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The oldest South American Cricetidae (Rodentia) and Mustelidae (Carnivora): Late Miocene faunal turnover in central Argentina and the Great American Biotic Interchange

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ABSTRACT

The discovery of a rich fauna from the late Miocene Cerro Azul Formation in Caleufú, central Argentina, is reported. This fauna includes vertebrate Holarctic immigrants, among which are the oldest South American records of mammals of the families Cricetidae (Rodentia) and Mustelidae (Carnivora). Stratigraphic, biochronological and taphonomic evidence indicates that the faunal assemblage from Caleufú is confidently synchronous and represents the late Huayquerian (Zone of *Xenodontomys elongatus*; late Miocene). Thus, this fauna supports hypotheses of the arrival of cricetids and mustelids prior to the Pliocene completion of the Panamanian isthmus. However, the new records do not permit inferences to be made about precise moments of entry of these groups into South America. Representation of the GABI in the fossil record is here interpreted as a major event integrated by a nested pattern of events, including geographically more restricted turnovers (implying particular taphonomic and geographic biases) and associated environmental changes. In such a hierarchical context, the record of Caleufú represents a local turnover different from those occurring with arrivals of these taxa, or their ancestors, into the continent. In accordance with biochronological data, the turnover recorded in Caleufú could be coeval with the global-scale glacial event detected for the late Miocene (ca. 5.7–5.8 Ma). In southern South America, this arid and cold pulse would have triggered the distribution drift to central Argentina of fauna previously restricted to western peri-Andean areas. Local turnovers such as the one reported here, and associated physical changes, have to be analyzed in detail as individual events in order to interpret the chronology, dynamics and paleoenvironmental context of hierarchically greater episodes such as the GABI.

1. Introduction

Different late Cenozoic faunal changes (distribution drift, speciation, extinction) linked to the Caribbean tectonics and the development of the present Panamanian isthmus (Marshall and Sempere, 1993; Iturralde-Vinent and MacPhee, 1999; Coates et al., 2004; Kirby and MacFadden, 2005), are among the most important historic events leading to the composition of the modern South American mammal fauna (Webb and Marshall, 1982). The faunal episodes are classically subsumed into a major event known as Great American Biotic Interchange (GABI; e.g. Reig, 1981; Webb, 1985; Pascual et al., 1985; Webb and Rancy, 1996; Webb, 1999; Pascual et al., 2001). Nevertheless, the fossil record attesting to the GABI is strongly diachronic, at least in South America (e.g. Cione and Tonni, 1995a,b, 2001; Cione et al., 2007). This fossil record encompasses almost 7 Ma between the late Miocene first occurrence of the Family Procyonidae (Butler et al., 1984) and the late Pleistocene–Holocene records of Hominidae, Leporidae and Sciuridae. In addition, the Holarctic immigrants of families Geomyidae, Heteromyidae and Soricidae are only known in South America through living representatives (see Tonni et al., 1992; Cione and Tonni, 1995b; Cartelle, 1999; Woodburne et al., 2006).

Chronological evidence of fossils attesting to the GABI in South America is usually assumed to reflect essentially the chronology of arrival of immigrants into the continent. In the exceptional case of the Cricetidae, the information supplied by living species has been used to challenge this interpretation, giving rise to long debates (see a synthesis in Engel et al., 1998; Pardiñas et al., 2002). But in any case, fossil record evidence of associated faunal and environmental changes occurring in the continent in the post-immigration interval (e.g. Marshall and Sempere, 1993) have been scarcely considered. This, in spite of the purported causal influence of those changes, along with the geographical bias of the fossiliferous sites, in the pattern of first appearances of species in the fossil record.

Abbreviations: AL, alveolar length; CL, coronal length; FMNH, Field Museum of Natural History, Chicago; GHUNLPam, Cátedra Geología Histórica, Universidad Nacional de La Pampa, Argentina; L, length; MLP, Museo de La Plata, Argentina; NISP, number of identified specimens per taxon; W, width.

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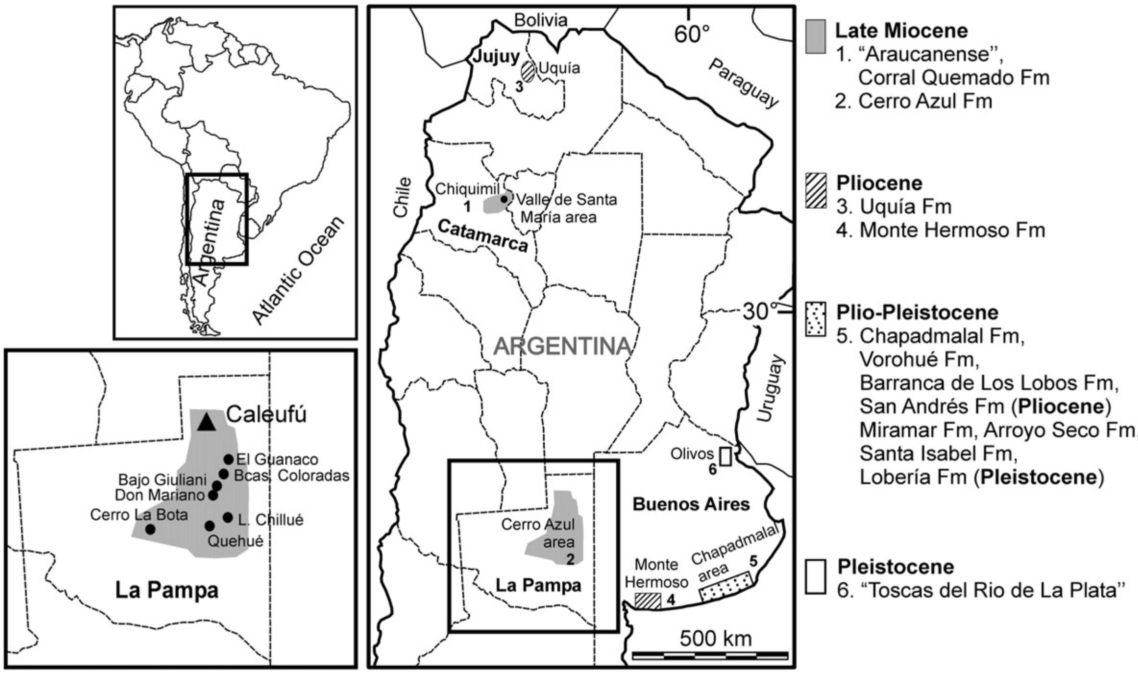


Fig. 1. Geographic location of deposits where first appearances of Holarctic immigrant mammals in South America are recorded.

Recently, a rich late Miocene fauna bearing Holarctic immigrants has been found in exposures of the Cerro Azul Formation in Caleufú, central Argentina. The discovery is the result of fieldwork over the last twenty years in upper Miocene outcrops of the Pampean area of this country (e.g. Montalvo and Casadío, 1988; Verzi et al., 1991, 1994, 1995; Goin et al., 2000; Montalvo, 2002; Verzi et al., 2003, 2008). The vertebrate assemblage of Caleufú is interpreted as representing a faunal turnover which includes the first appearance of rodents of the family Cricetidae and carnivores of the family Mustelidae in South America. In this paper, we report these new records of immigrant mammals, and discuss the biochronologic and paleoclimatic context of the faunal assemblage. A proposal for the significance of the faunal turnover detected in Caleufú in the context of the GABI, is given.

2. Geological setting

The analyzed deposits correspond to continental sediments of the Cerro Azul Formation (Linares et al., 1980) that crop out in central Argentina, mainly in eastern La Pampa province (Fig. 1), and western Buenos Aires province (as "Epecuén Formation", sensu Pascual, 1961). These exposures and their fauna belong to a sedimentary and faunal cycle, which followed the withdrawal (around 10 Ma; Haq et al., 1987; Schultz et al., 2004) of a widespread marine transgression that extended from central Argentina, to western Uruguay and southern Paraguay and Brazil (Pascual et al., 1985; Webb, 1995).

The lithology of these post-regression continental deposits of central Argentina is quite homogeneous, composed of loess and loess-like (aqueous reworked) sediments. A detailed description of the geology and stratigraphy of Cerro Azul Formation can be seen in Linares et al. (1980) and Goin et al. (2000). A new biostratigraphic scheme, including a biozonation, was recently proposed (Verzi et al., 2008). The exposures at Caleufú (northern La Pampa Province, 35°41′37″ S, 64°40′8″ W; Fig. 1) correspond to eolian deposits, ranging from 1.8 to 2.0 m in thickness, in which three levels are recognized (Fig. 2; Verzi et al., 2003; Albino and Montalvo, 2006). Fossils were recovered from the lower level composed of sandy siltstones diffusely stratified, 0.8 to 1.0 m thick, cemented by carbonates, and with abundant scattered calcareous concretions and rounded manganese nodules. This level shows evidence of pedogenesis and especially diagenesis. Middle and upper levels were devoid of fossils.

3. Faunal assemblage of Caleufú: the oldest South American Cricetidae and Mustelidae

The faunal assemblage of Caleufú is rich and taxonomically diverse, and spatially constrained. 6453 vertebrate remains were recovered from an area of about 1590 m^2. Taphonomic attributes suggest that micromammals were accumulated by mammal predator activities (Montalvo, 2002, 2004). A process of prey selection is evidenced by the predominance of remains of a few species of small rodents and notoungulates, high percentage of juveniles, breakage pattern, and tooth marks. Coprolites with strongly digested bone remains were found (Montalvo, 2004). These features suggest that the Caleufú assemblage is confidently synchronous from a stratigraphic point of view (Verzi et al., 2008).

At least 39 vertebrate taxa (Table 1) could be determined based on 2 257 specimens of the total sample recovered. Systematics of the

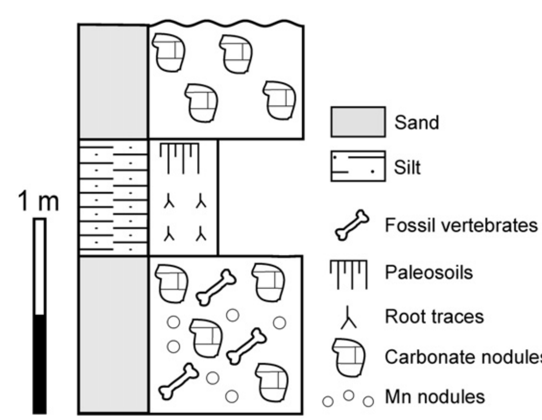


Fig. 2. Schematic stratigraphic profile of the Cerro Azul Formation in Caleufú (modified from Esteban et al., 2003).

Table 1
Faunal list of the late Miocene Cerro Azul Formation in Caleufú. 1. Albino et al. (2006); 2. Albino and Montalvo (2006); 3. Cenizo and Montalvo (2006); 4. Abello et al. (2002); 5. Esteban et al. (2003); 6. described or mentioned in this paper; 7. Montalvo and Rocha (2003); 8. Verzi et al. (2003). Supraspecific taxonomy of mammals follows Wilson and Reeder (2005), and McKenna and Bell (1997) for the extinct taxa

Class **REPTILIA** Laurenti
Order **SQUAMATA** Oppel
Suborder **LACERTILIA** Owen
Infraorder **SCINCOMORPHA** Camp
Family **Teiidae** Gray
Subfamily **Tupinambinae** Presch
Genus *Tupinambis* Daudin
[1]*Tupinambis* sp.
Suborder **SERPENTES** Linnaeus
Superfamily **Colubroidea** Oppel
Family "**Colubridae**" Oppel
[2]Gen. et sp. indet.
Family **Viperidae** Bonaparte
[2]Gen. et sp. indet.
Class **AVES** Linné
Order **PASSERIFORMES** (Linné)
Suborden **TYRANNI** Wetmore y Miller
Tyranni indet.
Order **ACCIPITRIFORMES** (Vieillot)
Family **Falconidae** (Shape)
Genus *Milvago* (Vieillot)
[3]*Milvago* sp.
Order **TINAMIFORMES** (huxley)
Family **Tinamidae** Gray
Genus *Eudromia* Geoffroy
[3]*Eudromia* sp.
Class **MAMMALIA** Linné
Order **DIDELPHIMORPHIA** Gill
Family **Didelphidae** Gray
Subfamily **Didelphinae** Gray
Didelphinae indet.
Tribe **Monodelphini** Talice, de Mosera, and Machado
[4]Monodelphini indet.
Genus *Hyperdidelphys* Ameghino
[4]*Hyperdidelphys* sp.
Family **Sparassocynidae** Reig
Genus *Sparassocynus* Mercerat
[4]*Sparassocynus* sp.
Order **INDET**. Abello, Montalvo, and Goin
Family **Argyrolagidae** Reig
Genus *Argyrolagus* Ameghino
[4]*Argyrolagus* sp.
Order **CINGULATA** Illiger
Family **Dasypodidae** Gray
Subfamily **Euphractinae** Winge
Tribe **Euphractini** Winge
Genus *Macroeuphractus* Ameghino
[5]*Macroeuphractus morenoi* (Lydekker)
Genus *Chorobates Reig*
[5]*Chorobates villosissimus* (Rovereto)
[5]*Chorobates* cf. *villosissimus* (Rovereto)
Genus *Proeuphractus* Ameghino
[5]*Proeuphractus* sp.
Tribe **Eutatini** Bordas
Genus *Chasicotatus* Scillato-Yané
[5]*Chasicotatus ameghinoi* Scillato-Yané
[5]*Chasicotatus* sp.
Genus *Doellotatus* Bordas
[5]*Doellotatus chapadmalensis* Bordas
[5]*Doellotatus inornatus* (Rovereto)
Genus *Ringueletia* Reig
[5]*Ringueletia simpsoni* (Bordas)
Family **Glyptodontidae** Gray
Glyptodontidae indet.
Order **PILOSA** Flower
Family **Scelidotheriidae** Ameghino
Subfamily **Scelidotheriinae** Ameghino
Scelidotheriinae indet.
Order **CARNIVORA** Bowdich
Family **Mustelidae** Fischer de Waldheim
[6]Mustelidae indet.
Order **LITOPTERNA** Ameghino
Family **Proterotheriidae** Ameghino
Proterotheriidae indet.
Order **NOTOUNGULATA** Roth
Suborder **TYPOTHERIA** Zittel
Family **Hegetotheriidae** Ameghino
Subfamily **Pachyrukhinae** Kraglievich
Genus *Paedotherium* Burmeister
Paedotherium minor Cabrera
Family **Mesotheriidae** Alston
Subfamily **Mesotheriinae** Simpson
Genus *Pseudotypotherium* Ameghino
Pseudotypotherium subinsigne (Rovereto)
Family **Toxodontidae** Owen
Toxodontidae indet.
Order **RODENTIA** Bowdich
Suborder **HYSTRICOMORPHA** Brandt
Infraorder **HYSTRICOGNATHI** Brandt
Family **Chinchillidae** Bennett
Genus *Lagostomus* Brookes
Lagostomus (Lagostomopsis) sp.
Family **Dinomyidae** Peters
Genus *Tetrastylus* Ameghino
Tetrastylus sp.
Family **Caviidae** Fischer de Waldheim
Genus *Neocavia* Kraglievich
[7]*Neocavia* cf. *Lozanoi*
Genus *Palaeocavia* Ameghino
Palaeocavia sp.
Genus *Orthomyctera* Ameghino
Orthomyctera sp.
Family **Echimyidae** Gray
Genus *Pampamys* Verzi, Vucetich, and Montalvo
Pampamys emmonsae Verzi, Vucetich, and Montalvo
Family **Octodontidae** Waterhouse
Genus *Phtoramys* Ameghino
Phtoramys homogenidens Ameghino
Genus *Neophanomys* Rovereto
Neophanomys biplicatus Rovereto.
Subfamily **Ctenomyinae** Lesson
Genus *Xenodontomys* Kraglievich
[8]*Xenodontomys elongatus* Verzi, Montalvo, and Tiranti
Subfamily **Octodontinae** Waterhouse
Genus *Pithanotomys* Ameghino
[6]*Pithanotomys macer* Ameghino
[6]Gen. et sp. nov.
Suborder **MYOMORPHA** Brandt
Superfamily **MUROIDEA** Illiger
Family **Cricetidae** Fischer de Waldheim
Subfamily **Sigmodontinae** Wagner
[6]Sigmodontinae indet.

recovered reptiles of the families Viperidae, Colubridae and Teiidae, Aves of the families Falconidae and Tinamidae, and mammals of the families (or subfamilies) Didelphidae, Sparassocynidae, Argyrolagidae (Metatheria), Dasypodidae (Xenarthra), Ctenomyinae and Caviidae (Rodentia), have been analyzed previously (Table 1). The record of Viperidae represents the first appearance of snakes of this family in South America (Albino and Montalvo, 2006).

Among mammals, two left mandibles (GHUNLPam 19611 and 21853) of a species of Cricetidae were found. This cricetid is smaller than *Auliscomys formosus* from the Montehermosan (early Pliocene) of the coastal region of central Argentina (Table 2), the oldest species previously known (Reig, 1978, fig. 5a; Pardiñas et al., 2002). GHUNLPam 19611 preserves a damaged fragment of the intra-alveolar portion of the incisor, and m1–3; GHUNLPam 21853 is more damaged, preserving only the m2 complete, the posterior portion of the m1 and a damaged intra-alveolar part of the incisor. The new material has terraced molars (sensu Hershkovitz, 1967) with the lophids of the m1–2 more transverse than those of *A. formosus* (cf. Fig. 3 and Reig, 1978, fig. 5). As in *A. formosus*, the procingulum of the m1 has a slight anteromedian flexid and a marked anterolabial cingulum; the m2 has a well developed protoflexid. The protoflexid of the m3 is a slight groove; the occlusal figure of this molar is not sigmoid-shaped as in *A. formosus*, but nearly figure-eight-shaped because the depths of meso- and hypoflexid are opposite.

The mammal sample also includes a left mandible fragment of a carnivore of the family Mustelidae (GHUNLPam 21722; Fig. 4). It is a very damaged anterior fragment, with the roots of the three incisors with a strongly staggered arrangement. The canine is cut off near the base of the crown. Behind the canine there is a small anterior root of a premolar, probably p2, and a larger posterolingual alveolus for the

Table 2
Dental measurements (mm) of Sigmodontinae indet. from Caleufú

	m1		m2		m3		m1–m3	
	L	W	L	W	L	W	AL	CL
GHUNLPam 19611	1.54	0.88	1.23	0.95	0.98	0.81	4.61	4.19
GHUNLPam 21853			1.16	0.77				

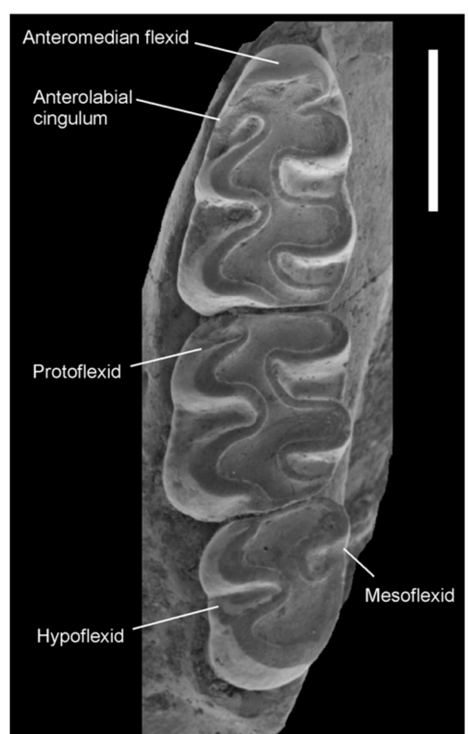


Fig. 3. Occlusal view of left m1–3 of Sigmodontinae indet. GHUNLPam 19611. Scale = 1 mm.

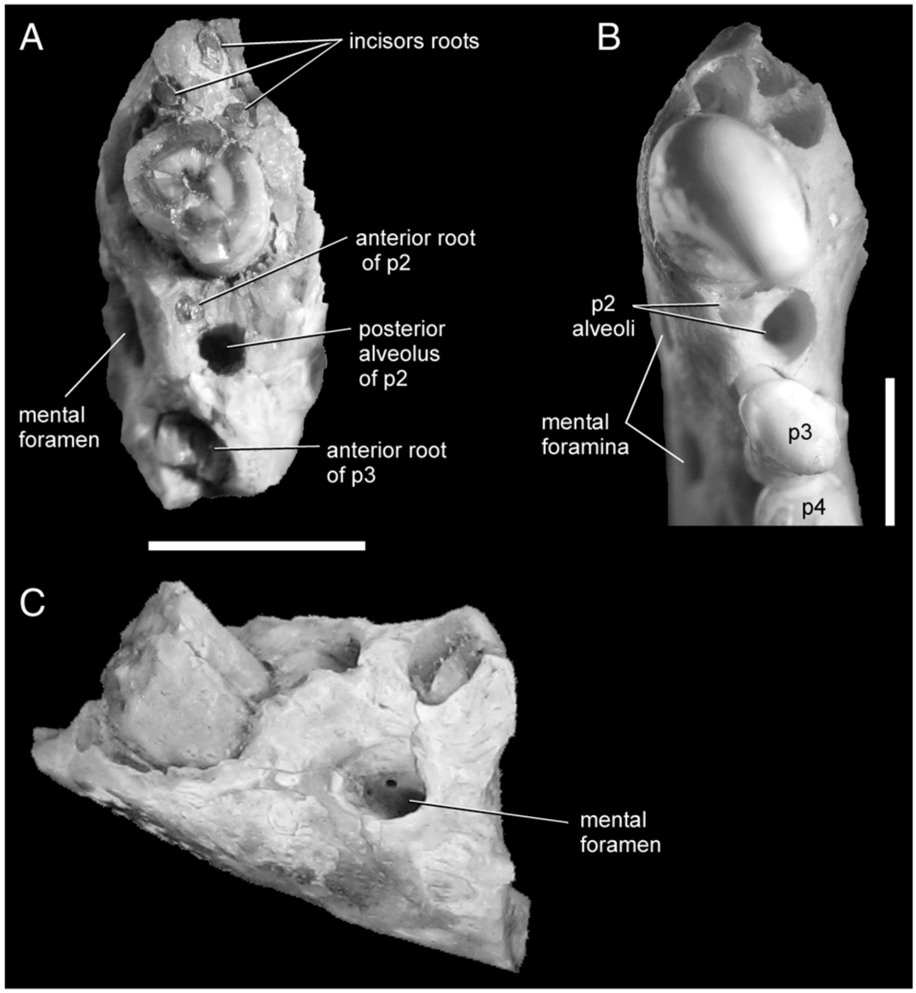


Fig. 4. Dorsal view of anterior portion of left hemimandible of Mustelidae: A, GHUNLPam 21722; B, *Lontra longicaudis* MLP 1702 (Recent). C, lateral view of GHUNLPam 21722. Scales = 5 mm.

posterior root of this tooth; posteriorly, there is the anterior alveolus of the following jugal tooth, probably p3, with a root fragment. The mental foramen is wide and circular. The position of the preserved roots and alveoli shows similarities with those of living Lutrinae (Fig. 4).

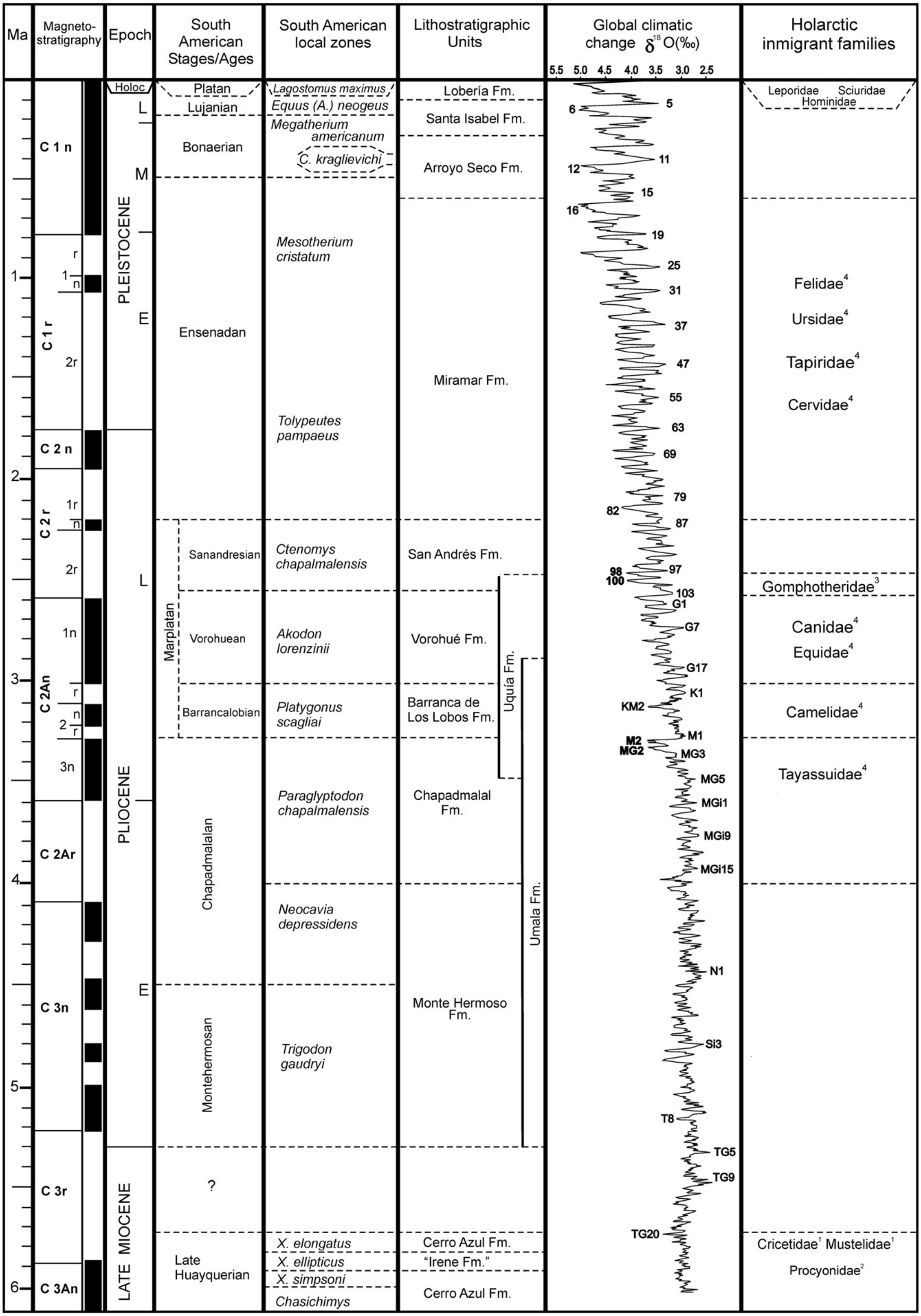
4. Biochronology

The Cerro Azul Formation as a whole was classically interpreted as Huayquerian (late Miocene; Fig. 5) in age based on its mammal fauna (Verzi et al., 1991 and references therein). Recently, a detailed biochronology of the Cerro Azul Formation and other late Miocene localities of the Argentinian pampas has been proposed (Verzi et al., 2008) on the basis of the evolution of caviomorph rodents of the superfamily Octodontoidea (Verzi, 1999; Verzi et al., 2003, 2004). This temporal interpretation is supported basically by evolutionary changes of hypsodonty within single lineages, applying a criterion of "stage of evolution" (Lindsay, 1990) which we assume implies irreversibility in a biochronological context. The hypothesized non-reversible condition, namely unequivocal evolutionary polarity, of phyletic sequences is a valuable correlation tool when there is no stratigraphic superposition of the bearing levels, as occurs in Cerro Azul Formation and other late Miocene localities from central Argentina (Verzi et al., 2008).

Dental evolution of the octodontoid rodents, in particular of the lineages *Chasichimys–Xenodontomys–Actenomys* and *Neophanomys*, suggests that Caleufú is the youngest exposure so far known of the Cerro Azul Formation and that it belongs to the late Huayquerian (Zone of *Xenodontomys elongatus*; late Miocene; Verzi et al., 2008). The ctenomyine rodent *Xenodontomys elongatus* is the most derived chronomorph (sensu Martin, 1993) of the phyletic sequence *Chasichimys–Xenodontomys* recorded in the Chasicoan–Huayquerian (late Miocene) of central Argentina (Verzi, 1999; Verzi et al., 2004). This chronomorph is, however, clearly more primitive than its derivative *Actenomys priscus* from the Montehermosan–Vorohuean of the coastal cliffs of east-central Argentina (early–late Pliocene; Figs. 1 and 5; Verzi, 2008), and a morphological gap between these chronomorphs, implying time, is evident.

Neophanomys is recorded both in the Cerro Azul Formation and the "Araucanense" from northwestern Argentina (Fig. 1; Verzi et al., 1999). In the "Araucanense" (Huayquerian, late Miocene) of the Chiquimil section, in northwestern Argentina, *Neophanomys biplicatus* was found in unit XVIIIa, below a tuff of the overlying unit XIX dated at 6.02 Ma (FMNH P14347, Marshall and Patterson, 1981, fig. 6 and appendix IV; Butler et al., 1984). This chronomorph is recorded in the Huayquerian exposures of the Cerro Azul Formation in the Pampean localities of Quehué, Estancia Don Mariano, and Bajo Giuliani (Fig. 1). The *Neophanomys* chronomorph from Caleufú is slightly more hypsodont than *N. biplicatus*, and thus, it is assumed to be more modern, but not younger than late Miocene in age (Verzi et al., 2008).

According to these biochronological data, the faunal assemblage of Caleufú is assigned to the late Huayquerian (late Miocene; see below). Consequently, the record of Cricetidae and Mustelidae from this


Ma
Magneto-stratigraphy
Epoch
South American Stages/Ages
South American local zones
Lithostratigraphic Units
Global climatic change δ18O(‰)
Holarctic inmigrant families
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PLIOCENE
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LATE MIOCENE
Platan
Lujanian
Bonaerian
Ensenadan
Marplatan
Sanandresian
Vorohuean
Barrancalobian
Chapadmalalan
Montehermosan
?
Late Huayquerian
Lagostomus maximus
Equus (A.) neogeus
Megatherium americanum
C. kraglievichi
Mesotherium cristatum
Tolypeutes pampaeus
Ctenomys chapalmalensis
Akodon lorenzinii
Platygonus scagliai
Paraglyptodon chapalmalensis
Neocavia depressidens
Trigodon gaudryi
X. elongatus
X. ellipticus
X. simpsoni
Chasichimys
Lobería Fm.
Santa Isabel Fm.
Arroyo Seco Fm.
Miramar Fm.
San Andrés Fm.
Vorohué Fm.
Barranca de Los Lobos Fm.
Chapadmalal Fm.
Monte Hermoso Fm.
Uquía Fm.
Umala Fm.
Cerro Azul Fm.
"Irene Fm."
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MG2
MG3
MG5
MGi1
MGi9
MGi15
N1
Sl3
T8
TG5
TG9
TG20
Leporidae Sciuridae
Hominidae
Felidae4
Ursidae4
Tapiridae4
Cervidae4
Gomphotheridae3
Canidae4
Equidae4
Camelidae4
Tayassuidae4
Cricetidae1 Mustelidae1
Procyonidae2

locality represents the oldest South American record of these Holarctic immigrant families (Verzi et al., 2008). To date, the Cricetidae had their oldest South American record in the Montehermosan of central Argentina (Monte Hermoso Formation; early Pliocene) through the presence of the species *Auliscomys formosus* (Reig, 1978; Pardiñas et al., 2002). Mustelidae was first recorded in the late Pliocene of central Argentina (Vorohué Formation; Marplatan stage, Vorohuean substage) through the galictine *Galictis sorgentinii* (Reig, 1957). The record of the mephitine *Conepatus altiramus*, originally described as coming from the upper early Pliocene of the Chapadmalal Formation (Reig, 1952), is still dubious (see Reig, 1957, p. 39; Hershkovitz, 1966, p. 742; Cione and Tonni, 1995b, p. 147).

Both in the Cerro Azul Formation (Quehué and Telén localities) and the Chiquimil section, the octodontid *Neophanomys* is found in the same levels as the procyonid *Cyonasua* (Carnivora). This latter is considered as the oldest Holarctic immigrant into South America (Butler et al., 1984, p. 634); however, according to the new discoveries in Caleufú, its occurrence in this continent could be as old as that of the first Cricetidae (Marshall, 1979) and Mustelidae.

5. Faunal turnovers and the Great American Biotic Interchange

The new late Miocene materials from Caleufú support hypotheses regarding the arrival of cricetids (Hershkovitz, 1966; Reig, 1978; Marshall, 1979; Reig, 1980; Engel et al., 1998) and mustelids prior to the Pliocene completion of the Panamanian isthmus, and also favor the proposal of dryland connections since the late middle Miocene (Iturralde-Vinent and MacPhee, 1999; Coates et al., 2004). Moreover, the almost coeval record of procyonids suggests that these three mammal taxa may have been part of a single early dispersal event as proposed in part by Marshall (1979, p. 129, for procyonids and cricetids). However, at least in this case, the records do not permit refinements as to the arrival times in South America or the dynamics of such arrival.

The entry of Holarctic immigrant mammals into South America has been alternatively interpreted as a gradual (e.g. Pascual et al., 1985) or an essentially episodic phenomenon (e.g.; Marshall and Sempere, 1993; Cione and Tonni, 1995b; Webb and Rancy, 1996; Woodburne et al., 2006). In these interpretations, the chronologic evidence of fossils attesting to the GABI in South America are assumed to reflect essentially the chronology of the arrival (except for Cricetidae, see Introduction); accordingly, the dynamics of such arrival are related to paleoenvironmental change (e.g. Vrba, 1992; Marshall and Sempere, 1993; Webb and Rancy, 1996). Cione and Tonni (1995a,b) have refined the stratigraphic and chronologic evidence of the record of Holarctic immigrants, which allowed a more precise acknowledgment of its episodic character. However, this does not allow to know if the entry of this fauna into the continent was in fact episodic. Primarily, fossils and associated paleoclimatic data represent key information for understanding the dynamics of the species in their area of occurrence. Fossil localities bearing Holarctic immigrants in South America are strongly biased geographically, mainly restricted to central Argentina in the southern portion of the continent (Cione and Tonni, 1995b, p. 147). Except for the late Pleistocene to Recent representatives (see above), nearly 80% of first appearances of immigrant families are recorded in the Miocene through the Pleistocene of central Argentina, especially in the Pliocene and Pleistocene sequences of the coast of Buenos Aires province (Figs. 1 and 5; Cione and Tonni, 1995b, 2001). Thus, both the chronology of these fossils and the related particular paleoenvironmental context should first be assumed as evidence associated with the first appearance of the involved species into this part of the continent, corresponding to the current Pampean region.

In this sense, we strongly agree with the scenario proposed by Marshall (1979, pp. 130–131), which emphasized the importance of the events (including biotic and physical changes) occurred deep in the continent after the arrival through the Panamian land bridge.

As stated by Vrba (1995a), faunal turnovers, including speciation, extinction and distribution drift (Vrba, 1992, p. 10), are triggered by physical changes (consequences of astronomical climatic cycles, and diastrophic events; Vrba, 2005), involving climatic changes. It seems clear that important physical changes determined the set of faunal events known as GABI (e.g. Vrba, 1992; Ortiz Jaureguizar and Cladera, 2006, pp. 518–519). Representation of the GABI in the fossil record may be interpreted as a major event encompassing a nested pattern of events, including more geographically restricted turnovers and associated environmental changes (see Vrba, 1995a). In such a hierarchical context, the record of Caleufú represents a local turnover that includes the appearance of cricetids and mustelids in this area. This implies, not only particular taphonomic and geographic biases associated with deposits, but also physical changes involved in this geographically restricted episode, different from those occurring during the arrival of these taxa or their ancestors into the continent.

The analysis of changes in faunas of octodontoid rodents among different localities of the Cerro Azul Formation shows a remarkable faunal turnover in Caleufú. From the oldest exposure of this formation in Cerro La Bota (Verzi, 1999), to the youngest one in Caleufú (Verzi et al., 2003, 2004), octodontoid rodents with rootless molars (Octodontidae) increase in dominance while protohypsodont ones (Echimyidae and Octodontidae) decrease (Fig. 6). This change involves the gradual local dissapearance of Echimyidae, today confined to subtropical and tropical habitats of northern South America, and the differentiation of modern Octodontidae in the south of the continent. This evolutionary trend among octodontoids was an adaptive response to the increasing aridity and consequent development of open environments in central Argentina (Verzi, 1999; Vucetich et al., 1999). Available data show the global character of this late Miocene cooling and drying pulse (e.g. Janis, 1993; Opdyke, 1995; Vrba, 1995b; MacFadden and Cerling, 1996; Cerling et al., 1997; Zachos et al., 2001; Bobe, 2006; Vrba and Haile-Selassie, 2006). In Caleufú, this gradual evolutionary trend is altered by a sudden and massive presence of euhypsodont Octodontinae rodents (NISP=64) previously restricted to western Argentina (Verzi, 1999). The record of Holarctic immigrant mammals and snakes is a part of this faunal turnover. The absence of these taxa in Cerro Azul Formation localities older than Caleufú could represent a taphonomic bias, as long as the fossil assemblage of Caleufú is an accumulation caused by predators' activities (Montalvo, 2002, 2004); however, taphonomic analyses in progress in one of these older localities (Bajo Giuliani), equally rich in fossils and temporally near to Caleufú, suggest a similar genesis to that of the latter, but none of the abovementioned taxa are recorded (Verzi et al., 2008).

In accordance with biochronological data, we suggest that the turnover recorded in Caleufú could be coeval with the global glacial event of latest Miocene, ca. 5.7–5.8 Ma (Opdyke, 1995: 109; OIS TG20-TG22 of Shackleton, 1995), reported at regional scale for the Andes of southern Argentina (>5.04, Ton-That et al., 1999). Coincidentally, 5.5–6.0 Ma has been assumed as an interval of increased intercontinental mammalian migration (Opdyke, 1995; Vrba, 1995b; Winkler, 2002; Vrba and Haile-Selassie, 2006). In southern South America, this cold and arid pulse would have triggered the arrival in central Argentina of

Fig. 5. Stratigraphic chart with a correlation to global climatic change. Stratigraphy modified from Cione and Tonni (1999), Verzi and Quintana (2005) and Verzi et al. (2008); magnetostratigraphic scale follows Berggren et al. (1995); isotopic curve is after Shackleton (1995). Holarctic immigrant families are not in order of first appearance within each stage/age (Cione and Tonni, 1995b): 1. first appearance in the late Miocene Cerro Azul Formation, central Argentina; 2. first appearance in the late Miocene "Araucanense", northwestern Argentina (Butler et al., 1984); 3. first appearance in the Pliocene of Uquía Formation (Reguero et al., 2007); 4. first appearance in the Pliocene or Pleistocene coastal deposits of central Argentina (Cione and Tonni, 1995b; see also Fig. 1).

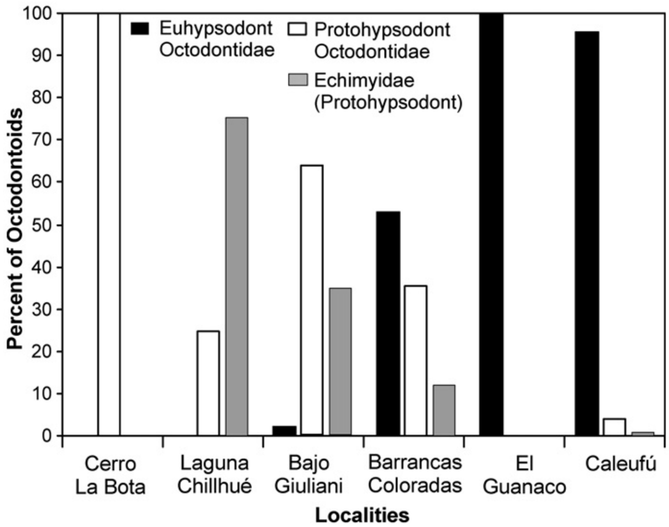

Fig. 6. Changes in the composition of the octodontoid communities from the Cerro Azul Formation (modified from Verzi et al., 2008). The relative abundance of each octodontoid group is expressed as percent of the total of octodontoid specimens. Protohypsodont octodontoids are represented by Octodontidae and Echimyidae; euhypsodont octodontoids are only Octodontidae.

species previously restricted to western periandean areas, through the expansion or drift of favorable environments. The west–east polarity of this distribution drift appears as a recurrent pattern in turnovers associated to cooling and drying pulses affecting micromammals in central Argentina (Verzi, 2001; Verzi and Quintana, 2005).

In this sense, the absence of the Holarctic taxa here described in late Miocene sediments of periandean areas, in western and northwestern Argentina, is noteworthy (Rovereto, 1914; Marshall and Patterson, 1981; Marshall and Sempere, 1993). Although the causes of this absence cannot be ascertained, a taphonomic bias is suggested by the peculiar conditions that favored the accumulation of remains in the Caleufú assemblage, and the differential preservation of the cricetid-sized *Neophanomys*, one of the smallest South American hystricognath rodents. One hemimandible of *Neophanomys* was found among 12 vertebrate remains in the late Miocene level XVIIIa of the Chiquimil locality in northwestern Argentina; a total of 71 vertebrate remains have been recovered from this entire deposit. A second hemimandible of *Neophanomys*, without precise provenance data, was also found in the Valle del Río Santa María (Fig. 1), among a total of 120 vertebrate remains collected throughout the 11 localities distributed in the area (Marshall and Patterson, 1981, figs. 1–3, and appendix IV). In contrast, 13 hemimandibles of *Neophanomys* have been recovered from the Cerro Azul Formation; 7 of them are part of a sample of 2 257 identifiable vertebrate remains collected from a single Caleufú level outcropping in a comparatively quite small area (see Section 3).

In brief, the record of Caleufú shows that the arrival in South America of immigrant Holarctic mammals of the families Cricetidae and Mustelidae, as well as the snakes of the family Viperidae, was quite probably prior to the end of the Miocene. A global climatic change would have triggered the presence of these taxa in their area of occurrence as result of a dispersal event involved in a local faunal turnover. The identity of this latter, including its chronology and paleoenvironmental context, must be differentiated from the event or events of entry into the continent of the involved species or their ancestors. Because of their potential significance, analyses of these local turnovers and associated physical changes as individual events can be important when interpreting the chronology, dynamics and paleoenvironmental context of hierarchically higher episodes such as the GABI.

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