middle Pliocene, Arroyo Las Brusquitas (MLP field number H-42, MMP 579-S, 1382-M); Playa La Estafeta (MLP field number

H-150); Playa Las Palomas (208-S, 1250-M); Playa Chapadmalal (2132-M); Pliocene, Paso Otero (MLP 87-V-20-1).

Echimyidae. *Thrichomys apereoides*: Brasil, Palmeiras (MMP 1242-1245); Pernambuco (MMP 1246); "Brasil" (MMP 1247, 1248, 1292); Pocoti-Fortaleza (MMP 1293, 1297); Baturite-Fortaleza (1294); Ipanema (MMP 1295, 1296).

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

1. Anterior extension of the maxillary into the posterior margins of the incisive foramina: scarcely developed or absent, posteriormost ends of the foramina behind the premaxillary-maxillary suture (0); near or in contact with the premaxillary portion of the septum level with the premaxillary-maxilar suture, foramina restricted posteriorly (1); dorsal to the premaxillary septum, foramina restricted posteriorly (2). In the Octodontidae other than *Octodontomys*, the alveolus of the dP^4 is inclined forwardly and medial to the incisor. Such disposition causes the extension of the maxillary which constraints the incisive foramen posteriorly. Glanz and Anderson (1990: 12) point this character as the presence of a short incisive foramen for the Octodontidae.

2. Premaxillary portion of the septum in the incisive foramina: with the posterior end joined medially forming a rather acute projection (0); with the posteriordorsal ends divergent, each one forming a lateral apophysis (1).

3. Sphenopalatine foramen (*sensu* Lavocat 1971, 1976: Fig. 3 I): oblique and extended posteriorly to the alveolar sheath of the M^1 or M^2 (0); vertical in front of the M^1 alveolar sheath, with or without independent relict posterior to the M^1 (1).

4. Alveolar sheath of the molars: not externally visible in the orbital region (0); protruding into the orbital region (1). This character is related to the development of hypsodonty in Octodontidae.

5. Alveolar sheath of M^1: not hidden inside the sphenopalatine foramen (0); hidden inside the foramen (1).

6. Joint of maxillary, lateral palatine plate and alisphenoid in the basitemporal region: posterior to the M^3 alveolus (0); posterolateral to the M^3 alveolus, maxillary with a slight posteroexternal margin or edge (1). Woods and Howland (1979) described the basitemporal morphology in Myocastoridae and Capromyidae. They named "pterygoid plate" the main portion (lateral) of the alisphenoid and did not mention the participation of the palatine, which according to the description takes also part of its "pterygoid plate". I name here lateral palatine plate the portion of this bone interposed between maxillary and alisphenoid.

7. Posterior portion of the maxillary: without apophysis (0); with one apophysis posterior to the M^3 alveolus, near or in contact to the alisphenoid (1); with one apophysis posterolateral to the M^3 alveolus strongly joined to the alisphenoid (2).

8. Lateral flange of the canal for the infraorbital nerve: well developed (0); reduced or absent (1). Glanz and Anderson (1990: 17) pointed that: "Among octodontids other than *Octodontomys*, this flange (...) is encroached upon and reduced by the backwardly extending incisor capsule in *Aconaemys* and even more so in *Spalacopus*...". However, *Aconaemys* has robust incisors and with alveoli more protruding than *Tympanoctomys*, and while *Aconaemys* retains this flange, *Tympanoctomys* almost does not. This suggests that these characters are partially independent.

9. Zygomatic arch: with high, deep and subhorizontal jugal fossa; maxillary with an extension dorsal to the jugal on the base of the antorbitary zygomatic ramus (0); with the fossa oriented more posteriorly (1); with a lower and slightly deep fossa (2); with a lower, slightly deep and posterior fossa (3); with a deep jugal fossa, very high level with the paraorbitary apophysis and oriented more posteriorly; if the maxillary extension is absent, the end of the jugal is wide and oriented anterodorsally (4).

10. Ventral zygomatic root (area for the origin of the masseter lateralis muscle): normally developed (0); wide and thin (1).

11. Paraorbitary process in lateral view: formed by a rather developed apophysis of the jugal reached posteriorly by the squamosal (0); formed only by the squamosal (1); formed only by the jugal (2).

12. Suborbitary fossa in the jugal (Osgood 1946, Contreras and Berry 1982): absent (0); present (1).

13. Frontals: with concave margins, excavated level with the orbits (0); with straight margins posteriorly divergent (1).

14. Paroccipital process: ventrally oriented, with its free end separated from the bulla and ventral to the latter (0); short, more laterally oriented and completely joined to the bulla (1) (Woods 1984: 427).

15. Root of the paroccipital process: posteriorly faced, on the plane of the occiput (0); more medially oriented by the development of the mastoid bulla (1); strongly medial and close to the condyle (2).

16. Length of the braincase (from the condyle up to the M^3 alveolus): less than 3.5 times the length dP^4-M^2 (0); longer, near 4 times the length of dP^4-M^2 (1).

17. Squamosal's posterior apophysis: straight, with the posterior end wide (0); with the posterior end narrow and ventrally inclined (1).

18. Dorsal wall of the epitympanic recess: as a small dorsal ossification on the braincase roof, or absent (0); forming a large bony "island" on the roof of the braincase (1).

19. Origin of the masseteric crest of the mandible: including the notch for the tendon of the masseter medialis (0); posterior to the notch (1). In the Octodontidae, the beginning of the masseteric crest on the mandible is posterior to the notch corresponding to the insertion of the tendon of the masseter medialis anterior (*sensu* Woods 1972), therefore not including it. This configuration may result of the insertion of the fiber lamina of the masseter medialis, posterior to the tendon (pars zygomaticomandibularis *sensu* Woods and Howland 1979) in a dorsal subdivision of the masseteric fossa, not reaching the crest (Woods 1972: 128, De Santis 1986: Figs 66–67).

20. Masseteric crest: posteriorly oriented in its origin (0); more vertical since its origin (1).

21. Adult dP^{4}_{4}-M^{3}_{3}: with paraflexus, metaflexus/id and posteroflexus (or the corresponding fossettes/ids) (0); without such flexi/flexids (neither the corresponding fossettes/ids) (1).

22. dP^{4}-M^{2}: with transverse lophs and persistent flexi (0); eight shaped, with two transverse lobes separated by the hipoflexus and mesoflexus (1); with the posterior lobe not labially extended and with a deep hipoflexus (2); with the posterior lobe not labially extended and without hipoflexus (3). *Abalosia*, *Octodon* and *Octodontomys* have upper molars with the posterior lobe not labially extended, unlike the remaining Octodontinae. Consequently, there is neither a mesoflexus limited by both lobes as in the remaining species. Reig and Quintana (1991) described the molariforms of *Octodon* and *Abalosia* as lacking the mesoflexus. However, in the ontogeny of the molars of *Octodon* and *Abalosia* there are no evidences of the close of this flexus, while in *Octodontomys*, instead, it can be clearly observed the close of the mesoflexus and later loss of the mesofossette (Verzi and Carrin Iglesias 1999).

23. dP_{4}-M_{2}: with transverse lophids (0); 8-shaped, with two transverse lobes separated by hypoflexid and mesoflexid (1); with subelliptic and oblique lobes separated by hypoflexid and mesoflexid (2); with rounded lobes slightly oblique, with only traces of hypoflexid and mesoflexid (3); semilunar and without flexids (4).

24. Secondary fold on the lingual face of the anterior lobe of the dP_{4}: absent (0); scarcely penetrating (1); well-developed (2).

25. Anterior face of the dP_{4}: rounded, not ending acutely (0); with its sharp end and a secondary fold on the labial and/or the lingual side (1).

26. Bottom of the hypo- and mesoflexid in $M_{1\text{-}2}$: separated (0); very close or in contact (1).

27. Anterior lobe of $M_{1\text{-}2}$: with persistent flexids or fossetids (0); triangular-like, nearly a scalene triangle (1); triangular-like, nearly an isosceles triangle (2); pyriform (3); rounded (4).

28. Mastication: oblique (0); propalinal with a slight oblique component (1); propalinal (2).

Genus	Characters																											
										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	6	7	8
Thrichomys	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0
Actenomys	2	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	3	4	0	0	?	?	0
Ctenomys	2	0	1	1	?	0	0	1	0	?	2	1	0	1	0	0	0	?	1	0	1	3	4	0	0	?	?	0
Octodontomys	0	1	0	1	0	0	0	0	2	0	0	0	0	1	1	0	0	0	1	0	1	3	3	0	0	0	4	0
Octodon	1	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	2	2	0	0	0	3	0
Spalacopus	1	1	1	1	?	1	2	1	3	1	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	2	1
Aconaemys	1	1	1	1	1	1	2	0	1	1	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1	2	2
Tympanoctomys	1	1	0	1	0	1	1	1	4	0	1	0	1	1	2	1	1	1	1	1	1	1	1	2	1	1	1	2
Octomys	1	1	0	1	0	1	1	0	1	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	2	2
Abalosia	1	?	0	1	0	1	1	1	4	0	?	0	1	?	2	1	?	?	1	1	1	2	1	2	1	0	1	2