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Palaeoecological implications of the mid-Pliocene faunal turnover in the Pampean Region (Argentina)

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Abstract

Known since Darwin's time, the Plio-Pleistocene succession exposed at the Chapadmalal sea cliffs have provided abundant mammal remains even though palaeobiological studies are scarce. Different authors have identified several assemblages in this stratigraphic interval of homogeneous lithology, which records an important mid-Pliocene faunal turnover dated at ca. 3.3 Ma. This paper examines the palaeoecological characteristics and the regional importance of this faunal turnover: 37% of all genera and 53% of all species became extinct between the older Chapadmalalan and the younger Barrancalobian chronostratigraphic units, a level that is actually higher than the percentage of genera extinct at the global-scaled Cretaceous–Tertiary extinction. The palaeoecological analysis permits to infer that the species-rich Chapadmalalan fauna seems to have been very balanced from the trophic–energetic point of view. On the other hand, the succeeding and less-explored Barrancalobian represents a relatively poorer environment, highly unbalanced in terms of the herbivore–carnivore relationships, due mainly to the absence of medium to large mammal and bird carnivores. The cause of the mid-Pliocene faunal turnover is still debatable. Climatic change has been traditionally related to this faunal turnover. Stratigraphically, an impact event dated at ca. 3.3 Ma is recorded in the succession. This event coincides with a change in the deep-sea stable isotopic record, reflecting a sudden change in climate and ocean circulation. This suggests that the impact might have induced regional faunal extinctions. Correlation with other areas different from the coast of Buenos Aires Province is needed to establish the geographic scale of the extinction. New fossils will provide a more complete and accurate picture of this remarkable faunal turnover.

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Keywords: Stratigraphy; South America; Mammals; Palaeoecology; Extinction

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1. Introduction

1.1. Background

The Chapadmalal sea cliffs, extending along 35 km of the southeastern coast of Buenos Aires Province, Argentina (Fig. 1), provide a quite complete sequence of Plio-Pleistocene mammal-bearing strata. Many fossil collections recovered since the visit of Darwin in 1833 are placed in several museums of Argentina and include abundant specimens.

To date, the study of the mammal assemblages recovered in the area has mostly focused on their taxonomy with general comments on the environmental setting and biostratigraphic implications inferred from the fossil record (Alberdi and Leone et al., 1995, and chapters therein; Tonni et al., 1992, Cione and Tonni, 1995a,b, Cione and Tonni, 1996; Tonni and Cione, 1999, and references therein). Few contributions, however, have been devoted to the study of palaeobiological questions of potential significance for palaeoecological reconstructions such

as morphology of rodent palaeocaves (Genise, 1989; Scognamillo et al., 1998) and their taphonomic significance (Peña, 1997).

Based on the information available, Tonni et al. (1992) identified several mammal assemblages (Table 1) recording the Plio-Pleistocene interval. The remarkable differences between the taxonomic lists of the Chapadmalalan and the Marplatano stages have been interpreted as an important faunal turnover stratigraphically placed in the mid-Pliocene, although a detailed chronology was not provided (Tonni et al., 1992, Cione and Tonni, 1995a,b). This general interpretation has been followed by other authors (Alberdi and Leone et al., 1995, and chapters therein).

The purpose of this paper is to contribute to the understanding of the inferred Pliocene faunal turnover by means of a community structure analysis according to the ecological energetics of the involved mammal assemblages. The causes and implications of the extinction are also discussed as well as its regional importance.

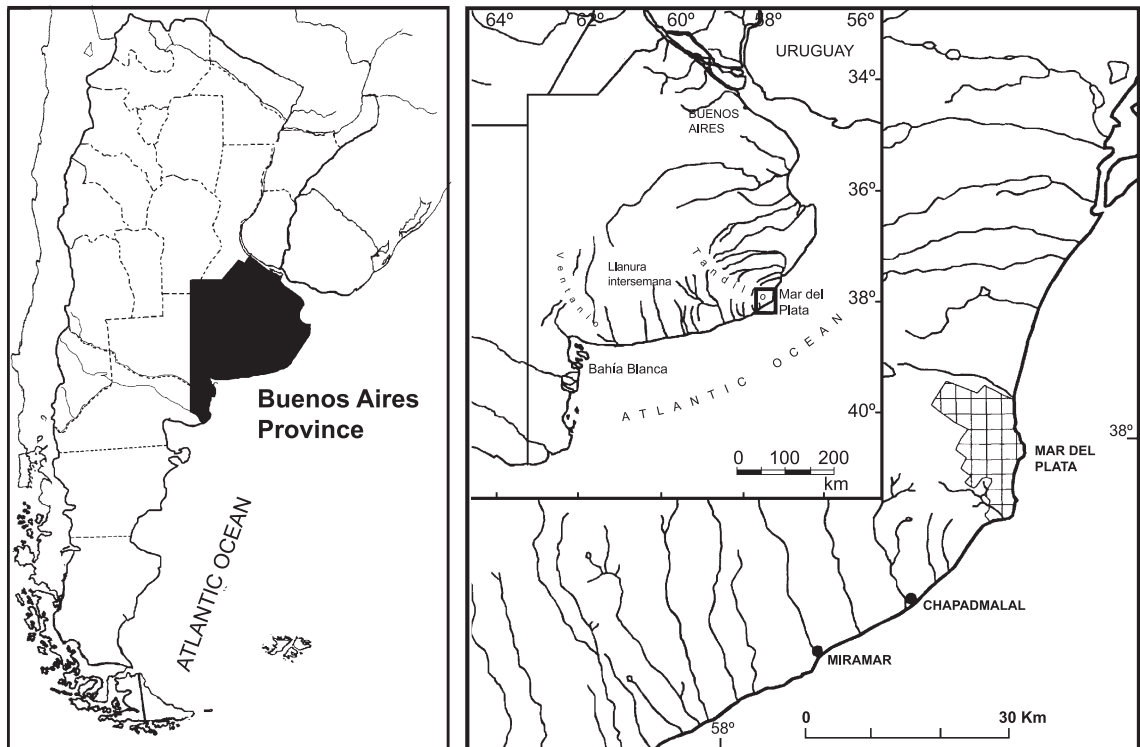


Fig. 1. Map of the Mar del Plata area, Buenos Aires Province, Argentina.

Table 1

Record of taxa during the Chapadmalalan and the Barrancalobian stages, taken from literature (see text Material and methods, Faunal lists)

Taxa	CH	BL
<i>Marsupialia</i>		
Microtragulidae		
<i>Microtragulus reigi</i>	x	x
<i>Argyrolagus scagliai</i>	x	–
Didelphidae		
<i>Lutreolina tracheia</i>	x	–
<i>Thylophrops chapalmalensis</i>	x	x
<i>Didelphis reigi</i>	x	–
<i>Didelphis crucialis</i>	x	–
<i>Hyperdidelphis inexpectata</i>	x	–
<i>Thylatheridium cristatum</i>	x	x
Thylacosmilidae		
<i>Thylacosmilus atrox</i>	x	–
Sparassocynidae		
<i>Sparassocynus derivatus</i>	x	x
<i>Xenarthra</i>		
Dasyopodidae		
<i>Doellotatus chapalmalensis</i>	x	– ^a
<i>Macrochorobates chapalmalensis</i>	x	– ^a
<i>Chorobates recens</i>	x	x
<i>Macroeuphractus retusus</i>	x	–
<i>Macroeuphractus outesi</i>	x	–
<i>Plaina intermedia</i>	x	–
<i>Ringueletia simpsoni</i>	x	x
<i>Tolypeutes</i> sp. A	x	–
<i>Tolypeutes</i> sp. B	–	x
<i>Pampatherium</i> sp.	x	x
<i>Chaetophractus villosus</i>	x	x
<i>Zaedyus pichiy</i>	x	x
Glyptodontidae		
<i>Plohophorus</i> sp. A	x	–
<i>Plohophorus</i> sp. B	–	x
<i>Plohophorus figuratus</i>	x	–
<i>Plohophoroides conterminus</i>	x	–
<i>Hoplophractus</i> sp.	–	x
<i>Urotherium</i> sp.	x	x
<i>Urotherium simplex</i>	x	–
<i>Trachycalyptus chapadmalensis</i>	x	x
<i>Paraglyptodon chapadmalensis</i>	x	–
Megatheriidae		
<i>Pronothrotherium typicum</i>	x	–
<i>Diheterocnus sanmartini</i>	x	–
<i>Plesiomegatherium</i> sp.	x	–
Mylodontidae		
<i>Proscelidodon patrius</i>	x	–
<i>Glossotheridium chapadmalense</i>	x	–
<i>Glossotherium</i> sp.	x	x
<i>Scelidotheridium parodii</i>	x	x
<i>Scelidotheridium</i> sp.	x	x
<i>Scelidodon copei</i>	–	x
<i>Rodentia</i>		
Cricetidae		
<i>Akodon kermacki</i>	x	x
<i>Reithrodon auritus</i>	x	–
<i>Graomys doriae</i>	x	–
<i>Dankomys simpsoni</i>	x	–
<i>Dankomys vorohuensis</i>	–	x
Echimyidae		
<i>Eumysops</i> sp.	x	x

Table 1 (continued)

Taxa	CH	BL
<i>Rodentia</i>		
Octodontidae		
<i>Actenomys</i> sp.	x	x
<i>Pithanotomys</i> sp.	x	x
<i>Eucoelophorus chapalmalensis</i>	x	– ^a
Myocastoridae		
<i>Paramyocastor diligens</i>	x	–
Caviidae		
<i>Palaeocavia</i> sp.	x	x
<i>Orthomyctera</i> sp.	x	x
<i>Neocavia depressidens</i>	x	–
<i>Caviodon australis</i>	x	–
<i>Dolicavia minuscula</i>	x	x
<i>Cardiomys australis</i>	x	–
<i>Microcavia</i> sp.	x	x
<i>Dolichotis</i> sp.	x	x
Hydrochoeridae		
<i>Protohydrochoerus perturbidus</i>	x	–
<i>Chapalmatherium novum</i>	x	x
Dinomyidae		
<i>Telicomys gigantissimus</i>	x	–
Chinchillidae		
<i>Lagostomus</i> sp.	x	x
<i>Carnivora</i>		
Procyonidae		
<i>Cyonasua lutaria</i>	x	–
<i>Chapalmalania ortognatha</i>	x	– ^a
<i>Litopterna</i>		
Proterotheriidae		
<i>Brachytherium</i> sp.	x	–
<i>Neolicaphrium</i> sp.	x	–
Macraucheniiidae		
<i>Promacrauchenia</i> sp.	–	x
<i>Promacrauchenia chapalmalense</i>	x	–
<i>Notoungulata</i>		
Toxodontidae		
<i>Xotodon</i> sp.	x	–
<i>Toxodon</i> sp.	–	x
<i>Toxodon chapalmalensis</i>	x	–
Mesotheriidae		
<i>Pseudotypotherium</i> sp.	x	x
Hegetotheriidae		
<i>Paedotherium typicum</i>	x	x
<i>Paedotherium bonaerense</i>	x	x
<i>Tremacyllus impresus</i>	x	x
<i>Artiodactyla</i>		
Tayassuidae		
<i>Argyrohyus chapadmalensis</i>	x	–
<i>Platygonus scagliai</i>	–	x
Camelidae		
<i>Lama</i> sp.	–	x

^a Recorded in next stage, Vorohuean.

1.2. Geologic Framework

The sedimentary record exposed along the Chapadmalal sea cliffs consists of sandy silts and silty sands which have been traditionally regarded as loess deposits, reworked and redistributed by fluvial and slope processes. The occurrence of pedogenic features throughout the succession permits to infer that soil

formation was a dominant process during sedimentation with several distinct paleosols laterally traceable for several kilometres indicating major intervals of landscape stability. Calcrete crusts and carbonate nodules typify the sedimentary record and originated by both pedogenesis and groundwater. Bioturbation structures constitute another remarkable characteristic of the Chapadmalal succession ranging from 2- to 3-cm-long meniscate and massive invertebrate tubules to vertebrate burrows and caves between 15–20 cm and 120 cm of diameter (Zárate, 1989). The mineralogical composition is dominated by plagioclase, volcanic shards, quartz and volcanic lithics, thereby implicating an Andean source (Teruggi, 1957). The most striking features of the sedimentary record are the escorias (glassy materials) and tierras cocidas that occur at a stratigraphic layer of the Pliocene section, which have been recently interpreted as the result of an impact event (Schultz et al., 1998).

As can be seen in Table 2, the sedimentary succession was divided into eight lithostratigraphic units (Kraglievich, 1952, 1953). However, their identification was mostly based on their faunal assemblages rather than their lithology, which is remarkable homogeneous throughout. Instead, several allostratigraphic units were identified constrained by paleosols and erosional unconformities (Zárate, 1989). More recently, based on the available information Cione and

Tonni, (1995a,b) divided the fossil mammal record into four stages ages, which basically followed the former subdivision of Kraglievich (1952).

The time span recorded by the Chapadmalal succession has been inferred from magnetostratigraphic analysis which yielded a Gilbert magnetic age between ca. 3.4 and >3.98 Ma for the lower section (Chapadmalalan stage) (Orgeira, 1990; Orgeira and Valencio, 1984). Recently, the Ar/Ar date of ca. 3.3 Ma obtained from escoria glasses (Schultz et al., 1998) allowed reinterpreting the magnetic age of the Playa San Carlos Alloformation (lower section of the Chapadmalal Formation, stratigraphically below the magnetostratigraphic profile of Orgeira and Valencio, 1984) as most likely deposited between 4 and 5 Ma (Zárate et al., 1998a). The impact event mentioned above as recorded by the escorias is stratigraphically located in paleosol P6 of the Playa Los Lobos Alloformation (Fig. 2). This roughly encompasses the upper section of the Chapadmalal Formation between 2 and 4 m below the boundary between the Punta Martínez de Hoz and Playa Los Lobos Alloformations. The 2- to 4-m-thick stratigraphic interval between the escoria-bearing unit containing fossil remains from the Chapadmalalan assemblage and the lowermost section of the Punta Martínez de Hoz Alloformation (bearing Barrancalobian fossil fauna) is a key segment for studying the proposed faunal turnover since it is

Table 2
Stratigraphic subdivisions of the Chapadmalal succession based on different criteria

Lithostratigraphic units (formation) Kraglievich (1952, 1953)	Allostratigraphic units (alloformation) Zárate (1989)	Land mammal ages (Marshall et al. 1984)	Chronostratigraphic units (stages, *substages) (Cione and Tonni, 1995a,b)
Holocene deposits	Arroyo Lobería	Holocene deposits	
Lobería		Lujanian	Lujanian
Santa Isabel	Punta San Andrés		
Arroyo Seco			
Miramar			
San Andrés			
Vorohué	Punta Martínez de Hoz	Uquian	* Sanandresian
Barranca de los Lobos			Marplatan
Chapadmalal	Playa Los Lobos	Chapadmalalan	* Barrancalobian
	Playa San Carlos		Chapadmalalan

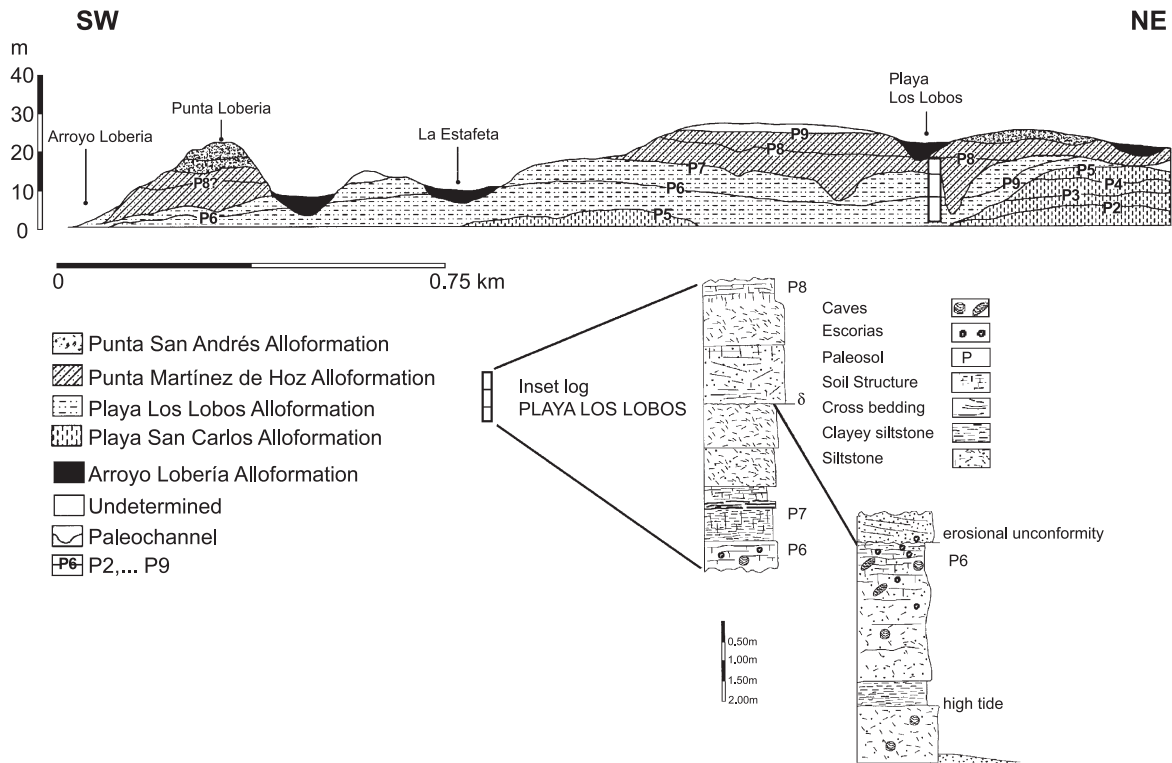


Fig. 2. Stratigraphic section of the Chapadmalal succession north of arroyo Lobería and inset log of Playa Los Lobos.

registering the Chapadmalalan/ Barrancalobian boundary. However, no detailed biostratigraphic analysis has been carried out so far. Thus, at this stage of our knowledge, the faunal turnover can be roughly bracketed between 3.3 ± 0.1 Ma (numerical age of the escoria glass) and 3.22 Ma (end of the Mammoth subchron recorded in the lower section of the Punta Martínez de Hoz Alloformation).

2. Materials and methods

2.1. Faunal lists

The lists of taxa used (Table 1) were taken from the literature, mainly from the exhaustive compilation of Tonni et al. (1992) and updated with the revision chapters (Tambussi, 1995; Goin, 1995; Scillato-Yané et al., 1995; Vucetich and Verzi, 1995; Pardiñas, 1995; Bond et al., 1995; Menegaz and Ortiz Jaureguizar, 1995) of the volumes edited by Alberdi and Leone et

al. (1995) and Tonni and Cione, (1999) and some specific articles (Quintana, 1998; Verzi et al., 2002).

At a very detailed scale, some constrains partially hinders the analysis. The stratigraphic boundaries of these units are poorly defined at field scale, making the stratigraphic location of fossil remains close to the boundary and their assignment to a particular stage-age unit difficult and sometimes subjective. A considerable number of the specimens previously collected have no detailed stratigraphic locations. Additionally, the Barrancalobian crops out in the upper part of the sea cliff, thereby making the main sections difficult to reach and thus have been less prospected. Finally, bioturbation structures of rodents and big mammals add further complications, since many fossil remains come from caves and burrows which are stratigraphically transgressive (Genise, 1989; Scognamillo et al., 1998; Peña, 1997; Zárate et al., 1998b). Hence, the study undertaken on the available database provides a preliminary and general picture of the faunal turnover.

2.2. Palaeoecology

When available, body mass estimations were taken from the literature (Tonni and Noriega, 1998; Bond, 1999, Elissamburu, 2001; Vizcaino and De Iuliis, 2003). Otherwise, skeletal remains of specimens of each species housed in the Museo de La Plata were geometrically compared with living analogues, which gave us estimates precise enough for the kind of calculation we make here. Those species whose masses were estimated as less than 10 kg were not considered in order to avoid the problem of the biases in fossilization, preservation and collection (Behrensmeyer and Hill, 1980; Damuth, 1982; Fariña, 1996; Palmqvist et al., 2003). On the other hand, those species of body mass estimated at more than 100 kg were assigned this figure, as further refinement would have changed very little the results. To estimate the population density of each herbivorous species, the general equation in Damuth (1981) was used:

$$\log D = -0.75 \log m + 4.23$$

where D is population density in number of individuals per square kilometre, and m is the body mass expressed in grams. This empirical equation was obtained from the study of many diverse modern ecosystems (Damuth, 1981). The standard error of the slope is 0.026. If the average minus one S.E. were used rather than -0.75 , there would be no important differences in the results. The basal metabolic rate of these herbivores was calculated following the equation in Peters (1983):

$$\log R = -0.25 \log m + 0.6128$$

where R is the per-second mass-specific metabolic rate (in $\text{J kg}^{-1} \text{s}^{-1}$), and m is the body mass expressed in grams.

In the case of the carnivores, their density was calculated after the equation in Damuth (1993) for African flesh eaters (same symbols as above):

$$\log D = -0.64 \log m + 2.23.$$

An appropriate equation, also quoted by Peters (1983), was used to estimate the basal metabolic rate

of these species of the order Carnivora (same symbols as above):

$$\log R = -0.27 \log m + 0.6551.$$

Tayassuids were considered omnivores, and therefore half their consumption was counted in each category. The on-crop biomass for each species was then obtained by multiplying the calculated popula-

Table 3

Species in the Chapadmalalan, their body mass (kg), on-crop biomass (kg km^{-2}) and basal metabolic rate ($\text{J kg}^{-1} \text{s}^{-1}$)

	Body mass (kg)	On-crop biomass (kg km^{-2})	Basal metabolic rate ($\text{J kg}^{-1} \text{s}^{-1}$)
<i>Chapadmalalan herbivore species</i>			
<i>Ringueletia simpsoni</i>	40	240.2	1.630
<i>Pampatherium</i> sp.	>100	302.0	1.297
<i>Plohophorus</i> sp. A	>100	302.0	1.297
<i>Plohophorus figuratus</i>	>100	302.0	1.297
<i>Plohophoroides conterminus</i>	>100	302.0	1.297
<i>Urotherium</i> sp.	>100	302.0	1.297
<i>Urotherium simplex</i>	>100	302.0	1.297
<i>Trachycalyptus chapadmalensis</i>	>100	302.0	1.297
<i>Paraglyptodon chapadmalalensis</i>	>100	302.0	1.297
<i>Pronothrotherium typicum</i>	>100	302.0	1.297
<i>Diheterocnus sanmartini</i>	>100	302.0	1.297
<i>Plesiomegatherium</i> sp.	>100	302.0	1.297
<i>Proscelidodon patrius</i>	>100	302.0	1.297
<i>Glossotheridium chapadmalense</i>	>100	302.0	1.297
<i>Scelidothidium parodii</i>	>100	302.0	1.297
<i>Scelidothidium</i> sp.	>100	302.0	1.297
<i>Protohydrochoerus perturbidus</i>	>100	302.0	1.297
<i>Chapalmatherium novum</i>	>100	302.0	1.297
<i>Telicomys gigantissimus</i>	>100	302.0	1.297
<i>Brachytherium</i> sp.	15	187.9	2.083
<i>Neolicaphrium</i> sp.	40	240.2	1.630
<i>Promacrauchenia chapadmalense</i>	>100	302.0	1.297
<i>Xotodon</i>	>100	302.0	1.297
<i>Toxodon chapadmalensis</i>	>100	302.0	1.297
<i>Pseudotypotherium</i> sp.	80	285.6	1.371
<i>Argyrohyus chapadmalensis</i>	50	151.0	1.542
<i>Chapadmalalan carnivore species</i>			
<i>Thylacosmilus atrox</i>	95	10.5	1.322
<i>Cyonasua lutatia</i>	>100	10.7	1.303
<i>Chapalmalania ortognatha</i>	>100	10.7	1.303
<i>Macroeuphractus retusus</i>	>100	10.7	1.303
<i>Macroeuphractus outesi</i>	>100	10.7	1.303
<i>Argyrohyus chapadmalensis</i>	50	8.3	1.572
<i>Psilopterus</i> sp.	40	7.7	2.039
<i>Hermosiornis rapax</i>	70	9.4	2.144
<i>Cathartidae</i> gen. et sp. nov.	24	6.4	6.111

tion density by its body mass. The energy requirements for each species (Tables 3 and 4) were obtained by multiplying its on-crop biomass by its basal metabolic rate.

2.3. Extinction

Taxa not recorded in the Barrancalobian but present in the following lower and upper strata were not considered extinct for this analysis. Differences in extinction rates between three chosen categories of size (smaller than 10 kg of body mass, between 10 and 100 kg, and larger than this figure) were assessed using a χ^2 . The same analysis was applied to assess the proneness to extinctions of those taxa according to their trophic habits, i.e., herbivorous, omnivorous and carnivorous (Lessa and Fariña, 1996; Lessa et al., 1997). A complementary analysis involving a stepwise, maximum likelihood logistic regression was also performed (see Lessa and Fariña, 1996; Lessa et al., 1997).

3. Results

3.1. Palaeoecology

In the Chapadmalalan, 18% or 50% of the mammals were estimated to have had a body mass under 10 kg, 12% or 17.6% between 10 and 100 kg and 22% or 32.4% above that figure. The figures for the Barrancalobian were smaller but percentages were comparable: 22 (52.4%), 8 (19.0%) and 12 (28.6%), respectively.

The mammals of body masses greater than 10 kg found in both Chapadmalalan and Barrancalobian faunas are listed in Tables 3 and 4, respectively. In the first case (Table 3), there are 25 species of herbivores, one omnivore and five mammalian carnivores (although the phororhacid birds *Psilopterus* sp. and *Hermosiornis rapax* were included in the calculations, as well as a very large fossil condor). Almost two-thirds of the herbivores (16) are edentates: one armadillo (*Ringueletia simpsoni*), one pampatherium (*Pampatherium* sp.), seven glyptodonts (*Plohophorus* sp. A, *Plohophorus figuratus*, *Plohophoroides conterminus*, *Urotherium* sp., *Urotherium simplex*, *Trachycalyptus chapadmalensis* and *Paraglyptodon*

Table 4

Species in the Barrancalobian, their body mass (in kg), on-crop biomass (in kg km⁻²) and basal metabolic rate (J kg⁻¹ s⁻¹)

	Body mass (kg)	On-crop biomass (kg km ⁻²)	Basal metabolic rate (J kg ⁻¹ s ⁻¹)
<i>Barrancalobian herbivore species</i>			
<i>Ringueletia simpsoni</i>	40	240.2	1.630
<i>Pampatherium</i>	>100	302.0	1.297
<i>Plohophorus</i> sp. B	>100	302.0	1.297
<i>Hoplophractus</i> sp.	>100	302.0	1.297
<i>Urotherium</i> sp.	>100	302.0	1.297
<i>Trachycalyptus chapadmalensis</i>	>100	302.0	1.297
<i>Glossotherium</i> sp.	>100	302.0	1.297
<i>Scelidotheridium parodii</i>	>100	302.0	1.297
<i>Scelidotheridium</i> sp.	>100	302.0	1.297
<i>Scelidodon copei</i>	>100	302.0	1.297
<i>Chapalmatherium novum</i>	>100	302.0	1.297
<i>Promacrauchenia</i> sp.	>100	302.0	1.297
<i>Toxodon</i> sp.	>100	302.0	1.297
<i>Pseudotypotherium</i> sp.	80	285.6	1.297
<i>Platygonus scagliai</i>	>100	302.0	1.297
<i>Lama</i> sp.	>100	302.0	1.297
<i>Barrancalobian carnivore species</i>			
<i>Chapalmalania ortognatha</i>	>100	13.8	1.081
<i>Platygonus scagliai</i>	>100	302.0	1.297

chapadmalensis), and seven sloths (*Pronothrotherium typicum*, *Diheterocnus sanmartini*, *Plesiomegathierium* sp., *Proscelidodon patrius*, *Glossotheridium chapadmalense*, *Scelidotheridium parodii*, *Scelidotheridium* sp.). The list is completed by three rodents (the hydrocherids *Protohydrochoerus perturbidus* and *Chapalmatherium novum*, and the dymomyid *Telicomys gigantissimus*), three litopterns (*Brachytherium* sp., *Neolicaphrium* sp. and *Promacrauchenia chapadmalense*) and three notoungulates (the toxodontids *Xotodon* sp. and *Toxodon chapadmalensis*, and the mesotheriid *Pseudotypotherium* sp.). There is one herbivore–omnivore artiodactyl, the tayasuid *Argyryohyus chapadmalensis*. The procyonids *Cyonasua lutatia* and *Chapalmalania ortognatha*, and the armadillos *Macroeufractus retusus* and *Macroeufractus outesi* are considered carnivore–omnivores. The only strict carnivore is the marsupial sabretooth *Achlysictis lelongi*.

In the Barrancalobian (Table 4), there are 16 species of herbivores, one omnivore and only one mammalian carnivore (and no avian carnivore found).

Again, more than half of the herbivores (10) are edentates: one armadillo (*Ringueletia simpsoni*), one pampatherid (*Pampatherium* sp.), four glyptodonts (*Plohophorus* sp. B, *Hoplophractus* sp., *Urotherium* sp. and *Trachycalyptus chapadmalensis*), four sloths (*Glossotherium* sp., *Scelidotheridium parodii*, *Scelidotheridium* sp. and *Scelidodon copei*). There are also one rodent (the hydrocherid *Chapalmatherium novum*), one litoptern (*Promacrauchenia* sp.), two notoungulates (the toxodontid *Toxodon* sp. and the mesotheriid *Pseudotypotherium* sp.) and one artiodactyl, the camelid *Lama* sp. There is one omnivore artiodactyl, the tayasuid *Platygonus scagliai*. Although there is no certain record of carnivorous mammals, following our assumption, they would be represented only by the procyonid *Chapalmalania ortognatha*.

The on-crop biomass for each species was estimated by multiplying the calculated population density by its body mass. The energy requirements for each species (Tables 3 and 4) were then obtained by multiplying its on-crop biomass by its basal metabolic rate. Following the normal values recorded for living mammals, a typical assimilation efficiency of 50% (of the edible material) was considered, and average actual maintenance metabolism was taken to be 2.5 times the basal rate (Peters, 1983). Adding up the requirements of all the species considered, and converting the units, it follows that the Chapadmalalan herbivores must have needed some 1.6 MJ m⁻² year⁻¹, or 29 g C m⁻² year⁻¹ to fulfill their requirements. In turn, the Barrancalobian herbivores must have needed 0.96 MJ m⁻² year⁻¹, or 17.6 g C m⁻² year⁻¹. The requirements of carnivores were 22.1 and 3.3 kJ m⁻² year⁻¹ for the Chapadmalalan and the Barrancalobian, respectively, as habitat secondary productivity to bear their basal metabolism.

3.2. Extinction

Thirty seven percent of the genera and 53% of the species recorded in the Chapadmalalan are not found in the Barrancalobian or upper Marplatian substages. Among them, differences in the proneness to extinction according to size ($\chi^2=3.54$; $p>0.17$; $df=2$) or trophic habits ($\chi^2=0.53$; $p>0.77$; $df=2$) were not granted when a contingency table was used, although the logistic regression did yield

significant results in the first case ($p<0.0067$). At the ordinal ($\chi^2=2.65$; $p>0.85$; $df=6$) and familial ($\chi^2=13.05$; $p>0.95$; $df=23$) levels, all groups were found to have no statistically significant differences in their proneness to extinction.

4. Discussion

4.1. Palaeoecology

According to our model, the Chapadmalalan fauna is rich in the number of species. Thus, those mammals must have required a rather high primary productivity, about 26.5 MJ m⁻² year⁻¹, or 480 g C m⁻² year⁻¹ if large herbivores consumed 6% or less of the primary productivity, as in modern mammalian faunas (Owen-Smith, 1988). Using McNaughton et al.'s (1989) equations, which are based on on-crop biomass, primary productivity must have been 19 MJ m⁻² year⁻¹, or 340 g C m⁻² year⁻¹. Both values correspond to very productive habitats, similar to today's tropical savannas (Margalef, 1980). Very large predatory birds were also included in the calculations, as they must have preyed upon the mammals. Their population density and metabolic rates were conservatively (Nagy, 2001) calculated as for mammals of the same size. The metabolism of the condor was calculated after the equations in Palmqvist et al. (1996). This fauna seems to be reasonably well balanced in terms of its secondary productivity and the requirements of the carnivores. This is because the requirements of the carnivores are not much below the secondary productivity or even closer, as calculated using McNaughton et al.'s (1989) equations (Table 5). Smaller than average populations or lower metabolic rates, perhaps in Xenarthra (McNab, 1980, 1989; Vizcaino, submitted for publication), may account for that disparity. Although the appropriate figures fit very well in both present day and northern hemisphere Pleistocene faunas, as La Brea in North America (Fariña, 1996) and Venta Micena in Europe (Palmqvist et al., 2003), the balance found here is much better than in the other South American fossil fauna studied (the Pleistocene Luján local fauna), where difference in favour of secondary productivity were fourfold (Fariña, 1996).

Table 5
Energetics of the two faunas studied in this paper

Requirements of the herbivores in Chapadmalalan	1.6 MJ m ⁻² year ⁻¹
Requirements of the carnivores in Chapadmalalan	22 kJ m ⁻² year ⁻¹
Secondary productivity of Chapadmalalan	36 kJ m ⁻² year ⁻¹
Secondary productivity of Chapadmalalan (McNaughton et al., 1989)	27 kJ m ⁻² year ⁻¹
Requirements of the herbivores in Barrancalobian	0.96 MJ m ⁻² year ⁻¹
Requirements of the carnivores in Barrancalobian	3.3 kJ m ⁻² year ⁻¹
Secondary productivity of Barrancalobian	24 kJ m ⁻² year ⁻¹
Secondary productivity of Barrancalobian (McNaughton et al., 1989)	19 MJ m ⁻² year ⁻¹

On the other hand, Barrancalobian fauna represents a relatively poorer environment. This inference is on the primary productivity, which must have been between 15 and 20 MJ m⁻² year⁻¹, the range depending on whether McNaughton et al.'s (1989) equations or Peters', (1983) model is used. Those values, however, correspond to a rather productive habitat, twice as rich as a good quality present day cattle field (Cayssials, 1979). Moreover, this fauna was highly unbalanced in terms of the herbivore–carnivore relationships. Indeed, secondary productivity is about five to eightfold greater than the requirements of the predators.

4.2. The Barranca de los Lobos Paradox

The Barrancalobian name refers to the Barranca de los Lobos site, the type locality of the Barranca de los Lobos Formation according to Kraglievich (1952). As indicated above, it is part of the cliffs by the Atlantic Ocean at the southeastern coast of Buenos Aires Province. A literal translation of Barranca de los Lobos from Spanish to English would be “Wolves’ Cliff,” which might suggest a great abundance of those carnivorans. Paradoxically, wolves do not presently exist in the region or in the rest of South American subcontinent. Indeed, the name refers to sea lions (*Otaria flavescens*, Mammalia: Carnivora: Pinnipedia), or “lobos marinos” in Spanish, which used to

be found there but are not no longer settled in the area. This paradox also applies to the Pliocene, because one of the most relevant features of the Barrancalobian fauna, as it is known today, is the absence of medium to large carnivores, both mammals and birds.

Although there were some carnivores among the Barrancalobian marsupials, they were small forms (less than 10 kg). The largest is one Sparassocynidae that must have occupied the adaptive zone of the mustelids or the Australian dasyurids (Goin, 1995). In spite of the probable presence of a large procyonid, hard evidence indicates that other placental carnivores, such as mustelids (*Galictis*) and canids (*Pseudalopex* and *Canis*), are recorded for the first time at the Vorohuean substage (Vorohue Formation), and the large felids (*Smilodon* and *Felis*) and ursids (*Arctotherium*) in the Ensenadan (Miramar Formation).

Among birds, the last phorroracids are recorded in the Upper Chapadmalalan. They belong to two different groups, the Hermosiorinithinae (*Hermosiorinis rapax*) and the Psilopterinae (*Psilopterus* sp.). The species belonging to the genus *Hermosiorinis* are medium-size phorroracids considered predators or alternatively scavengers on large carcasses (Tonni and Noriega, 1998). In addition, a large condor is also known from those levels. Only a herbivorous ratite (Tinamiformes) is known from the Barrancalobian levels, which probably reflects a record defect (Tambussi, 1995).

4.3. Extinction

As noted above, 37% of all genera and 53% of all species became extinct, which qualifies for a mass extinction of intermediate level according to the criterion proposed by Sepkoski (1986) at a global scale. Such a level is actually higher than the percentage of genera extinct at the Cretaceous–Tertiary event.

Both theory and observations in other extinction events predict that large animals become extinct at higher proportions than smaller ones (Martin and Klein, 1984; Benton, 1990; Raup, 1993; Lessa and Fariña, 1996; Lessa et al., 1997). Also, carnivores have been proposed (and observed) to be more likely to go extinct than species of lower trophic levels (Patterson, 1984). Therefore, it is rather surprising that

in the case studied here no difference has been found in the proportion of extinctions among mammals of different trophic habits. It should be noted that little change in the statistical figures is obtained if *Macro-euphractus* spp. or the procyonids are assigned different habits. In the case of body size, results are less clear, as this variable did not seem to be related when a contingency table was used but it did when a nonlinear model (logistic regression) was applied. Another intriguing result is that taxonomic groups go extinct at the same rate as the whole set at the order or family levels, suggesting an extrinsic factor among the possible causes of this turn over.

Several factors have been suggested as the possible causes triggering the Pliocene faunal turnover. [Tonni et al. \(1992\)](#) and [Cione and Tonni \(1995a,b\)](#) interpreted the Chapadmalalan/Barrancalobian faunistic change in response to climatic changes. According to these authors, the remarkable number of mammal caves of different sizes found at the Chapadmalalan beds (also present but not as abundant in the Barrancalobian) suggest arid environments. [Cione and Tonni, \(1995a,b\)](#) stated “that the local climatic indicators of the Chapadmalal “Formation” are in agreement with the global climatic changes indicating a cold period during part of the late Pliocene followed by a climatic amelioration”.

A different interpretation is proposed by [Ortiz Jaureguizar et al. \(1995\)](#). They suggested that the Chapadmalalan/Barrancalobian faunal turnover is associated with the global climatic change observed at the 2.6 to 2.4 Ma interval ([Berggren, 1972](#); [Shackleton and Kennett, 1975](#)) when warm and humid conditions dominant during the Chapadmalalan shifted towards cold and arid conditions prevalent in the Barrancalobian. They remark again that the presence of numerous rodent caves in the Chapadmalalan diminish in the Barrancalobian, which would indicate the beginning of arid and cold conditions.

The faunal turnover just above the escoria-bearing layer is intriguing. [Schultz et al. \(1998\)](#) pointed out that the time of the impact event coincides with “a pulselike change in the deep-sea stable isotopic record, reflecting a sudden change in climate and ocean circulation”. This suggests that “the impact may have directly induced regional faunal extinctions or triggered broader environmental changes leading to ecosystem collapse”.

More recently, [Cione and Tonni \(2001\)](#) added new interpretations on the causes of the faunal turnover. They pointed out that the Chapadmalalan/early Marplatán turnover seems to be caused not by competition with North American immigrants but by an important tectonic event (Diaguita orogenic phase) that triggered important environmental modifications throughout southern South America.

Sedimentological analysis and paleosol morphology now allow interpreting the depositional environment of the lower Chapadmalal beds between 3.3 and 4–5 Ma. These beds record environmental conditions characterized by high water availability, at least enough for the leaching of calcium carbonate from soil systems. The upper Chapadmalalan beds represented by the Playa de los Lobos Alloformation are composed of some paleosols with carbonate nodules and loess facies. Such precipitates would suggest slightly greater water deficiency relative to conditions represented in the lower Chapadmalalan section. The lower section of Punta Martínez de Hoz (younger than 3.3 Ma and older than the Kaena event), however, represents a demonstrably drier environment than both lower sections with seasonality and unstable climatic conditions during its deposition ([Zárate, 1989](#)). These interpretations do not support the arid environments pointed out by [Tonni et al. \(1992\)](#) and [Cione and Tonni \(1995a,b\)](#). Moreover, [Peña \(1997\)](#) points out that present-day ecological factors (predation, reproduction, competition) demonstrate that factors other than climate may have accounted for the occurrence of caves and burrows. Paleoclimatic inferences by [Ortiz Jaureguizar et al., \(1995\)](#) are more in agreement with those resulting from the sedimentology, at least for the lower section of the Chapadmalalan beds. The magnetic ages proposed for a section of the Chapadmalal Formation ([Orgeira, 1990](#)) along with the new magnetic ages based on the numerical ages ([Zárate et al., 1998a](#)) however, do not support the correlation of the Chapadmalalan record with the 2.6–2.4 Ma global changes ([Ortiz Jaureguizar et al., 1995](#)), which should be recorded in the upper beds of the Marplatán (Vorohuean and Sanandresian beds).

Although the size of the probable Chapadmalalan impact crater remains unknown, the large sizes of the impact glass and their regional distribution suggest a diameter of at least 5–10 km ([Schultz et al., 1998](#)). A crater of this size is unlikely to have induced a global extinction since much larger craters are known with-

out severe biologic consequences (e.g., Chesapeake Bay and Popigai impacts at 35 Ma; Poag, 2002). Smaller impacts could induce temporary deterioration of the climate with consequent patterns of faunal disappearance proportional to body size. The absence of such a record just above the Chapadmalalan sequences, however, suggests a devastation consistent with faunal lethality produced by being close to the event. In this case, local faunal stress would have been induced not only by the impact itself (blast, etc.) but also by the drastic changes in the landscape comparable to a volcanic eruption. This change in habitat would have extended well beyond 10 crater radii thereby affecting most of the middle Pliocene age fauna exposed south of Mar del Plata. The consequence should have affected fauna of all body sizes, consistent with our observations, although a trend of opportunistic reinvasion of smaller, faster recovering species is also likely and congruent with our results. The dramatic change in landscape (new drainage, new habitats) should have changed the surviving faunal assemblages. Possible impact induced climate changes augmented by the deteriorating Pliocene climate (Schultz et al., 1998), which then could have permanently altered rehabilitation. Such speculation can be tested by careful and systematic studies of the fossil record.

4.4. *Caveats and prospects*

The Barrancalobian and the subsequent Vorohuean and Sanandresian are considered as substages of the Marplatan stage (Cione and Tonni, 1995a). Correlation with other areas different from the coast of Buenos Aires Province are mandatory if the extinction represents an event at the local, regional or continental scale. According to Cione and Tonni (1995a), other beds that might be correlated with this part of the Chapadmalalan and Marplatan ages would be the lower and upper parts of the Uquía Formation, respectively, although this reference does not provide evidence for differentiating levels that could correlate with those subages. However, studies in progress (Reguero et al., 2003) point out that the lower section of the Uquía Formation is assigned to the Late Chapadmalalan, the middle section to the Late Vorohuean and Sanandresian, and the upper section to the Ensenadan. This evidence precludes correlation

with the Barrancalobian and prevents detailed comparisons at the present. Equally importantly, the Uquía Formation outcrops in a high altitude mountain setting of northwestern Argentina, about 2000 km from the Chapadmalal sea cliffs. Taxonomic differences could be easily attributed to geographical and environmental reasons. New fossil collections considering all these potential problems will provide a more complete and accurate picture of this remarkable faunal turnover.

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