Available online at www.sciencedirect.com
SCIENCE DIRECT®
ELSEVIER
Palaeogeography, Palaeoclimatology, Palaeoecology 219 (2005) 303–320
PALAEO
www.elsevier.com/locate/palaeo

The caviomorph rodents from the San Andrés Formation, east-central Argentina, and global Late Pliocene climatic change

Diego H. Verzi[a,*], Carlos A. Quintana[b]

[a]Departamento Zoología Vertebrados, Museo de La Plata, 1900 La Plata, Argentina. CONICET
[b]Laboratorio de Arqueología, UNMDP, Mar del Plata, Argentina

Received 19 October 2004; received in revised form 5 January 2005; accepted 5 January 2005

Abstract

The caviomorph rodents from the San Andrés Formation are revisited. The fossiliferous stratigraphic unit outcrops in the coastal cliffs of the Chapadmalal area (east-central Argentina), and represents the Late Pliocene (Upper Marplatan Stage, Sanandresian Substage). A new species of *Cavia* (Caviidae) and unpublished materials of *Dolichotis salinicola* (Caviidae) and *Abrocoma* (Abrocomidae) are described, and the taxonomic status of the previously described taxa is briefly discussed. The living taxa *Cavia, D. salinicola* and *Abrocoma* are first recorded in the San Andrés Formation, and the extinct *Abalosia* (Octodontidae) is exclusive of this formation. The specimens of *Abrocoma* represent the single undoubted record of the living genus. The record of *D. salinicola, Abalosia, Abrocoma* and the octodontid *Ctenomys* represents an immigration event to east-central Argentina. This fauna from San Andrés is the extinct caviomorph assemblage most clearly indicative of arid environments so far recorded. Its episodic character and composition, and the available palaeomagnetic data, reinforce the hypothesis that it is probably coeval with the profound Late Pliocene cooling and drying pulse detected worldwide around 2.5 Ma. The Sanandresian immigrant taxa would have inhabited the emergent semi-deserts of western Argentina, and may have reached the more eastern Chapadmalal area during an expansion of such arid environments triggered by this Late Pliocene cooling and drying pulse.

Keywords: Caviomorph rodents; Late Pliocene; Argentina; Palaeoclimate

1. Introduction

Coastal cliffs of the Chapadmalal area, in east-central Argentina, are among the best Plio-Pleistocene exposures in South America. These exposures were subject of numerous seminal geologic and paleontologic studies focused to the knowledge of fossil vertebrates and stratigraphy of the Late Cenozoic, and the palaeoclimatic and palaeogeographic context (e.g. Ameghino, 1908; L. Kraglievich, 1934; J. Kraglievich, 1952; Reig, 1952, 1958a,b, 1978; Pascual et al., 1965; Marshall et al., 1983, 1984; Zárate and Fasano, 1989; Orgeira, 1987, 1990, 1991; Alberdi et al., 1995; Cione and Tonni, 1995a, 1996). Their rich

* Corresponding author. Fax: +54 221 4257527.
E-mail addresses: dverzi@museo.fcnym.unlp.edu.ar (D.H. Verzi), quintana@copetel.com.ar (C.A. Quintana).

0031-0182/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2005.01.003

fossil record yielded valuable information to the knowledge of the diversity and evolution of the Late Cenozoic South American mammals, including the dramatic faunistic turnover known as Great American Faunistic Interchange, extensively recorded in these cliffs (e.g. Webb, 1976; Reig, 1981; Tonni et al., 1992; Marshall and Sempere, 1993; Cione and Tonni, 1996).

However, despite the large efforts, single taxa throughout complete faunas of different units require new collections and deep systematic, biostratigraphic and biochronologic review (e.g. Alberdi et al., 1995). Systematics and biostratigraphy of caviomorph rodents from the cliffs of Chapadmalal area have been partially revisited (Vucetich and Verzi, 1999 and references therein). In this context, limited data from the Late Pliocene caviomorphs of the San Andrés Formation show the record of peculiar taxa, members of a significant faunal change probably related to climatic fluctuations (Vucetich and Verzi, 1995, 1999; Verzi, 2001). In this paper, the systematics of caviomorphs from the San Andrés Formation is revisited, and new taxa, only mentioned in previous lists (Quintana, 1994) are described for the first time. The palaeoclimatic and palaeogeographic meaning of this caviomorph fauna, and its probable relationship with global climatic events, is discussed.

2. Material and methods

The material of extinct and living caviomorphs analyzed belong to the collections of: Museo de Ciencias Naturales de Mar del Plata “L. Scaglia”, Argentina (MMP); Museo de La Plata, Argentina (MLP); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina (MACN); Museo de Biología, Universidad Central de Venzuela, Caracas, Venezuela (MBUCV). In addition, materials of extant species of Abrocomidae (including holotypes) were studied through illustrations (Glanz and Anderson, 1990; Emmons, 1999; unpublished illustrations of materials belonging to the Natural History Museum, London, BMNH). The taxa described are based on materials collected by the authors, as well as on previous collections. The provenance of most taxa could be refined through samplings made especially by one of the authors (CAQ). Previously collected materials assigned to the ‘Formación San Andrés’ (*in schedis*) but found in localities where this unit is not exposed (see Reig and Quintana, 1991; Quintana, 1994; Cione and Tonni, 1995a), were excluded from the analysis. Skulls and mandibles were measured with a dial caliper nearest 0.01 mm. Tooth measurements were taken through the reticule eyepiece of a Wild M5 stereomicroscope. The following cranial, mandibular and dental measurements were taken: BLI, breadth of lower incisor; BUI, breadth of upper incisor; DLI, depth of lower incisor; DM, mandibular height below dp4 or p4; DUI, depth of upper incisor; LLD, length of lower diastema; LM1, anteroposterior length of M1; Lm1, anteroposterior length of m1; LM2, anteroposterior length of M2; Lm2, anteroposterior length of m2; LM3, anteroposterior length of M3; LP4, length of P4 (or DP4); Lp4, length of p4 (or dp4); LP4-M3, length of P4-M3; LUD, length of upper diastema; TM1: maximum transverse diameter of M1; Tm1, maximum transverse diameter of m1; TM2, maximum transverse diameter of M2; Tm2, maximum transverse diameter of m2; TM3, maximum transverse diameter of M3; TP4, maximum transverse diameter of P4 (or DP4); Tp4, maximum transverse diameter of p4 (or Dp4).

3. Geological and stratigraphic setting

Coastal cliffs of the Chapadmalal area, south of Mar del Plata City (Buenos Aires Province, east-central Argentina) enclose near 30 km of almost continuous exposures, ranging from 12 to 25 m in thickness (Zárate and Fasano, 1989). Along these cliffs the following litostratigraphic units, from bottom to top, can be recognized: Chapadmalal, Barranca de los Lobos, Vorohué, San Andrés, Miramar, Arroyo Seco, Santa Isabel and Lobería formations (Fig. 1). For a description of the geology and stratigraphy of these units see Kraglievich (1952), Teruggi et al. (1974) and Zárate and Fasano (1989).

The San Andrés Formation is composed of massive clayey siltstones, and some sandy lenses. These sediments would have been deposited mainly in shallow water ponds (Kraglievich, 1952; Zárate and Fasano, 1989). Pedogenetic processes and calcareous accumulations partially modified the primary depositional features (Zárate and Fasano, 1989). Teruggi et

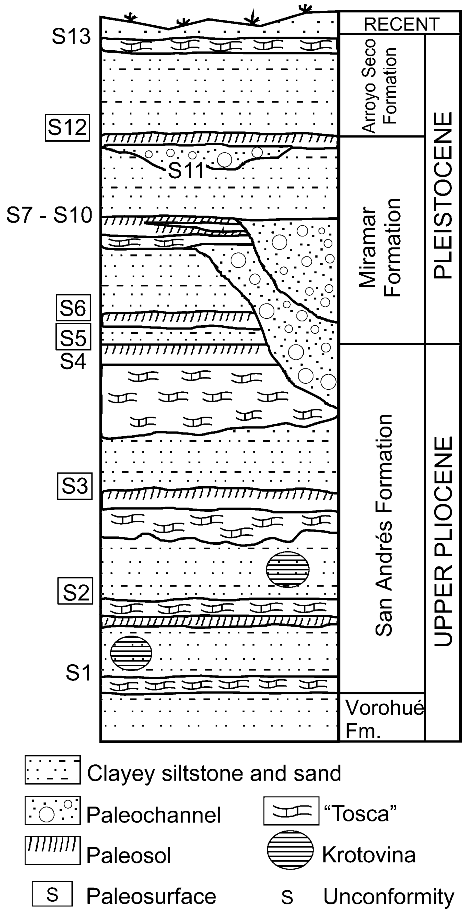

Fig. 1. Schematic stratigraphic profile of the Santa Isabel locality (mofidied from Teruggi et al., 1974).

al. (1974) recognized two paleosols, two middle levels of calcretes ('toscas'), and a multiple calcrete crust at the top (Fig. 1).

Magnetostratigraphic analyses of the San Andrés Formation, and underlying and overlying units were performed by Orgeira (1987, 1990, 1991). This author suggested as the most reliable interpretation the one in which reversed polarity within the lower levels of San Andrés Formation correlates with the Kaena Event (younger than 3.110 Ma, Berggren et al., 1995), and the normal polarity in the top with the upper Gauss Chron (older than 2.581 Ma, Berggren et al., 1995). There are no radiometric dates for San Andrés Formation. An ^{40}Ar–^{39}Ar date of glassy materials ('escorias') in the top of the underlying Chapadmalal Formation (Fig. 2) yielded as most precise ages 3.27±0.08 and 3.33±0.10 Ma (Schultz et al., 1998). The 'escoria'-bearing level occurs just before the onset of the Mammoth subchron, which is consistent with the radiometric ages (Schultz et al., 1998). Later revisions of the magnetostratigraphy supported by these results (Cione and Tonni, 2001) and correlation with other units of northwestern Argentina and Bolivia (Cione and Tonni, 1995a, 1996), assigned the reversed polarity within the San Andrés Formation to the lower Matuyama Chron (younger than 2.581 Ma, Berggren et al., 1995). The normal polarity SRM stretch in the uppermost San Andrés may correspond to the Reunión event (2.150–2.140 Ma, Berggren et al., 1995; Cione and Tonni, 1995a) or to the lower part of the Olduvai event (younger than 1.950 Ma, Berggren et al., 1995; Cione and Tonni, 1996). If it is accepted that the boundary between the San Andrés Formation and the overlying Miramar Formation is older than 2 Ma (Cione and Tonni, 2001), the first alternative is more feasible (Fig. 2).

Fossils from the San Andrés Formation were found between Arroyo Lobería and Punta Vorohué (General Pueyrredón County, Buenos Aires Province), especially in Santa Isabel and Punta San Andrés localities (Fig. 3). The studied unit is between the first and fourth unconformities (S1 and S4) of Teruggi et al. (1974), that represent the bottom and top of the San Andrés Formation, respectively (Fig. 1). The fauna was partially assigned to the 'Horizonte Chapadmalalense' by Ameghino (1908). Reig (in Marshall et al., 1984), recognizing the identity of this fauna, proposed the Sanandresian as a Subage of the Uquian Age. Cione and Tonni (1995a) followed this proposal and included the Sanandresian as the Upper Substage of the local Marplatan Stage (Late Pliocene; Fig. 2). The biostratigraphic base of this Substage is the Zone of *Paractenomys* (=*Ctenomys*) *chapalmalensis* (Cione and Tonni, 1995b, 2001). Other presumably Sanandresian localities have proved to be younger than the localities here studied, according to their faunal content (see Cione and Tonni, 1995a).

4. Systematics

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tullberg, 1899

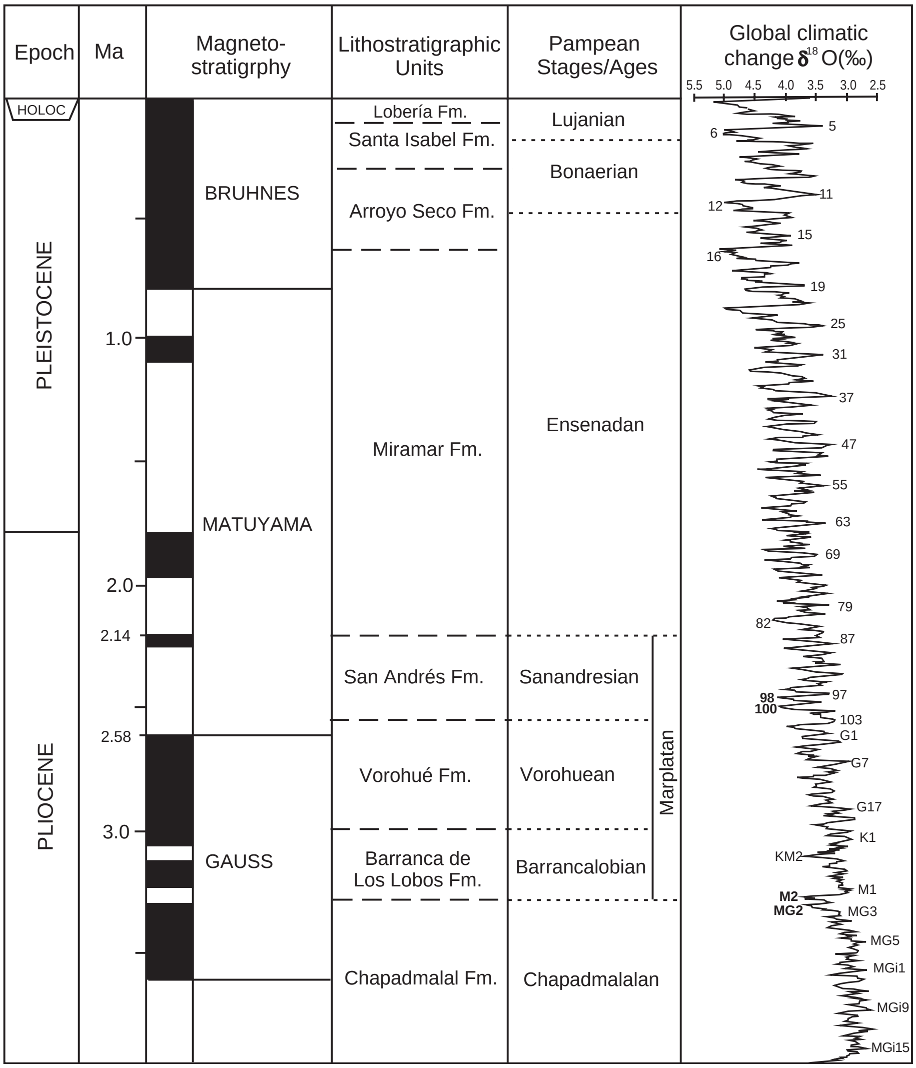

Fig. 2. Stratigraphic chart with a correlation to global climatic change. Stratigraphy modified from Cione and Tonni (1999); isotopic curve after Shackleton (1995); the Plio–Pleistocene boundary follows Berggren et al. (1995).

Infraorder CAVIOMORPHA Wood and Patterson in Wood, 1955

Family CAVIIDAE Fischer de Waldheim, 1817

Subfamily CAVIINAE Fischer de Waldheim, 1817

Genus *Cavia* Pallas, 1766

Cavia galileoi sp. nov. (Fig. 4)

Holotype: MACN 19721

Hypodigm: The type and MACN 19720 (Appendix A).

Geographic and stratigraphic provenance: Santa Isabel (General Pueyrredón County, Buenos Aires Province, Argentina); San Andrés Formation, between the second and third paleosurfaces (S2 and S3) of Teruggi et al. (1974) (Figs. 1 and 3).

Derivation of name: galileoi, in memory of Galileo Scaglia, for his perseverance and pioneering search for fossils, that led to countless studies on Plio-Pleistocene mammals of the Chapadmalal area.

Diagnosis: Species of *Cavia* of smaller size than *Cavia aperea* and *Cavia magna*. Second crest of p4-m1 narrow, without the anterolingual widening present in the extant species. Deep lingual flexid.

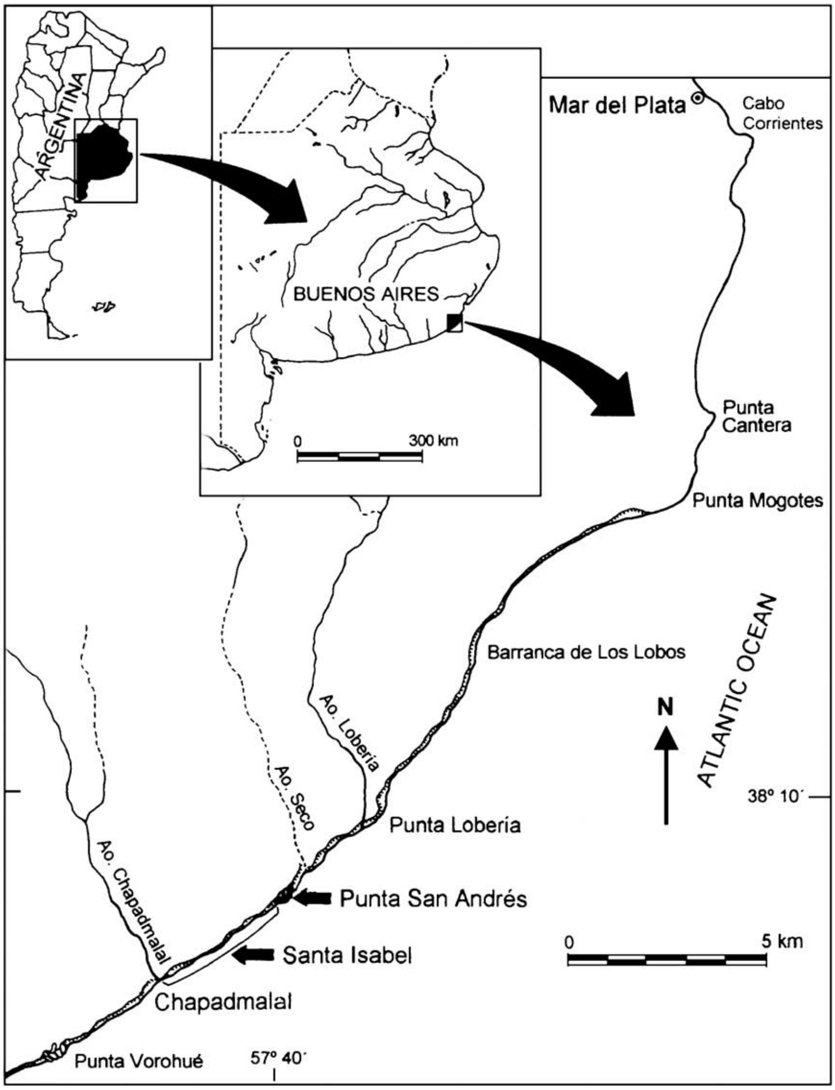

Fig. 3. Geographic localization of the fossil bearing beds of the San Andrés Formation.

Cement filling only in the hypoflexid. m1 proportionally narrower than that of the living species.

Description: The new species is smaller than adult specimens of the living *C. aperea* and *C. magna*. The second crest of p4-m1, posterior to the hypoflexid, slightly narrows medially, in contrast to the living species of *Cavia* in which this crest has a marked anterolingual widening. As in the other species of the genus, the crest of the new species is wider than in *Palaeocavia*, *Microcavia* and *Dolicavia*. The first lobe of p4-m1 of *C. galileoi* joins the second crest through a narrow enamel layer. Cement is only present in the hypoflexid as in *Palaeocavia*, and unlike the extant species of *Cavia* in which cement also fills the inner flexid (Fig. 4). The hypoflexid is deeper than the lingual flexid and it has more cement than in *Palaeocavia*. As in the other species of *Cavia*, the lingual flexid is markedly more developed than in *Palaeocavia*, *Microcavia* and *Dolicavia*. The m1 is proportionally narrower than that of the living species. The incisor and mandibular remains (Fig. 4) show no signifi-

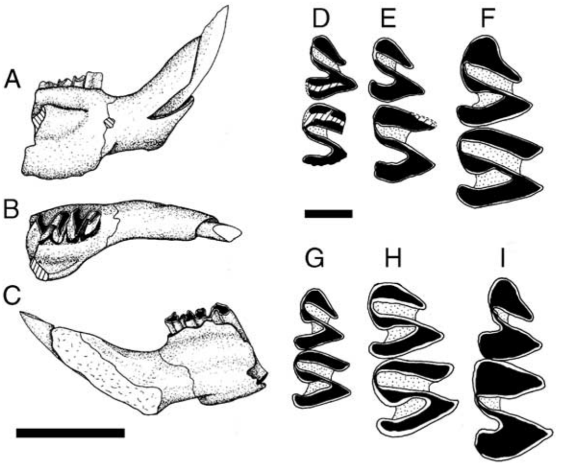

Fig. 4. External (A), occlusal (B) and internal (C) views of the right mandible of *Cavia galileoi* sp. nov. MACN 19721 (holotype), Santa Isabel, San Andrés Formation, Late Pliocene; scale=10 mm. Occlusal view of the right p4-m1 of *Cavia* (D–H) and *Palaeocavia* (I); (D) *C. galileoi* sp. nov. MACN 19720, Santa Isabel, San Andrés Formation, Late Pliocene; (E) *C. galileoi* sp. nov. MACN 19721 (holotype), Santa Isabel, San Andrés Formation, Late Pliocene; (F) *Cavia aperea* MMP 2824, Recent, Chapadmalal, Buenos Aires Province, Argentina; (G) *C. aperea* MMP 314 (juvenile), Recent, Arroyo Las Brusquitas, Buenos Aires Province, Argentina; (H) *Cavia guianae* MBUCV I-5826, Recent, Caripe Department, Venezuela; (I) *Palaeocavia impar* MACN 7658, Chapadmalal Formation, Early–Late Pliocene; scale=2 mm.

cant morphological differences with respect to the extant species.

Among the traits described for p4-m1, the following derived character-states support the inclusion of *C. galileoi* in the genus: a) second crest proportionally wide, b) tendency toward lamination of lobes, c) lingual flexid deep, and d) abundant cement in the hypoflexid. The absence of anterolingual widening on the second crest and the lack of cement in the lingual flexid suggest that the new species is more primitive than the living members of the genus (Fig. 4).

Measurements (mm): MACN 19721 (holotype), Lp4=3.38; Tp4=3.05; Lm1=4.16; Tm1=3.27; DLI=1.53; BLI=1.49. MACN 19720, Lp4=2.88; Tp4=2.22; DLI=1.97; BLI=1.52.

Remarks: The species *C. galileoi* is exclusive of the San Andrés Formation, and represents the oldest record of the genus.

Genus *Microcavia* Gervais and Ameghino, 1880

Microcavia reigi Quintana, 1996

Referred material: Appendix A.

Geographic and stratigraphic provenance: Between Arroyo Lobería and Punta Vorohué (General Pueyrredón County, Buenos Aires Province, Argentina); San Andrés Formation, between S1 and S3 of Teruggi et al. (1974) (Figs. 1 and 3).

Remarks: The taxon *Caviops chapalmalensis* Rovereto, 1914 is a senior synonym of *M. reigi*, but the combination *Microcavia chapalmalensis* is not available because it is occupied by another Pliocene species of *Microcavia* (Ameghino, 1908; see Quintana, 1996). The taxa *C. chapalmalensis* Ameghino, 1908 and *Caviops duplicatus* Ameghino, 1908, previously included in the synonymy of *M. reigi* (Quintana, 1996), are here regarded as nomina nuda and excluded from the formal synonymy because of the lack of materials or illustrations that may be related to such names (Rovereto, 1914: 205; Mones, 1986).

Microcavia is recorded since the Montehermosan Stage (Lower Pliocene) and has the longest biochron among the living caviines. *M. reigi* is exclusive from the Vorohué and San Andrés formations.

Subfamily DOLICHOTINAE Pocock, 1922

Genus *Dolichotis* Desmarest, 1820

Dolichotis salinicola Burmeister, 1876 (Fig. 5)

Referred material: MMP 885-M (Appendix A).

Geographic and stratigraphic provenance: Punta San Andrés (General Pueyrredón County, Buenos

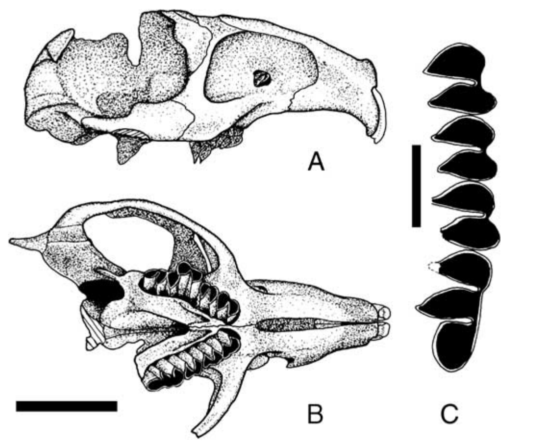

Fig. 5. Lateral (A) and ventral (B) views of the skull (scale=20 mm), and occlusal (C) view of left DP4-M3 (scale=2.5 mm) of *Dolichotis salinicola* MMP 885-M, Punta San Andrés, San Andrés Formation, Late Pliocene.

Aires Province, Argentina); San Andrés Formation (Fig. 3).

Description: The preserved remain is indistinguishable from the skulls of the living specimens. The diastema is straight, somewhat longer than the dental series and the cranial height, and proportionally shorter than that of *Dolichotis patagonum*. The incisive foramina are very narrow, as in the extant species of *Dolichotis*, and occupy almost the whole diastema. There is a very small interpremaxilar foramen. The mesopterygoid fossa is V shaped and reaches the anterior lobe of the M2. The alveolar foramen is very small, and is behind the alveolar sheath of the P4. The top of the alveolar sheath of the M1 is not observed in the rostrum, unlike in *D. patagonum*. The lachrymal bone is very wide and its anterior portion does not split the upper zygomatic portion of the maxillary. The lachrymal foramen is on the end of an elongate depression externally oriented. The zygomatic arch has no deep muscle insertions. The incisors are orthodont, deeper than wide and with the enamel surface slightly convex. Molariforms are like those of the living species of *Dolichotis*. The M3 have a third lobe well defined by a narrow and deep lingual flexus, unlike those of *Orthomyctera* and *Dolicavia*.

Measurements (mm): LP4=4.25; TP4=3.8; LM1=3.80; TM1=3.49; LM2=3.93; TM2=3.93; LM3=6.77; TM3=3.8; LP4-M3=22.21; DUI=2.97; BUI=2.40.

Remarks: Fossil remains assigned to *D. salinicola* (as *Pediolagus*) were known only for the Late Pleistocene of the Buenos Aires province and the Holocene of Salta province, Argentina (Tonni, 1981). The material here described represents the oldest record of this species.

Family ABROCOMIDAE Miller and Gidley, 1918

Genus *Abrocoma* Waterhouse, 1837 (Fig. 6)

Referred material: MMP 1059-M and MACN 19722 (Appendix A).

Geographic and stratigraphic provenance: MACN 19722, Santa Isabel; San Andrés Formation, between S2 and S3 of Teruggi et al. (1974) (Figs. 1 and 3). MMP 1059-M, Punta San Andrés; San Andrés Formation (Fig. 3).

Description: Species similar in size to the living ones of the *Abrocoma cinerea* species complex (Braun and Mares, 2002), *A. bennetti* and *A. boliviensis*. More gracile than the extinct *Protabrocoma antiqua* from the Late Miocene of western Argentina (Rovereto, 1914). The notch for the tendon of the M. masseter medialis in the mandible, is wide and deep. It is placed half the height of the mandibular body, level with the dp4-m1. The preserved portion of the coronoid process is high, as in *A. cinerea* complex and *A. bennetti*, but in contrast to *A. boliviensis* and *Cuscomys* where this process is low (Fig. 6; Emmons, 1999, Fig. 6). Lower and upper molariforms are very similar to those of the *A. cinerea* complex and *A. bennetti*, with lobes narrower anteroposteriorly than in the living *A. boliviensis*, *Cuscomys*, and the extinct *Protabrocoma* (Fig. 6; Glanz and Anderson, 1990, Fig. 9; Emmons, 1999, Figs. 4 and 7). The DP4-M1 cannot be separated from those of *A. cinerea* complex or *A. bennetti*. As in these species, lobes are narrow anteroposteriorly; the anterior lobe is subrectangular and with the anterior face slightly concave. In *P. antiqua*, *A. boliviensis* and *Cuscomys*, especially the anterior lobe is wider anteroposteriorly, subtriangular and with its anterior face more plane or slightly convex (Fig. 6; Emmons, 1999, Fig. 7). As in *A. cinerea* and *A. bennetti* the anterior margin of the metaflexus is more transverse than in *P. antiqua*, *A. boliviensis* and *Cuscomys*. In these latter, the margin is more oblique posterolingually.

Measurements (mm): MACN 19722: Lp4=2.64; Tp4=1.98; Lm1=2.52; Tm1=2.2; Lm2=2.73; Tm2=2.14; DLI=1.34; BLI=0.96; DM=5.86; LLD=7.32. MMP 1059-M, LP4=2.54; TP4=2.03; LM1=2.16; DM1=2.35.

Remarks: The family Abrocomidae includes the extinct genus *Protabrocoma* from the Late Miocene of Argentina and Bolivia (Rovereto, 1914; Kraglievich, 1927; Marshall and Patterson, 1981; Villarroel and Marshall, 1989; Cione et al., 2000) and two living genera, *Abrocoma* and *Cuscomys*, distributed in west-central South America from southern Peru and Bolivia southward to central Chile and west-central Argentina (Fig. 7; Glanz and Anderson, 1990; Emmons, 1999; Braun and Mares, 2002). Currently, *Abrocoma* includes the living *A. cinerea* species complex, *A. bennetti* and *A. boliviensis* (Braun and Mares, 2002). We suggest that according to the morphology of its low coronoid process and the occlusal figure of the molariforms (cf. Glanz and Anderson, 1990, Figs. 9

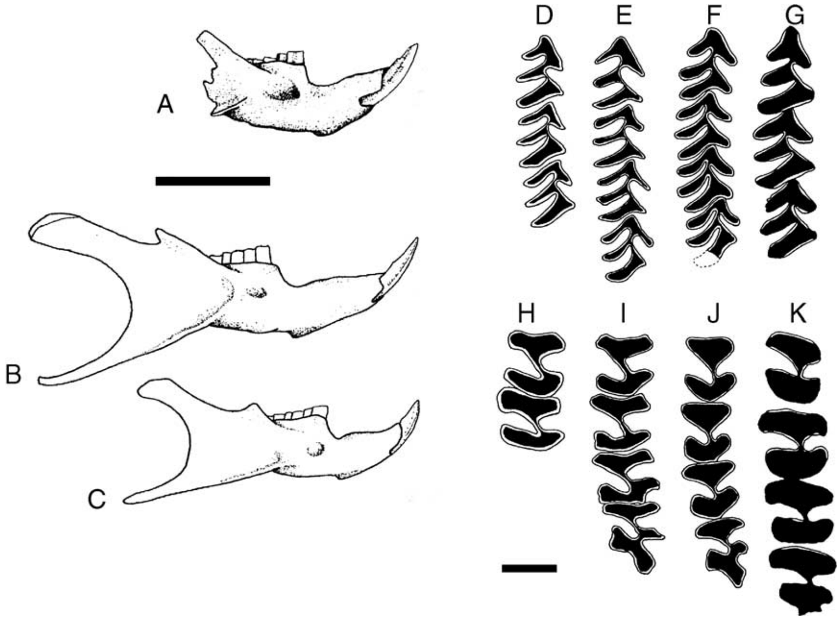

Fig. 6. Lateral view of right mandibles (A–C) and occlusal view of lower right (D–G) and upper left (H–K) molariforms of Abrocomidae. (A) *Abrocoma* MACN 19722, Santa Isabel, San Andrés Formation, Late Pliocene; (B) *Abrocoma cinerea* MACN 18828, Recent, "Los Andes", Argentina (reversed for comparison); (C) *Abrocoma* (=*Cuscomys*) *boliviensis* BMNH 34.9.2.171 (holotype), Recent, Caramapa, Santa Cruz, Bolivia (modified from Glanz and Anderson, 1990, Fig. 10); scale=10 mm. (D) *Abrocoma* MACN 19722, right dp4-m2, Santa Isabel, San Andrés Formation, Late Pliocene; (E) *Abrocoma cinerea* MACN 26117, right dp4-m3, Recent, "Los Andes", Argentina; (F) *Abrocoma* (=*Cuscomys*) *boliviensis* MVZ120238, left dp4-m3 (reversed for comparison), Recent, Caramapa, Santa Cruz, Bolivia (modified from Glanz and Anderson, 1990, Fig. 9); (G) *Protabrocoma antiqua* MACN 8563, right dp4-m2, Huayquerías de San Carlos, Mendoza Province, Argentina, Late Miocene; (H) *Abrocoma* MMP 1059-M, left DP4-M1, Punta San Andrés, San Andrés Formation; (I) *Abrocoma cinerea* BMNH 19.8.2.29 (holotype), left DP4-M3, Recent, Casabindo, Jujuy Province, Argentina; (J) *Abrocoma* (=*Cuscomys*) *boliviensis* MVZ120238, left DP4-M3, Recent, Caramapa, Santa Cruz, Bolivia (modified from Glanz and Anderson, 1990, Fig. 9); (K) *Protabrocoma antiqua* MACN 8357, left DP4-M3, Andalhualá, Catamarca, Late Miocene.

and 10, and Emmons, 1999, Figs. 6 and 7), the living species *A. boliviensis* should be transferred to the genus *Cuscomys.*

The maxilla from the San Andrés Formation was first mentioned by Reig (1987), who underlined the significance of the record. This material and the mandible found afterwards represent the single undoubted records of the extant genus *Abrocoma*. According to the morphology of the coronoid process and molariforms, the abrocomid from San Andrés is clearly related to the living *A. cinerea* species complex and *A. bennetti*. It differs from them in its wider notch for the tendon of the M. masseter medialis in the mandible. But the diagnostic value of this character is not clear, and may only represent individual variation. Given the scarcity of materials from San Andrés and the complexity of the systematics of *Abrocoma* (Braun and Mares, 2002), the remains described are assigned only up to the genus level.

Family ECHIMYIDAE Gray, 1825

Subfamily EUMYSOPINAE Rusconi, 1935

Genus *Eumysops* Ameghino, 1888

Referred material: Appendix A.

Geographic and stratigraphic provenance: Punta San Andrés and Santa Isabel; San Andrés Formation, between S1 and S3 of Teruggi et al. (1974) (Figs. 1 and 3).

Remarks: The systematics of this genus is complex, and in need of deep revision. Kraglievich (1965) mentioned the record of *Eumysops paracavioides* as a new species for the San Andrés Formation. But this name is not valid since the species was never formally published. Vucetich and Verzi (1995: 215) recognized two morphotypes for the San Andrés Formation: 'morphotype 2' (=*Eumy-*

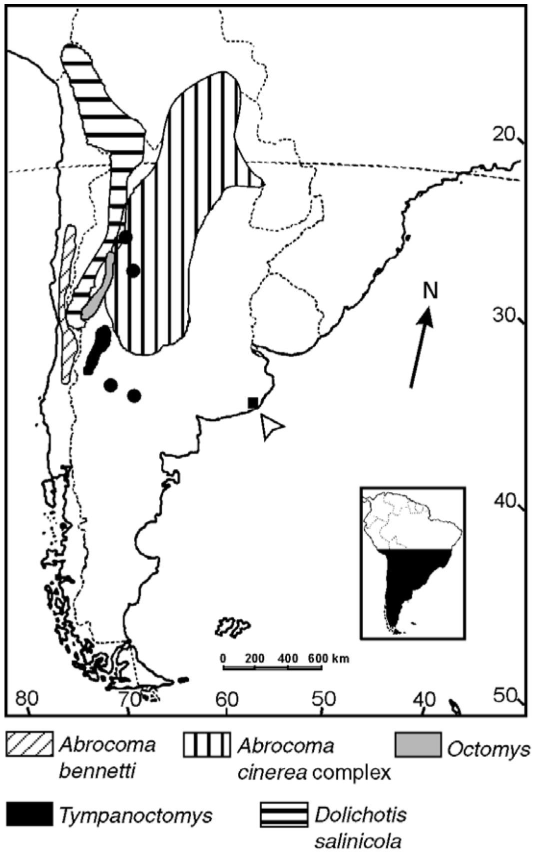

Fig. 7. Geographic distribution of the extant species related to the Sanandresian caviomorphs (after Glanz and Anderson, 1990; Redford and Eisenberg, 1992; Ojeda et al., 1996; Braun and Mares, 2002).

sops laeviplicatus=*Eumysops chapalmalensis*?) and 'morphotype 3' (=*Eumysops cavioides*?).

The record of *Eumysops* in the San Andrés Formation is the last one for the pampean area, but the genus is recorded again in Quaternary sediments of Entre Ríos in eastern Argentina (Vucetich et al., in press).

Family OCTODONTIDAE Waterhouse, 1839

Genus *Abalosia* Reig and Quintana, 1991

Abalosia castellanosi (Rusconi, 1933)

Referred material: Appendix A.

Geographic and stratigraphic provenance: Santa Isabel and Punta San Andrés; San Andrés Formation, between S1 and S3 of Teruggi et al. (1974) (Figs. 1 and 3).

Remarks: Reig and Quintana (1991) interpreted *Abalosia* as ancestral to the living octodontine *Octodon*. In a morphological phylogeny proposed by Verzi (2001), this genus was a member of a clade of desert-specialist octodontines together with the living genera *Tympanoctomys* and *Octomys*.

Abalosia is an exclusive taxon of the San Andrés Formation.

Genus *Pithanotomys* Ameghino, 1887

Referred material: Appendix A.

Geographic and stratigraphic provenance: Punta San Andrés; San Andrés Formation (Fig 3).

Remarks: The systematics of the genus *Pithanotomys* is complex, and in need of deep revision (Verzi et al., 2002). Ameghino (1908: 425) proposed two names for the materials found in the sequence of the Chapadmalal area: *Pithanotomys chapalmalensis* and *Pithanotomys ortorhynchus*. Rovereto (1914: 199–200) reported a brief description of these materials. Although the original materials could not be found in the collections, the review of the available remains suggests that only one species is recorded in the Chapadmalal, Barranca de Los Lobos and Vorohue formations. The name *P. chapalmalensis* corresponds by priority. The specimen recorded in San Andrés (Appendix A) cannot be distinguished from *P. chapalmalensis* at cranial level, but it lacks the molariforms. Since molariforms are diagnostic at species level, the determination of the material from San Andrés is kept at genus level until new materials are found.

The presence of *Pithanotomys* in the San Andrés Formation represents the last record of the genus.

Family CTENOMYIDAE Lesson, 1842

Genus *Ctenomys* de Blainville, 1826

Ctenomys chapalmalensis (Ameghino, 1908)

Referred material: Appendix A.

Geographic and stratigraphic provenance: Punta San Andrés and Santa Isabel; San Andrés Formation, between S1 and S3 of Teruggi et al. (1974) (Figs. 1 and 3).

Remarks: Ameghino (1908) described *P. chapalmalensis* on the basis of materials found in the 'Piso Chapalmalense' of the sequence of Chapadmalal area. Later prospecting efforts determined that this species is exclusive from the San Andrés Formation (Quintana, 1994; Vucetich and Verzi, 1995). Rovereto (1914) included the species in the genus *Ctenomys*, and Rusconi (1930) gave it the category of subgenus, *Ctenomys* (*Paractenomys*). Verzi and Lezcano (1996) and Verzi (2002) suggested that this species might be a member of the basal group from which the modern species derived, but it lacks apomorphies to assign it a supraspecific category.

C. chapalmalensis is an exclusive taxon from the San Andrés Formation, and it represents the oldest record of *Ctenomys* in the pampean area of central Argentina. Older records, probably related to the differentiation of the genus, are known for southwestern Bolivia and northwestern Argentina (Reig et al., 1990; Walther et al., 1998; Verzi, 2002).

Genus *Eucelophorus* Ameghino, 1908

Eucelophorus chapalmalensis Ameghino, 1908

Referred material: Appendix A.

Geographic and stratigraphic provenance: Punta San Andrés; San Andrés Formation, between S1 and S3 of Teruggi et al. (1974) (Figs. 1 and 3).

Remarks: The variability displayed by the genus *Eucelophorus* (Kraglievich, 1927, 1940; Reig and Quintana, 1992) suggests that it likely represents an undivided lineage with an anagenetic evolutionary pattern (Verzi, 2002). According with this pattern, we include in *E*. *chapalmalensis* all the materials from the Chapadmalal, Vorohué and San Andrés formations (including the hypodigm of the species *E*. *zaratei* Reig and Quintana, 1992).

5. Palaeoclimatic and geographic significance

Because of the doubtful provenance of the materials, the genera *Orthomyctera, Palaeocavia, Neochoerus*, and *Lagostomus*, listed as from the San Andrés Formation in previous works (e.g. Tonni et al., 1992; Vucetich and Verzi, 1995), were not included in the analysis.

The caviomorph fauna from the San Andrés Formation is very peculiar (Quintana, 1994; Vucetich and Verzi, 1995, 1999; Verzi, 2001). The long-lived genera *Eucelophorus, Pithanotomys, Microcavia*, and *Eumysops* are recorded. On the other hand, the living taxa *D. salinicola, Abrocoma* and *Cavia,* and the extinct *Abalosia*, are first recorded in this formation. The presence of *Cavia* is preceded by that of the older related genus *Palaeocavia* in the Chapadmalal Formation (Quintana, 1998). But the sudden appearance of the remaining first records is not preceded by ancestrals or sister taxa presumably related. No taxon related to *D. salinicola, Abalosia*, *Ctenomys* and *Abrocoma* is recorded neither in the underlying Chapadmalal, Barranca de los Lobos and Vorohué formations (Reig in Marshall et al., 1984; Vucetich and Verzi, 1995), nor in any other of the rich Pliocene deposits outcropping between Mar del Plata and Bahía Blanca (east-central Argentina; Vucetich and Verzi, 1995; Deschamps and Borromei, 1992). This suggests that they are immigrant taxa to east-central Argentina (Vucetich and Verzi, 1995, 1999; Verzi, 2001).

From the standpoint of its palaeoclimatic meaning, this assemblage of the San Andrés Formation is the caviomorph extinct fauna most clearly indicative of arid environments so far recorded (Verzi, 2001). This hypothesis is supported by two types of evidence, anatomical and systematic. The best anatomical signal of adaptation to arid environments in the skull of rodents is the hypertrophy of the auditive bullae. Large auditory bullae were acquired independently in several lineages of desert rodents, probably as a strategy to detect predators in open environments (Mares, 1980; Randall, 1994; Ojeda et al., 1996, 1999). Large bullae increase sensitivity for low frequency sounds by diminishing the stiffness of the middle ear (Lombard and Hetherington, 1993). The subterranean ‘tuco-tuco’ *C. chapalmalensis* shows auditive bullae hypertrophied in their tympanic and mastoid regions, as in the extant species *C. azarae* and *C. mendocinus* of the ‘mendocinus’ group (Massarini et al., 1991) which inhabit the Monte desert biome (see Mares et al., 1985) from western Argentina (Fig. 8). Although the known skulls of the octodontine *Abalosia* do not preserve the auditory region, this genus also shows evidences in its occiput and basicranium of the presence of hypertrophied auditive bullae, as in the related living species *Octomys mimax* and especially *Tympanoctomys barrerae* (Verzi, 2001).

The systematic evidence is based on the environmental requirements of the living representatives most closely related (Vucetich and Verzi, 1995; Vrba, 1992: 3). According to this criterion, *D. salinicola, Abrocoma* and *Abalosia* are also clear indicators of arid environments (Figs. 7 and 8). The living maras of the genus *Dolichotis* are cavies specialized for a cursorial life in arid environments. The chacoan mara *D. salinicola* currently occupies salt pit areas in the arid chaco of Bolivia and Paraguay, and the arid chaco and

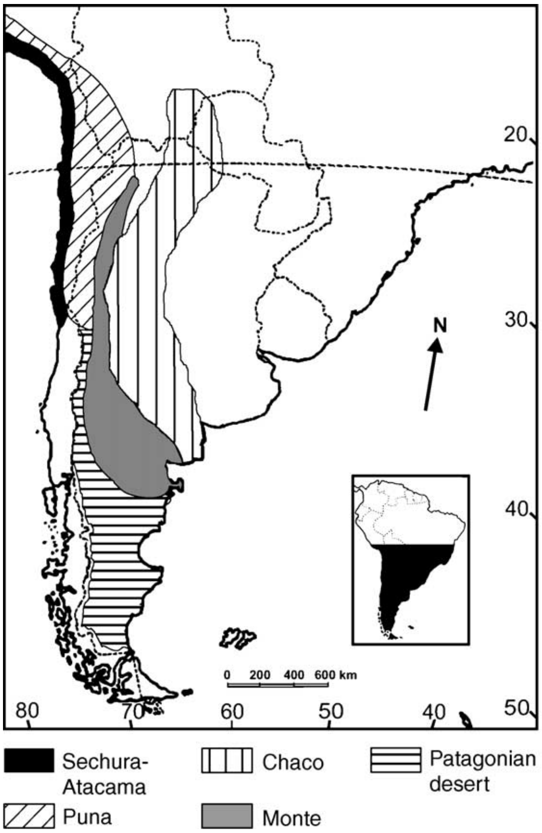

Fig. 8. Arid and semiarid areas of southern South America (modified from Mares, 1993).

the Monte biome in north and central-west of Argentina (Tonni, 1981; Redford and Eisenberg, 1992). The materials of *Abrocoma* from the San Andrés Formation are the single known record closely related to the living chinchilla rats of the complex *A. cinerea* and *A. bennetti*. These species are the abrocomids most strongly adapted to arid rocky habitats in Andean and pre-Andean regions of southern South America (Glanz and Anderson, 1990; Emmons, 1999). The octodontine *Abalosia* is a member of a desert specialists clade together with *Octomys* and *Tympanoctomys* today distributed in the Monte desert of western Argentina (Verzi, 2001). Its sister genus, the viscacha rat *Tympanoctomys*, is the South American living rodent more strongly adapted to desert conditions (Mares, 1993; Bozinovic and Contreras, 1990; Ojeda et al., 1999).

Finally, according to the present distribution of related taxa (Figs. 7 and 8), we propose that the Sanandresian immigrant caviomorphs *Abalosia, D. salinicola*, *Abrocoma* and *C. chapalmalensis* would have inhabited the emergent semi-deserts of western Argentina, as it was suggested by Verzi (2001) for *Abalosia*. These deserts probably began their development during the Late Miocene, 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 (Pascual et al., 1985; Pascual and Ortiz Jaureguizar, 1990; Mares et al., 1985). The immigrant caviomorphs may have reached the more eastern Chapadmalal area during an expansion of such arid environments triggered by the Late Pliocene cooling and drying pulse (Verzi, 2001).

6. Sanandresian caviomorphs and Late Pliocene global climatic change

There is overwhelming evidence of an important Late Pliocene global cooling and drying event in the 2.8–2.4 Ma interval (Fig. 2; isotopic stages 104, 100 and 98 after Shackleton, 1995), which is generally dated as 'around 2.5 Ma' (e.g. Vrba et al., 1995). This evidence includes vegetation changes, faunal turnovers (first appearances of cooler- and more open-adapted taxa and disappearance of subtropical taxa) and onset of glaciation in both hemispheres (e.g. Bonadonna and Alberdi, 1987; Janis, 1993; Marshall and Sempere, 1993; Vrba, 1985, 1989, 1992; Vrba et al., 1995; Alberdi et al., 1995; de Menocal, 1995, 2004; Kennett, 1995; Opdyke, 1995; Shackleton, 1995; Webb and Opdyke, 1995; Willis et al., 1999). This cooling began ca 3.2 Ma as a trend changing the warmer and more stable climate prevalent before this age by increasingly colder and more variable climatic conditions (Kennett, 1995: 57; Schultz et al., 1998).

In the Chapadmalal cliffs, a major mammalian extinction (including caviomorphs) was detected in the top of the Chapadmalal Formation, ca 3.3 Ma (Tonni et al., 1992; Vucetich and Verzi, 1995, 1999; Cione and Tonni, 2001). This faunistic turnover is coeval with a maximum in the benthic $\delta^{18}O$ values interpreted as a cooling of the Atlantic bottom (Schultz et al., 1998: 2062), and is near concurrent with the beginning of the Late Pliocene global cooling trend. A second important faunistic turnover in this sequence was recognized for the San Andrés Formation by Tonni and Cione (1994, 1995), Vucetich and Verzi (1995, 1999) Cione and Tonni (2001), and Verzi (2001). Tonni and Cione (1994, 1995), and Verzi (2001) related this faunistic turnover to the Late Pliocene global cooling near 2.5 Ma. Such proposal was partially based on the extinction recorded between the Sanandresian and Ensenadan stages. A similarity analysis performed by Vucetich and Verzi (1995, Fig. 1) using caviomorph genera of the Chapadmalalan to Lujanian stages (Early Pliocene–Late Pleistocene), showed that the most important change would have occurred by extinction between the Sanandresian and Ensenadan. However, this change may be actually representing a bias of the record, rather than a real extinction, since there is a hiatus between both units. The caviomorph faunas listed as 'Ensenadenses' by Cione and Tonni (1995b, 1996), Cione et al. (1999), and Vucetich and Verzi (1995, 1999) correspond to the uppermost Ensenadan–Bonaerian (Middle Pleistocene, Table 1; Verzi et al., 2002; Verzi et al., 2004), and actually there are no records of the underlying 'Preensenadense' and 'Ensenadense basal' (Early Pleistocene; see Rusconi,

Table 1
Record of the caviomorph rodents in the pampean area during the Late Pliocene–Middle Pleistocene

Epoch	Late pliocene		Middle pleistocene	
Taxa / Stage/Age	Vorohuean	Sanandresian	Late Ensenadan	Bonaerian
Echimyidae				
Eumysops morphotype 2	◄—	—		
Eumysops morphotype 3	◄—	—		
Dicolpomys				—►
aff. Clyomys				—►
Myocastoridae				
Myocastor			—	—►
Abrocomidae				
Abrocoma		—►		
Octodontidae				
Pithanotomys	◄—	—		
Abalosia castellanosi		—		
Tympanoctomys cordubensis			—	
Eucelophorus chapalmalensis	◄—	—	—►	
Ctenomys		◄—	—	—►
Ctenomys chapalmalensis		—		
Caviidae				
Microcavia	◄—	—	—►	
Microcavia reigi	—	—		
Cavia galileoi		—		
Galea				—►
Dolichotis salinicola		—►		
Hydrochoeridae				
Hydrochoeridae indet.	—			
Neochoerus				—►
Dasyproctidae				
Plesiaguti totoi				—►
Chinchillidae				
Lagostomus	◄—		—	—►

Early Pleistocene is not included because it represents a hiatus for the caviomorph record.

1937-1938; Marshall et al., 1984; Cione and Tonni, 1999). Thus, the change detected between the Sanandresian and the 'Ensenadan' cannot be examined as a single event.

On the contrary, given the richness and relative continuity of the Pliocene record in the Chapadmalal area, the significant faunal changes detected between the San Andrés Formation and underlying units can be assumed as a real turnover. Except for *Lagostomus* and an isolated record of a Hydrochoeridae indet, no other taxon of the underlying Vorohué Formation is absent in San Andrés. Moreover, the absence of *Lagostomus* represents clearly a bias in the record, or a local extinction event. In contrast, the first records cause a dramatic shift in the San Andrés caviomorph fauna respect to those of previous units, leading to its peculiar composition characterized by dryer-adapted immigrant taxa (Table 1).

These results reinforce the hypothesis that the fauna of the San Andrés Formation is probably coeval with a profound Late Pliocene climatic change. The caviomorph fauna that has been collected in the lower and middle levels of the unit may represent locally the cooling and drying pulse detected worldwide near 2.5 Ma. As said above, the arrival of immigrant taxa characterizes the faunistic turnover represented by this fauna. The lack of extinctions may be explained because the cooling and drying pulse represented in San Andrés belongs to a long-term climatic trend that began around 3.2 Ma (top of the Chapdamalal Formation), which has the same sense of change.

The climatic-sensitive caviomorphs recorded in the San Andrés Formation are clearly indicative of arid conditions, although not extremely cold. However, this may reflect an interpretive bias arisen in the evidence of the recent fauna: surprisingly, the arid and cold Patagonian steppe of southern Argentina (Fig. 8) has no endemic caviomorph genera, despite the long history of caviomorphs in this area (Vucetich et al., 1999) and the early differentiation of Patagonia as a bioma (Pascual et al., 1996). In spite of this, we assume that the global Late Pliocene cooling pulse, related to glacial conditions in both the southernmost portion of South America and Andean regions (Mörner and Sylwan, 1989; Cione and Tonni, 2001), would have triggered essentially arid conditions in the Pampean area where Sanandresian caviomorph are recorded (see Nabel et al., 2000).

Aknowledgements

We thank J. Bonaparte, A. Dondas, A. Kramarz, M. Reguero and R. Pascual for permission to study the materials under their care. We are especially grateful to A. Olivares for assistance with table and figures, and C. Deschamps for translation. The suggestions of two anonymous reviewers improved the manuscript. This paper was partially supported by CONICET and UNLP grants.

Appendix A. Material of caviomorphs from the San Andrés Formation analyzed

A.1. Abrocoma

MACN 19722, right mandible with incisor and dp4-m2; MMP 1059-M, fragment of left maxillary with DP4-M1.

A.2. Cavia galileoi

MACN 19721(holotype), incomplete right mandible with incisor and p4-m1, and incomplete left mandible with incisor and p4; MACN 19720, incomplete right mandible with incisor and p4-m1 (m1 broken).

A.3. Microcavia reigi

MACN 5186, 10005, 10936, 10972, 17154 and 19652–19657; MLP 52-X-1-31; MMP 614-S, 1056-M, 1162-M, 1478-M and 1621-M (see description in Quintana, 1996).

A.4. Dolichotis salinicola

MMP 885-M, anterior portion of skull with the incisors and molarifoms, and right zygomatic arch.

A.5. Ctenomys chapalmalensis

MACN 13839, left mandible with the incisor and molariforms; MACN 19242, incomplete mandible with dp4-m2; MACN 19243, right mandible with incisor and dp4-m1; MACN 19245, anterior portion of the left mandible with incisor and dp4; MACN

19246, incomplete mandible with dp4-m1; MACN 19247, posterior portion of the left mandible with m1-3; MACN 19248, incomplete rostrum with incisors; MACN 19249, anterior portion of skull with incisors, left DP4-M2, right DP4-M1, right humerus, ulna, radius and basipodial bones, incomplete right femur and tibia, scapula, posterior portion of pelvic bones and left calcaneus; MACN 19250, anterior portion of skull with the incisors; MACN 19251, palate with the molariforms and right incisor; MACN 19252, incomplete mandible with dp4; MACN 19253, incomplete mandible with dp4-m2; MACN 19254, anterior portion of right mandible with incisor and dp4-m1; MACN 19255, anterior portion of left mandible with incisor and dp4-m1; MACN 19256, left mandible with the incisor and molariforms; MLP 52-IX-27-53, anterior portion of right mandible with incisor and dp4-m1; MLP 90-IV-4-1, anterior portion of skull with the incisors and molariforms; MLP 90-IV-4-2, incomplete right mandible; MLP 90-IV-4-3, incomplete right mandible with the incisor and molariforms; MMP 298-S, anterior portion of skull with the incisors and molariforms, and both mandibles with incisors and dp4-m2; MMP 356-S, left mandible with incisor and dp4-m2, and maxillary with left DP4-M2 and right M1; MMP 358-S, both mandibles the with incisors and molariforms, and left humerus, ulna and radius; MMP 377-M, left mandible with incisor and dp4; MMP 444-S, anterior portion of the skull with the incisors and molariforms, and both mandibles with incisors and dp4-m2; MMP 481-S, skull with the incisors and molariforms; MMP 483-M, left portion of skull with the incisor and molariforms; MMP 575-S, anterior portion of skull with incisors, left DP4-M3 and right DP4-M1; MMP 601-M, left mandible with incisor and dp4-m2; MMP 606-S, anterior portion of skull with incisors and DP4-M2, and incomplete left mandible with incisor and dp4-m2; MMP 613-S, right mandible with incisor and dp4-m2; MMP 642-S, left mandible with incisor and dp4-m2; MMP 646-M, anterior portion of skull with the incisors and molariforms, and right mandible with incisor and dp4-m2; MMP 845-M, anterior portion of skull with the incisors and molariforms; MMP 889-M, right mandible with incisor and dp4-m3; MMP 890-M, right mandible with incisor and dp4-m3; MMP 891-M, anterior portion of skull with incisors and left DP4-M2; MMP 1061-M, right maxillary with incisor and DP4-M2 and both mandibles with incisors and dp4-m2; MMP 1214-M, anterior portion of skull with incisors, left DP4 and right DP4-M1; MMP 1223-M, ventral portion of skull with the incisors and molariforms; MMP 1225-M, anterior portion of skull without left M3; MMP 1227-M, fragment of skull with occipital portion, and the incisors and molariforms; MMP 1229-M, left mandible with dp4-m2; MMP 1319-M, anterior portion of skull with incisors and DP4-M2; MMP 1449-M, anterior portion of skull with incisors and DP4-M2; MMP 1526-M, left mandible with incisor and dp4-m3; MMP 1620-M, right mandible with incisor and dp4-m2; MMP 1622-M, right mandible with incisor and dp4-m1 and left mandible with incisor and dp4-m3; MMP 1730-M, anterior portion of skull with incisors and DP4-M1, and mandible with incisor and dp4-m3.

A.6. *Eucelophorus chapalmalensis*

MMP 448-S, 449-S, 485-S, 600-M, 610-S, 756-S, 613-M, 645-M. 668-M, 840-M, 1070-M, 2013-M, 2014-M and 2015-M (see description in Reig and Quintana, 1992).

A.7. *Pithanotomys sp.*

MMP 644-M, almost complete skull without teeth.

A.8. *Abalosia castellanosi*

MMP 572-M, 1060-M, 1439-M, 1450-M, 1452-M, 1522-M; 1523-M and 1524-M (see description in Reig and Quintana, 1991).

A.9. *Eumysops*

MMP 482-S, both maxillaries with DP4-M3, right mandible with the incisor and molariforms, left femur and fragments of pelvis; 484-S, right maxillary with DP4-M2 and left maxillary with DP4-M3; 557-M, left maxillary with DP4-M3 and right maxillary with DP4 and M2-3; 839-M, almost complete skull; 1052-M, complete skull; 2055-M, right mandible with m2-3. MACN 19698, right maxillary with DP4-M1; 19699, left mandible with ml-3; 19700, middle region of the skull without left M3, right tibia without proximal epiphysis; 19701, portion of right maxillary with

DP4-M2; 19702, left mandible with ml-3; 19703, left mandible with m1-2; 19704, portion of left maxillary with DP4-M1; 19705, right dp4-m2.

References

Alberdi, M.T., Leone, G., Tonni, E.P. (Eds.), 1995. Evolución biológica y climática de la región pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo occidental, Monografías Museo Nacional de Ciencias Naturales Madrid, vol. 12, pp. 423.

Ameghino, F., 1908. Las formaciones sedimentarias de la región litoral de Mar del Plata y Chapalmalán. An. Mus. Nac. B. Aires 3 (10), 343–428.

Berggren, W.A., Kent, D.V., Swisher III, C.C., Aubry, M.-P., 1995. A revised Cenozoic geochronology and chronostratigraphy. In: Bergreen, W.A., Kent, D.V., Aubry, M.-P, Hardenbol, J. (Eds.), Geochronology, time scales and global stratigraphic correlation, Soc. Sediment. Geol. Spec. Publ., vol. 54, pp. 129–212.

Bonadonna, F.P., Alberdi, M.T., 1987. The N/Q boundary at 1.64 Ma? Mediterránea 6, 115–130.

Bozinovic, F., Contreras, L.C., 1990. Basal rate of metabolism and temperature regulation of two desert herbivorous octodontid rodents: *Octomys mimax* and *Tympanoctomys barrerae*. Oecologia 84, 567–570.

Braun, J.K., Mares, M.A., 2002. Systematics of the *Abrocoma cinerea* species complex (Rodentia: Abrocomidae), with a description of a new species of *Abrocoma*. J. Mammal. 83, 1–19.

Cione, A.L., Tonni, E.P., 1995a. Chronostratigraphy and "Land-mammal ages" in the Cenozoic of southern South America: principles, practices and the "Uquian" problem. J. Paleontol. 69, 135–159.

Cione, A.L., Tonni, E.P., 1995b. Bioestratigraía y cronología del Cenozoico Superior de la región pampeana. In: Alberdi, M.T., Leone, G., Tonni, E.P. (Eds.), Evolución Biológica y Climática de la Región Pampeana durante los últimos Cinco Millones de Años. Un Ensayo de Correlación con el Mediterráneo Occidental, Monografías Museo Nacional de Ciencias Naturales Madrid, vol. 12, pp. 49–74.

Cione, A.L., Tonni, E.P., 1996. Reassesment of the Pliocene–Pleistocene continental time scale of Southern South America: Correlation of the type Chapadmalalan with Bolivian sections. J. S. Amer. Earth Sci. 9, 221–236.

Cione, A.L., Tonni, E.P., 1999. Biostratigraphy and chronological scale of upper-most Cenozoic in the Pampean Area, Argentina. In: Tonni, E.P., Cione, A.L. (Eds.), Quaternary vertebrate paleontology in South America, Quaternary of South America and Antarctic Peninsula, vol. 12, pp. 23–51.

Cione, A.L., Tonni, E.P., 2001. Correlation of Pliocene to Holocene southern South American and European vertebrate-bearing units. Bollet. Soc. Paleontol. Ital. 40, 167–173.

Cione, A.L., Tonni, E.P., Bond, M., Carlini, A.A., Pardiñas, U.F.J., Scillato Yané, G.J., Verzi, D.H., Vucetich, M.G., 1999. Occurrence charts of Pleistocene mammals in the Pampean area, eastern Argentina. In: Tonni, E.P., Cione, A.L. (Eds.), Quaternary vertebrate palaeontology in South America, Quaternary of South America and Antarctic Peninsula, vol. 12, pp. 53–59.

Cione, A.L., Azpelicueta, M.M., Bond, M., Carlini, A.A., Casciotta, J.R., Cozzuol, M.A., De La Fuente, M., Gasparini, Z., Goin, F.J., Noriega, J., Scillato-Yane, G.J., Soibelzon, L., Tonni, E.P., Verzi, D.H., Vucetich, M.G., 2000. Miocene vertebrates from Entre Ríos, eastern Argentina. In: Aceñolaza, F.G., Herbst, R. (Eds.), El Neógeno de Argentina, INSUGEO, Serie Correlación Geológica, vol. 14, pp. 191–237.

de Menocal1, P.B., 1995. Plio–Pleistocene African climate. Science 270, 53–59.

de Menocal, P.B., 2004. African climate change and faunal evolution during the Pliocene–Pleistocene. Earth Planet. Sci. Lett. 220, 3–24.

Deschamps, C.M., Borromei, A.M., 1992. La fauna de vertebrados del Bajo San José (provincia de Buenos Aires, Argentina). Aspectos paleoambientales. Ameghiniana 29, 177–183.

Emmons, L.H., 1999. A new genus and species of Abrocomid rodent from Peru (Rodentia: Abrocomidae). Am. Mus. Novit. 3279, 1–14.

Glanz, W.E., Anderson, S., 1990. Notes on Bolivian mammals: 7. A new species of *Abrocoma* (Rodentia) and relationships of the Abrocomidae. Am. Mus. Novit. 2991, 1–32.

Janis, C.M., 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. Ann. Rev. Ecolog. Syst. 24, 467–500.

Kennett, J.P., 1995. A review of polar climatic evolution during the Neogene, based on the marine sediment record. In: Vrba, E.S., Denton, G.H., Partidge, T.C., Burcle, L.H. (Eds.), Paleoclimate and evolution with emphasis on human origins. Yale University Press, pp. 49–64.

Kraglievich, J.L., 1952. El perfil geológico de Chapadmalal y Miramar, Provincia de Buenos Aires. Rev. Mus. Mun. Cienc. Nat. Tradic. Mar del Plata 1, 8–37.

Kraglievich, J.L., 1965. Speciation phylétique dans les rongeurs fossiles du genre *Eumysops* Amegh. (Echimyidae, Heteropsomyinae). Mammalia 29, 258–267.

Kraglievich, L., 1927. Nota preliminar sobre nuevos géneros y especies de roedores de la fauna argentina. Physis 8, 591–598.

Kraglievich, L., 1934. La antigüedad Pliocena de las faunas de Monte Hermoso y Chapadmalal deducidas de su comparación con las que le precedieron y sucedieron. Imprenta El Siglo Ilustrado, 133.

Kraglievich, L., 1940. Descripción detallada de diversos roedores argentinos terciarios clasificados por el autor. In: Torcelli, A.J. (Ed.), Obras completas y trabajos científicos inéditos de Lucas Kraglievich, Obras de geología y paleontología, vol. 2. pp. 297–330.

Lombard, R.E., Hetherington, T.E., 1993. Evolution of the ear. In: Hanken, J., Hall, B.K. (Eds.), The vertebrate skull: 3. Functional and evolutionary mechanisms. University of Chicago Press, Chicago, pp. 241–302.

Mares, M.A., 1980. Convergent evolution among desert rodents: a global perspective. Bull. Carnegie Mus. Nat. Hist. 16, 1–51.

Mares, M.A., 1993. Heteromyids and their ecological counterparts: a pandesertic view of rodent ecology and evolution. In: Genoways, H.H., Brown, J.H. (Eds.), Biology of the Heteromyidae, The Amer. Soc. Mammal, vol. 10, pp. 652–714. Spec. Publ.

Mares, M.A., Morello, J., Goldstein, G., 1985. The Monte Desert and other subtropical semiarid biomes of Argentina with comments on their relation to North America arid areas. In: Evenari, M., Noy-Meir, I., Goodall, D.W. (Eds.), Ecosystems of the World: Hot Deserts and Arid Shrublands. Elsevier, New York, pp. 203–237.

Marshall, L.G., Patterson, B., 1981. Geology and geochronology of the mammal-bearing Tertiary of the Valle de Santa María and Río Corral Quemado, Catamarca Province, Argentina. Fieldiana, Geol. 9, 1–80.

Marshall, L.G., Sempere, T., 1993. Evolution of the Neotropical Cenozoic Land Mammal Fauna in its geochronologic, stratigraphic, and tectonic context. In: Godblatt, P. (Ed.), Biological Relationships Between Africa and South America. Yale University Press, New Haven, pp. 329–392.

Marshall, L.G., Hoffstetter, R., Pascual, R., 1983. Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. Palaeovertebrata, Mém. Extr., 1–93.

Marshall, L.G., Berta, A., Hoffstetter, R., Pascual, R., Reig, O.A., Bombin, M., Mones, A., 1984. Mammals and stratigraphy: geochronology of the continental mammal-bearing Quaternary of South America. Palaeovertebrata, Mém. Extr., 1–76.

Massarini, A.I., Barros, M.A., Ortells, M.O., Reig, O.A., 1991. Chromosomal polymorphism and small karyotypic differentiation in a group of *Ctenomys* species from Central Argentina (Rodentia: Octodontidae). Genetica 83, 131–144.

Mones, A., 1986. Palaeovertebrata Sudamericana. Catálogo sistemático de los vertebrados fósiles de América del Sur: Parte I. Lista preliminar y bibliografía. Courier Forschungsinstitut Senckenberg 82, 1–625.

Mörner, N.A, Sylwan, C., 1989. Magnetostratigraphy of the Patagonian moraine sequence at Lago Buenos Aires. J. S. Amer. Earth Sci. 2, 385–390.

Nabel, P.E., Cione, A.L., Tonni, E.P., 2000. Environmental changes in the Pampean area of Argentina at the Matuyama–Bruhnes (C1r–C1n) Chrons boundary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 162, 403–412.

Ojeda, R.A., Gonnet, J.M., Borghi, C.E., Giannoni, S.M., Campos, C.M., Diaz, G.B., 1996. Ecological observations of the red vizcacha rat, *Tympanoctomys barrerae* in desert habitats of Argentina. Mast Neotrop. 3, 183–191.

Ojeda, R.A., Borghi, C.E., Diaz, G.B., Giannonni, S.M., Mares, M.A., Braun, J.K., 1999. Evolutionary convergence of the highly adapted desert rodent *Tympanoctomys barrerae* (Octodontidae). J. Arid Environ. 41, 443–452.

Opdyke, N.D., 1995. Mammalian migration and climate over the last seven millions years. In: Vrba, E.S., Denton, G.H., Partidge, T.C., Burcle, L.H. (Eds.), Paleoclimate and evolution with emphasis on human origins. Yale University Press, pp. 109–114.

Orgeira, M.J., 1987. Estudio paleomagnético de sedimentos del Cenozoico tardío en la costa atlántica bonaerense. Rev. Asoc. Geol. Argent. 42, 326–376.

Orgeira, M.J., 1990. Palaeomagnetism of late Cenozoic fossiliferous sediments from Barranca de los Lobos (Buenos Aires Province, Argentina): the magnetic age of the South American land-mammal ages. Phys. Earth Planet. Inter. 64, 121–132.

Orgeira, M.J., 1991. Correlación magnetoestratigráfica de secuencias cenozoicas tardías de la República Argentina y Bolivia. Rev. Asoc. Geol. Argent. 46, 127–135.

Pascual, R., Ortega, E.J., Gondar, D., Tonni, E.P., 1965. Las Edades del Cenozoico mamalífero de la Argentina con especial atención a aquellas del territorio bonaerense. An. Com. Investig. Cient., Prov. B. Aires 6, 165–193.

Pascual, R., Vucetich, M.G., Scillato-Yané, G.J., Bond, M., 1985. Main pathways of mammalian diversification in South America. In: Stehli, F.G., Webb, S.D. (Eds.), The Great American Biotic Interchange: Series Topics in Geobiology 4. Plenum Press, New York, pp. 219–247.

Pascual, R., Ortiz Jaureguizar, E., 1990. Evolving climates and mammal faunas in Cenozoic South America. J. Hum. Evol. 19, 23–60.

Pascual, R., Ortiz Jaureguizar, E., Prado, J.L., 1996. Land mammals: paradigm for Cenozoic South American geobiotic evolution. In: Arratia, G. (Ed.), Contributions of southern South America to vertebrate paleontology: Münchner Geowissenschaftliche Abhandlungen (A), vol. 30, pp. 265–319.

Quintana, C.A., 1994. Notas para la actualización del conocimiento de la fauna de la Formación San Andrés (Pleistoceno inferior), provincia de Buenos Aires. Ameghiniana 31, 331–332.

Quintana, C.A., 1996. Diversidad del roedor *Microcavia* (Caviomorpha: Caviidae) de América del Sur. Mast Neotrop. 3, 63–86.

Quintana, C.A., 1998. Relaciones filogenéticas de roedores Caviinae (Caviomorpha: Caviidae), de América del Sur. Bol. R. Soc. Esp. Hist. Nat., (Ser. Biol.) 94 (3–4), 125–134.

Randall, J.A., 1994. Convergences and divergences in communication and social organization of desert rodents. Austral. J. Zool. 42, 405–433.

Redford, K.H., Eisenberg, J.F., 1992. Mammals of the neotropics. 2: the southern cone. The University of Chicago Press, pp. 1–430.

Reig, O.A., 1952. Descripción previa de nuevos ungulados y marsupiales fósiles del Plioceno y del Eocuartario argentinos. Rev. Mus. Munic. Cienc. Nat. Tradic. Mar del Plata 1, 119–129.

Reig, O.A., 1958a. Notas para una actualización del conocimiento de la fauna de la Formación Chapadmalal: I. Lista faunística preliminar. Acta Geol. Lilloana 2, 241–253.

Reig, O.A., 1958b. Notas para una actualización de la fauna de la Formación Chapadmalal: II. Amphibia, Reptilia, Aves, Mammalia (Marsupialia: Didelphiidae, Borhyaenidae). Acta Geol. Lilloana 2, 255–283.

Reig, O.A., 1978. Roedores cricétidos del Plioceno superior de la Provincia de Buenos Aires (Argentina). Publ. Mus. Munic. Cienc. Nat. Mar del Plata 2, 164–190.

Reig, O.A., 1981. Teoría del origen y desarrollo de la fauna de mamíferos de América del Sur. Mus. Munic. Cienc. Nat. Mar del Plata, Monographie Naturae 1, 1–162.

Reig, O.A., 1987. An assessment of the systematics and evolution of the Akodontini, with the description of new fossil species of *Akodon* (Cricetidae: Sigmodontinae). In: Patterson, B.D., Timm, R.M. (Eds.), Studies in Neotropical Mammalogy: Essays in Honor of Philip Hershkovitz, Fieldiana, Zool., vol. 39, pp. 347–399.

Reig, O.A., Quintana, C.A., 1991. A new genus of fossil octodontine rodent from the Early Pleistocene of Argentina. J. Mammal. 72, 292–299.

Reig, O.A., Quintana, C.A., 1992. Fossil ctenomyine rodents of the genus *Eucelophorus* (Caviomorpha: Octodontidae) from the Pliocene and Early Pleistocene of Argentina. Ameghiniana 29, 363–380.

Reig, O.A., Busch, C., Ortells, M.O., Contreras, J.R., 1990. An overview of evolution, systematics, molecular biology and speciation in *Ctenomys*. In: Nevo, E., Reig, O.A. (Eds.), Evolution of Subterranean Mammals at the Organismal and Molecular Levels. Wiley-Liss, New York, pp. 71–96.

Rovereto, C., 1914. Los estratos araucanos y sus fósiles. An. Mus. Nac. Hist. Nat. B. Aires 25, 1–247.

Rusconi, C., 1930. Una nueva especie de roedor del subgénero *Paractenomys*. An. Soc. Cient. Argent. 110, 153–158.

Rusconi, C., 1937-1938. Contribución al conocimiento de la geología de la ciudad de Buenos Aires y sus alrededores y referencia de su fauna. Actas Acad. Nac. Cien. Córdoba 10, 177-294, 295-384.

Shackleton, N.J., 1995. New data on the evolution of Pliocene climatic variability. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins. Yale University Press, pp. 242–248.

Schultz, P.H., Zárate, M., Hames, W., Camilión, C., King, J., 1998. A 3.3-Ma impact in Argentina and possible consequences. Science 282, 2061–2063.

Teruggi, M.E., Andreis, R.H., Mazzoni, M.M., Dalla Salda, L.H., Spalletti, L.A., 1974. Nuevos criterios para la estratigrafía del Cuaternario de las barrancas de Mar del Plata-Miramar. An. LEMIT 268, 134–148. ser. 2.

Tonni, E.P., 1981. *Pediolagus salinicola* (Rodentia, Caviidae) en el Pleistoceno tardío de la provincia de Buenos Aires. Ameghiniana 18, 123–126.

Tonni, E.P., Alberdi, M.T., Prado, J.L., Bargo, M.S., Cione, A.L., 1992. Changes of mammal assemblages in the pampean region (Argentina) and their relation with the Plio–Pleistocene boundary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 95, 179–194.

Tonni, E.P., Cione, A.L., 1994. Los mamíferos y el clima en el Pleistoceno y Holoceno de la provincia de Buenos Aires. Actas Jornadas de Arqueología e Interdisciplinas, Programa de Estudios Prehistóricos, pp. 127–142.

Tonni, E.P., Cione, A.L., 1995. Los mamíferos como indicadores de cambios climáticos en el Cuaternario de la región pampeana de la Argentina. In: Argollo, J., Mourguiart, Ph. (Eds.), Los Climas Cuaternarios en América del Sur. Orstom, La Paz, pp. 319–326.

Verzi, D.H., 2001. Phylogenetic position of *Abalosia* and the evolution of the extant Octodontinae (Rodentia, Caviomorpha, Octodontidae). Acta Theriol. 46, 243–268.

Verzi, D.H., 2002. Patrones de evolución morfológica en Ctenomyinae (Rodentia, Octodontidae). Mast Neotrop. 9, 309–328.

Verzi, D.H., Lezcano, M., 1996. Status sistemático y antigüedad de *Megactenomys kraglievichi* Rusconi, 1930 (Rodentia, Octodontidae). Rev. Mus. La Plata (Paleont.) 9, 239–246.

Verzi, D.H., Tonni, E.P., Scaglia, O.A., San Cristóbal, J.O., 2002. The fossil record of the desert-adapted South American rodent *Tympanoctomys* (Rodentia, Octodontidae): paleoenvironmental and biogeographic significance. Palaeogeogr. Palaeoclimatol. Palaeoecol. 179, 149–158.

Verzi, D.H, Deschamps, C.M., Tonni, E.P., 2004. Biostratigraphic and palaeoclimatic meaning of the Middle Pleistocene South American rodent *Ctenomys kraglievichi* (Caviomorpha, Octodontidae). Palaeogeogr. Palaeoclimatol. Palaeoecol. 212, 315–329.

Villarroel, A.C., Marshall, L.G., 1989. A new fossil land mammal locality of Late Miocene (Huayquerian) Age from Muyu Huasi, southcentral Bolivia. Bol. Serv. Geol. Bolivia 4, 27–40. ser. A.

Vrba, E.S., 1985. African Bovidae: evolutionary events since the Miocene. Suid-Afrikaanse Tydskrif vir Wetenskap 81, 263–266.

Vrba, E.S., 1989. The environmental context of the evolution of early hominids and their culture. In: Bonnichsen, R., Sorg, M.H. (Eds.), Bone Modification. Center for the Study of the first Americans, Orono, Maine, pp. 27–42.

Vrba, E.S., 1992. Mammals as a key to evolutionary theory. J. Mammal. 73, 1–28.

Vrba, E.S., Denton, G.H., Partidge, T.C., Burcle, L.H. (Eds.), 1995. Paleoclimate and Evolution with Emphasis on Human Origins. Yale University Press, pp. 1–547.

Vucetich, M.G., Verzi, D.H., 1995. Los roedores caviomorfos. In: Alberdi, M.T., Leone, G., Tonni, E.P. (Eds.), Evolución Biológica y Climática de la Región Pampeana durante los últimos cinco millones de años. Un Ensayo de Correlación con el Mediterráneo Occidental, Monografías del Museo Nacional de Ciencias Naturales, Madrid, vol. 12, pp. 213–225.

Vucetich, M.G., Verzi, D.H., 1999. Changes in diversity and distribution of the caviomorph rodents during the Late Cenozoic in Southern South America. In: Tonni, E.P., Cione, A.L. (Eds.), Quaternary Vertebrate Paleontology in South America, Quaternary of South America and Antarctic Peninsula, vol. 12, pp. 207–223.

Vucetich, M.G., Verzi, D.H., Hartenberger, J.-L., 1999. Review and analysis of the radiation of the South American Hystricognathi (Mammalia, Rodentia). C. R. Acad. Sci. Paris (Paléont.) 329, 763–769.

Vucetich, M.G., Vieytes, E.C., Verzi, D.H., Noriega, J.I., Tonni, E.P., in press. Unexpected primitive rodents in the Quaternary of Argentina. J. South Amer. Earth Sci.

Walther, A.M., Orgeira, M.J., Reguero, M., Verzi, D.H., Vilas, J.F.A., Alonso, R., Gallardo, E., Kelley, S., Jordan, T., 1998. Estudio Paleomagnético, Paleontológico y radimétrico de la Formación Uquía (Plio–Pleistoceno) en Esquina Blanca (Jujuy). X Cong. Lat. Geol. y VI Cong. Nac. Geol. Económ. 1, 77.

Webb, S.D., 1976. Mammalian faunal dynamics of the Great American Interchange. Paleobiology 2, 216–234.

Webb, S.D., Opdyke, N.D., 1995. Global climatic influence on Cenozoic land mammal faunas. Board on Earth Sciences and

Resources, Effects of Past Global Change on Life. National Academy Press, Washington, pp. 184–208.

Willis, K.J., Kleczkowski, A., Crowhurst, S.J., 1999. 124,000-Year periodicity in terrestrial vegetation change during the late Pliocene epoch. Nature 397, 685–688.

Zárate, M.A., Fasano, J.L., 1989. The Plio–Pleistocene record of the central eastern pampas, Buenos Aires Province, Argentina: the Chapadmalal case study. Palaeogeogr. Palaeoclimatol. Palaeoecol. 72, 27–52.