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Ancient feeding, ecology and extinction of Pleistocene horses from the Pampean Region, Argentina

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Abstract. To reconstruct the diet and habitat preference of fossil horses, we measured the carbon and oxygen isotope composition of 35 bone and tooth samples of *Equus* (*Amerhippus*) *neogeus* Lund, *Hippidion principale* (Lund), and *Hippidion devillei* (Gervais) from 10 different Pleistocene localities in the Pampean region (Argentina). To compare the three species by stratigraphic age, we divided the samples into three groups: lower Pleistocene, middle-late Pleistocene and latest Pleistocene. Samples of *Hippidion devillei* from the lower Pleistocene were more homogeneous, with $\delta^{13}C$ values ranging between -11.73 to -9.79‰. These data indicate a diet exclusively dominated by C_3 plants. In contrast, *Hippidion principale* and *Equus* (*Amerhippus*) *neogeus* from middle-late Pleistocene showed a wide range of feeding adaptations (with a range of $\delta^{13}C$ values between -12.05 to -8.08 ‰ in *Hippidion* and $\delta^{13}C$ values between -11.46 to -7.21 ‰ in *Equus* (*Amerhippus*)). These data seem to indicate a mixed C_3 - C_4 diet, while data from the latest Pleistocene suggest a tendency toward an exclusively C_3 diet for both species. Furthermore, the results of $\delta^{18}O$ indicate an increase of approximately 4ºC from the early to latest Pleistocene in this area. Several nutritional hypotheses explaining latest Pleistocene extinctions are based on the assumption that extinct taxa had specialized diets. The resource partitioning preference of these species from latest Pleistocene in the Pampean region supports these hypotheses.

Resumen. PALEODIETA, ECOLOGÍA Y EXTINCIÓN DE LOS CABALLOS DEL PLEISTOCENO DE LA REGIÓN PAMPEANA, ARGENTINA. Para comprender las variaciones en la dieta de los équidos, hemos analizado la composición isotópica del oxígeno y del carbono del carbonato en 35 restos fósiles de *Equus* (*Amerhippus*) *neogeus* Lund, *Hippidion principale* (Lund) e *Hippidion devillei* (Gervais) procedentes de 10 localidades del Pleistoceno de la Región Pampeana (Argentina). Para poder comparar las variaciones temporales de los resultados isotópicos, hemos agrupado las muestras según su procedencia estratigráfica en tres grupos: Pleistoceno inferior, Pleistoceno medio y superior y Pleistoceno tardío. Los datos indican que las muestras del Pleistoceno temprano de *Hippidion devillei* son las más homogéneas, con un rango de variación de los valores de $\delta^{13}C$ entre -11,73 y -9,79‰. Estos resultados sugieren una dieta compuesta exclusivamente por plantas C_3. Por el contrario los resultados de las muestras de *Hippidion principale* y *Equus* (*Amerhippus*) *neogeus* del Pleistoceno medio y superior presentan un mayor rango de variación (con valores de $\delta^{13}C$ entre -12,05 y -8,08 ‰ para *Hippidion* y valores de $\delta^{13}C$ entre -11,46 y -7,21 ‰ para *Equus*). Estos resultados indican una adaptación a una dieta mixta C_3-C_4. Por su parte los especímenes del Pleistoceno tardío muestran nuevamente una tendencia hacia una dieta compuesta exclusivamente por plantas de tipo C_3 para ambas especies. Además, los resultados de $\delta^{18}O$ registran un aumento en la temperatura de alrededor 4 ºC en el área de estudio desde el inicio del Pleistoceno hasta el final. Algunos autores sugieren que un estrés nutricional, producto de un cambio rápido en las comunidades vegetales, podría ser una de las causas que expliquen la extinción del final del Pleistoceno. La especialización que observamos en la dieta en los caballos del final del Pleistoceno podría ser una evidencia en favor de esta teoría.

Key words. *Equus* (*Amerhippus*). *Hippidion.* Paleodiet. Ecology. Extinction. Pleistocene. Pampean region. South America.

Palabras clave. *Equus* (*Amerhippus*). *Hippidion.* Paleodieta. Ecología. Extinción. Pleistoceno. Región Pampeana. América del Sur.

Introduction

The Equidae family in South America is represented by two genera, *Hippidion* and *Equus* (*Amerhippus*). Both genera can be differentiated by their small and large forms, probably as a consequence of having adapted to similar environments. These immigrant genera dispersed into South America using two different routes. During the Plio-Pleistocene, two corridors developed that shaped the paleobiogeographic history of most of the North American mammals in South America (Webb, 1991). The most viable model postulated for the horse's dispersal process seems to indicate that the small forms utilized the Andes corridor, while larger horses dispersed through the Eastern route and through some coastal areas. The Pampean Region represents the most austral distribution for large horses that dispersed through the Eastern route, while the group of small horses that arrived as far as the southern

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Patagonia dispersed via the Western route. The dispersal route of each form seems to reflect an adaptive shift in their ecology (Alberdi and Prado, 1992; Alberdi *et al.*, 1995). Recently, a similar pattern of dispersion in South America was postulated for gomphotheres (Sánchez *et al.*, 2004).

Horses have been recorded in the Pampean Region from the late Pliocene to the latest Pleistocene (Alberdi and Prado, 1993; Prado and Alberdi, 1994). Three species are recognized: *Equus* (*Amerhippus*) *neogeus* Lund, 1840, *Hippidion principale* (Lund, 1846), and *Hippidion devillei* (Gervais, 1855).

In this paper we compare the results of carbon and oxygen isotopic composition from tooth, enamel, dentine and bone of these three species of equids, in order to determine the paleodiet and habitat preferences of Pleistocene horses in the Pampean Region, and show how variations in these preferences may have been related to their extinction.

Isotopic background

Previous studies have shown that the carbon isotope ratio ($\delta^{13}C$) of fossil teeth and bones can be used to obtain dietary information about extinct herbivores (De Niro and Epstein, 1978; Vogel, 1978; Sullivan and Krueger, 1981; Lee-Thorp *et al.*, 1989, 1994; Koch *et al.*, 1990, 1994; Quade *et al.*, 1992; Cerling *et al.*, 1997; MacFadden, 2000). This carbon isotope ratio is influenced by the type of plant material ingested, which is in turn influenced by the photosynthetic pathway utilized by the plants. During photosynthesis, C_3 plants in terrestrial ecosystems (trees, bushes, shrubs, forbs, and high elevation and high latitude grasses) discriminate more markedly against the heavy ^{13}C isotope during fixation of CO_2 than do tropical grasses and sedges (C_4 plants). Thus, C_3 and C_4 plants have different $\delta^{13}C$ values. C_3 plants have $\delta^{13}C$ values of -22 per mil (‰) to -30‰, with an average of approximately -26‰, whereas C_4 plants have $\delta^{13}C$ values of -10 to -14‰, with an average of about -12‰ (Smith and Epstein, 1971; Vogel *et al.*, 1978; Ehleringer *et al.*, 1986, 1991; Cerling *et al.*, 1993). Animals then incorporate carbon from food into their tooth and bone with an additional fractionation of 12 to 14‰. Mammals feeding on C_3 plants (fruit, leaves, etc.) characteristically have $\delta^{13}C$ values between about -10 and -16‰, while animals that eat C_4 tropical grasses (including blades, seeds, and roots) have $\delta^{13}C$ values between +2 and -2‰. A mixed-feeder would fall somewhere in between these two extremes (Lee-Thorp and van der Merwe, 1987; Quade *et al.*, 1992). Hence, the relative proportions of C_3 and C_4 vegetation in an animal diet can be determined by analyzing its teeth and bone $\delta^{13}C$.

In recent decades, there has been an increasing use of oxygen and carbon isotope analyses to reconstruct paleoenvironmental and paleoclimatical conditions. In the case of homeothermic animals in general, the oxygen isotope composition of apatite depends primarily on the oxygen balance of the animal (Longinelli, 1984; Luz *et al.*, 1984). Influxes of oxygen include ingested water (drinking water + water from plants) as well as inspired O_2 gas; oxygen is lost from the body as liquid water in urine, sweat, and feces, and as CO_2 and H_2O in respiratory gases. Factors acting on this balance are both internal (related to the physiology of the animal) and external (related to ecology and to climate). Oxygen isotope variations in large mammals depend largely on external factors such as the $\delta^{18}O$ of ingested water. Because the oxygen isotopic composition of phosphate in mammalian bones and teeth ($\delta^{18}O_p$) is related to that of ingested water, and ingested water comes ultimately from precipitation, the $\delta^{18}O$ of enamel and bone phosphate can be used to infer past climatic conditions (Longinelli and Nuti, 1973; Kolodny *et al.*, 1983; D'Angela and Longinelli, 1990; Bryant *et al.*, 1994; Sánchez *et al.*, 1994; Bryant and Froelich, 1995; Delgado *et al.*, 1995; Kohn, 1996; Kohn *et al.*, 1996, 1998).

Material and methods

Sampled area. The Pampa Plains contains extensive formations of superficial sand and loess that are known as the Pampean Formation (Teruggi, 1957). Paleomagnetic stratigraphy and radiometric data suggest that most of this formation was deposited over the last 3.3 Ma. (Schultz *et al.*, 1998). The stratigraphy of pampean loess typically consists of superposed beds, 1-2 m thick, separated by either erosional discontinuities or palaeosols. The majority of these palaeo-aeolian features lie in areas presently supporting vegetation communities dominated by grassland. Most of the late Pleistocene and Holocene deposits were assigned to either the Luján Formation (including three members: La Chumbiada, Guerrero and Río Salado) or to the La Postrera Formation (Fidalgo *et al.*, 1973, 1975, 1991; Dillon and Rabassa, 1985). Luján deposits are fluvial-lacustrine and those of La Postrera are eolian. The eolian deposits, which cover extensive parts of the southern Pampean Region, are comprised of sandy loess, very fine sand sheets, and dunefields (Zárate and Blasi, 1993).

At present, the Pampean plains has a subtropical climate, wich varies from humid in the east to arid in the west. This climatic pattern reflects the dominant effects of the ocean in the southern half of South America (Iriondo and García, 1993). The mean annu-

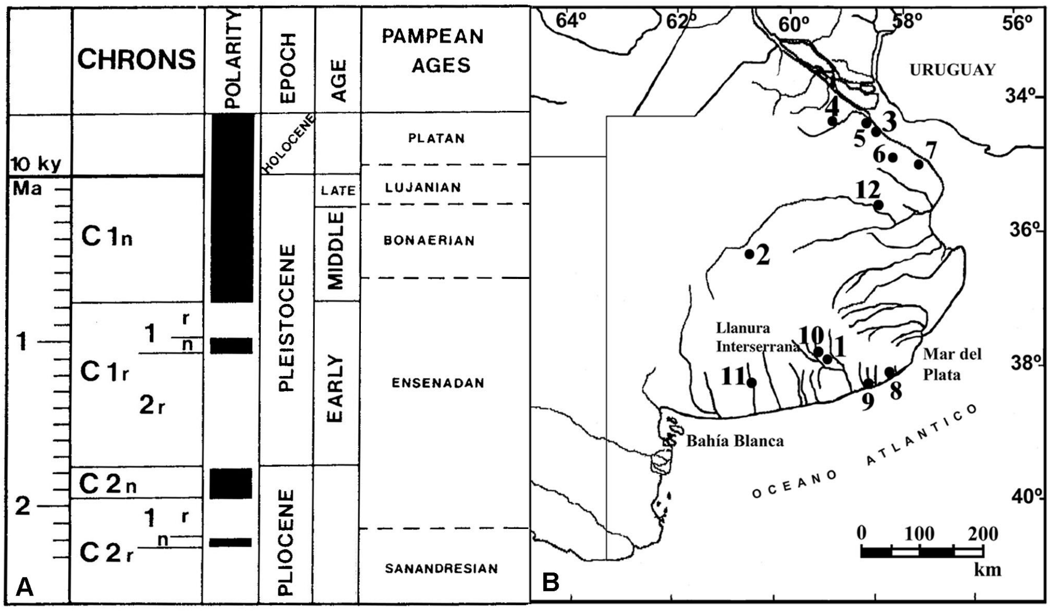

Figure 1. A, Pleistocene to Holocene chronology and mammal biostratigraphy of Pampean Region following Cione and Tonni (1999). The Holocene is not in scale. **B,** Geographical distribution of analyzed samples of horses from the Pleistocene of Buenos Aires Province (Argentina). 1: Quequén Grande; 2: Arroyo Tapalqué; 3: Buenos Aires; 4: Río Luján; 5: Olivos; 6: Cantera Vialidad Provincial; 7: Magdalena; 8: Punta Hermengo; 9: Centinela del Mar; 10: Zanjón Seco; 11: Río Quequén Salado; 12: Río Salado / ***A,*** *Cronología y bioestratigrafía de los mamíferos del Pleistoceno al Holoceno de la Región Pampeana siguiendo a Cione y Tonni (1999). El Holoceno no está a escala.* ***B,*** *Distribución geográfica de las muestras analizadas de los caballos procedentes del Pleistoceno de la provincia de Buenos Aires (Argentina). 1: Quequén Grande; 2: Arroyo Tapalqué; 3: Buenos Aires; 4: Río Luján; 5: Olivos; 6: Cantera Vialidad Provincial; 7: Magdalena; 8: Punta Hermengo; 9: Centinela del Mar; 10: Zanjón Seco; 11: Río Quequén Salado; 12: Río Salado.*

al temperatures is approximately 17°C and mean annual precipitation is around 800 mm.

In order to recognize the Ensenadan, Bonaerian, Lujanian and Platan ages, Cione and Tonni (1995, 1999) proposed several biozones for the Pleistocene and Holocene sedimentary rocks of the Pampean Region. Most of the *Equus* (*Amerhippus*) and *Hippidion* remains come from the localities assigned to these ages (figure 1).

Samples selection. Thirty-five horse samples from 10 different South American Pleistocene localities in the Pampean Region were measured to obtain oxygen and carbon isotopic composition of bone and tooth enamel carbonate (figure 1). Fossil samples were collected from specimens stored at the Museo de La Plata (MLP) and the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN). The museum collection number and the locality of each sample are reported in table 1. In order to complete the discussion we also included previously published results by Sánchez *et al.* (2003) for *Stegomastodon platensis* Ameghino, 1888 from the Pampean Region. To compare the different specimens, we divided the samples into three groups, taking into account the age of the corresponding deposits. The three groups are represented in figure 2: (A) lower Pleistocene, (B) middle to late Pleistocene and (C) latest Pleistocene specimens.

Samples preparation and analysis. The samples (including bones) were finely ground in an agate mortar. The chemical pre-treatment of the samples was preformed as described in Koch *et al.* (1997) in order to eliminate secondary carbonate. About 40-50 mg of powdered dentine and bone samples were soaked in 2% NaOCl for three days at room temperature to oxidize the organic matter. Residues were rinsed and centrifuged five times with deionized water, and later treated with 1M acetic acid for one day to remove diagenetic carbonates. Pre-treatment of the enamel differed slightly as samples were soaked in 2% NaOCl for one day only. Carbon dioxide was obtained by reacting approximately 40-50mg of treated powder with 100% H_3PO_4 for five hours at 50°C. This CO_2 was then isolated cryogenically in a vacuum line. Results are reported as $\delta = ([R_{sample}/R_{standard}]-1) \times 1000$, where R= $^{13}C/^{12}C$ or $^{18}O/^{16}O$, and the standards are PDB for carbon and V-SMOW for oxygen. We applied data corrections for calcite to calculate the magnitude of the oxygen isotopic fractionation between apatite CO_2 and H_3PO_4 at 50°C (Koch *et al.*, 1989). Analytical precision for repeated analyses was 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{18}O$.

Statistical analyses. We performed both parametric (t-test) and nonparametric (Wilcoxon Signed-Rank) statistical tests to evaluate $\delta^{13}C$ and $\delta^{18}O$ differences in middle and late Pleistocene populations, accepting the null hypothesis of no differences among means unless $p < 0.05$. SPSS 11.0 software was used for the statistical analysis.

Analytical results and discussion

Previous results of carbon isotope analyses of *Stegomastodon platensis* from the Pampean Region suggest they had various types of feeding preferences throughout the Pampean record (Sánchez *et al.* 2003, 2004). Initial evaluation and analysis of $\delta^{13}C$ showed that horses also developed various different feeding patterns over the same record.

Parametric (t-test) and non-parametric (Wilcoxon) statistical tests (table 2) confirm significant differences between *Equus* (*Amerhippus*) and *Hippidion* $\delta^{13}C$ values (t-test = 2.58, p = 0.022; Wilcoxon, *Z* = -2.10, *p* = 0.036). These results indicate that the two genera must be considered separately throughout the record.

Samples from the lower Pleistocene suggest that *Hippidion devillei* fed mostly on C_3 plants, while *Stegomastodon platensis* were mostly mixed-feeders (figure 2). Substantial differences in isotopic composition are also observed between gomphotheres and horses from the middle to the latest Pleistocene. There are also significant $\delta^{13}C$ differences between *Equus* (*Amerhippus*) *neogeus* and *Stegomastodon platensis* (t-test = -2.88, p = 0.011; Wilcoxon, Z = -2.58, p = 0.010), and between *Hippidion principale* and *Stegomastodon platensis* (t-test = -3.05, p = 0.019; Wilcoxon, *Z* = -2.24, *p* = 0.025). During this time interval, *Stegomastodon platensis* had a mixed diet, confirmed by more homogeneous isotopic values, ranging from -9.08 to -6.09 ‰. In contrast, both horses exhibit a wide range of dietary adaptations (between -12.05 to -8.08 ‰ for *Hippidion principale* and between -11.50 to -7.20 ‰ for *Equus* (*Amerhippus*) *neogeus*), that indicate they changed from a mixed C_3 -C_4 diet to an exclusively C_3 diet (table 3).

Samples from the latest Pleistocene show that there are no significant differences between horses (t-test=0.35, p=0.752; Wilcoxon, Z=0.37, p=0.751) or between horses and gomphotheres (between *Hippidion*

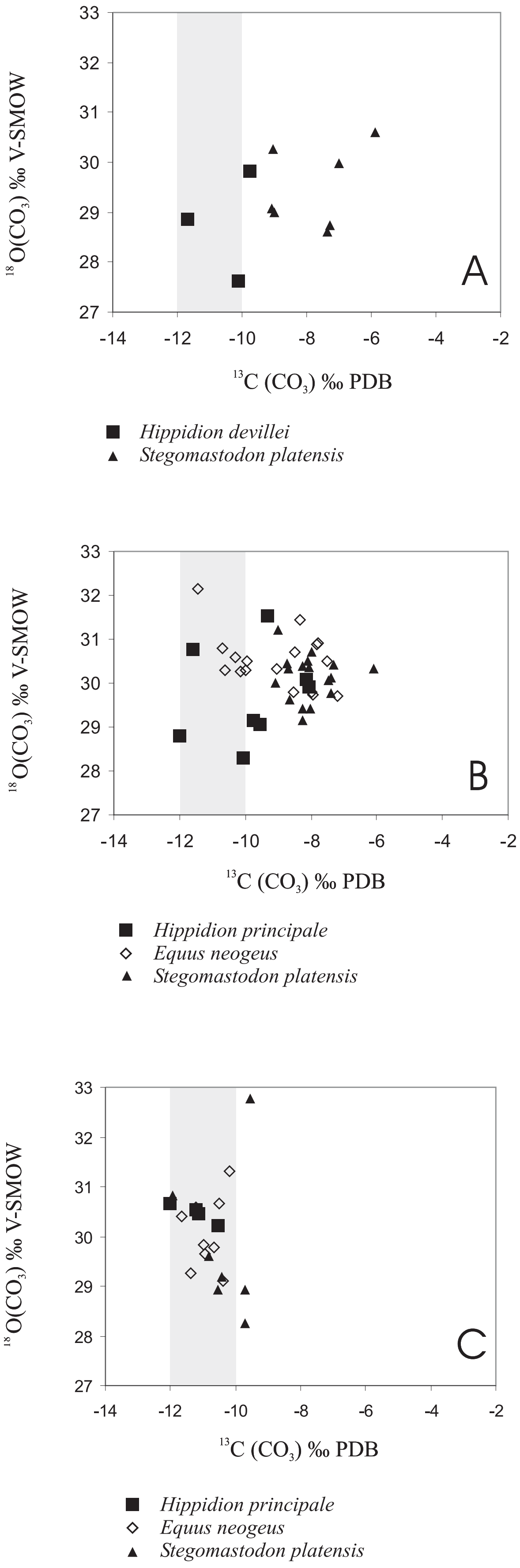

Figure 2. $\delta^{13}C$ *versus* $\delta^{18}O$ for: **A, *Hippidion devillei*** and ***Stegomastodon platensis*** from lower Pleistocene; **B, *Hippidion principale*, *Equus* (*Amerhippus*) *neogeus*** and ***Stegomastodon platensis*** from middle-late Pleistocene; **C, *Hippidion principale*, *Equus* (*Amerhippus*) *neogeus*** and ***Stegomastodon platensis*** from latest Pleistocene of Buenos Aires Province (Argentina) / *$\delta^{13}C$ versus $\delta^{18}O$ para:* ***A,* Hippidion devillei** *y* **Stegomastodon platensis** *del Pleistoceno inferior;* ***B,* Hippidion principale**, **Equus (Amerhippus) neogeus** *y* **Stegomastodon platensis** *desde el Pleistoceno medio al superior;* ***C,* Hippidion principale, Equus (Amerhippus) neogeus** *y* **Stegomastodon platensis** *del Pleistoceno final de la provincia de Buenos Aires (Argentina).*

Table 1. $\delta^{18}O$ and $\delta^{13}C$ isotopic values for skeletal elements of ***Hippidion devillei***, ***Hippidion principale*** and ***Equus*** **(*Amerhippus*)** ***neogeus*** from Pampean Region. e = enamel; d = dentine; b = bone; t = tooth (enamel + dentine). Skeletal samples with the same specimen number correspond to the same individual. * taken from MacFadden *et al.* (1996, 1999) / *resultados isotópicos de* $\delta^{18}O$ *y* $\delta^{13}C$ *de las muestras analizadas de* **Hippidion devillei**, **Hippidion principale** *y* **Equus (Amerhippus) neogeus** *de la Región Pampeana. e = esmalte; d = dentina; b = hueso; t = diente (esmalte + dentina). Las muestras con el mismo número corresponden a un mismo individuo. * datos tomados de MacFadden* et al. *(1996, 1999).*

Species name (age)	Specimen number	Skeletal tissue	Locality	Latitude (°S)	$\delta^{13}C$ (CO_3) ‰ PDB	$\delta^{18}O$ (PO_4) ‰ V-SMOW	$\delta^{18}O$ (CO_3) ‰ PDB	$\delta^{18}O$ (CO_3) ‰ V-SMOW
Equus sp. (middle-late Pl)*	AMNH.11154	e	Buenos Aires	35	-10,7		-0,1	30,8
Equus sp. (middle-late Pl)*	AMNH.11154	e	Buenos Aires	35	-10,3		-0,3	30,6
Equus sp. (middle-late Pl)*	MLP.91.VI.5-1	e	Magdalena	35	-10,6		-0,6	30,3
E. neogeus (middle-late Pl)	MLP s/s	t	Cant. Vial. Prov.	35	-7,51	21,24	-0,40	30,5
E. neogeus (middle-late Pl)	MLP s/s	b	Cant. Vial. Prov.	35	-11,46	20,76	1,19	32,1
E. neogeus (middle-late Pl)	MACN 6116	t	Arroyo Tapalqué	38	-8,52	17,27	-1,07	29,8
E. neogeus (middle-late Pl)	MACN 6116	b	Arroyo Tapalqué	38	-7,94	21,21	-1,14	29,7
E. neogeus (middle-late Pl)	MLP s/s	t	Punta Hermengo	38	-7,21	20,10	-1,18	29,7
E. neogeus (middle-late Pl)	MLP s/s	t	Centinela del Mar	38	-9,99	19,11	-0,60	30,3
E. neogeus (middle-late Pl)*	MLP.52.X.5-3	e	Rio Quequén Salado	38	-8,5		-0,2	30,7
E. neogeus (middle-late Pl)*	MLP.52.X.5-3	e	Rio Quequén Salado	38	-7,8		0	30,9
E. neogeus (middle-late Pl)	MACN 9753	e	Rio Quequén Salado	38	-9,93	21,26	-0,39	30,5
E. neogeus (middle-late Pl)	MACN 9753	d	Rio Quequén Salado	38	-10,13	21,26	-0,62	30,3
E. neogeus (middle-late Pl)	MACN 9753	b	Rio Quequén Salado	38	-7,98	20,39	-1,08	29,8
E. neogeus (middle-late Pl)	MACN 9751	b	Rio Quequén Salado	38	-7,81	21,01	-0,04	30,9
E. neogeus (middle-late Pl)	MACN 9751	d	Rio Quequén Salado	38	-8,34	22,86	0,52	31,4
E. neogeus (middle-late Pl)	MLP 63-VI-1017	b	Rio Quequén Salado	38	-9,03	20,67	-0,58	30,3
E. neogeus (latest Pl)	MACN 11636	b	Río Luján	35	-11,66	21,24	-0,49	30,4
E. neogeus (latest Pl)	MLP 6-402	b	Río Luján	35	-11,20	20,12	-0,32	30,6
E. neogeus (latest Pl)	MLP 80-VIII-13-63	b	Paso Otero	38	-11	18,41	-1,04	29,8
E. neogeus (latest Pl)	MLP 80-VIII-13-4	b	Paso Otero	38	-10,65	20,13	-1,09	29,8
E. neogeus (latest Pl)*	MLP.80.VIII.13-93	e	Paso Otero	38	-10,2		0,4	31,3
E. neogeus (latest Pl)	MACN 14417	d	Zanjón Seco	38	-11,39	20,27	-1,60	29,3
E. neogeus (latest Pl)	MACN 14417	t	Zanjón Seco	38	-10,40	21,11	-1,74	29,1
E. neogeus (latest Pl)	MACN 14417	e	Zanjón Seco	38	-10,51	21,20	-0,23	30,7
E. neogeus (latest Pl)	MACN 14417	b	Zanjón Seco	38	-10,94	19,86	-1,22	29,7
H. devillei (early Pl)	MACN 2140	t	Olivos	23	-9,79	21,53	-1,03	29,8
H. devillei (early Pl)	MACN 2138	t	Olivos	23	-11,73	20,24	-1,96	28,9
H. devillei (early Pl)	MACN 2155	b	Olivos	23	-10,16	19,68	-3,15	27,7
H. principale (middle-late Pl)	MACN 1735	t	Arroyo Tapalqué	38	-9,79	20,19	-1,67	29,2
H. principale (middle-late Pl)	MACN 5265	b	Arroyo Tapalqué	38	-9,61	20,09	-1,76	29,1
H. principale (middle-late Pl)	MACN 1734	t	Arroyo Tapalqué	38	-9,37	22,11	0,62	31,5
H. principale (middle-late Pl)	s/s	b	Arroyo Tapalqué	38	-11,64	19,54	-0,12	30,8
H. principale (middle-late Pl)	MACN 5667	t	Río Salado	36	-12,05	19,82	-2,02	28,8
H. principale (middle-late Pl)	MACN 5667	b	Río Salado	36	-10,1	19,87	-2,50	28,3
H. principale (middle-late Pl)	MACN 5056	b	Río Salado	36	-8,16	20,19	-0,78	30,1
H. principale (middle-late Pl)	MACN 9739	b	Rio Quequén Salado	38	-8,08	21,18	-0,94	29,9
H. principale (latest Pl)	MACN 10441	e	Río Luján	35	-10,6	21,16	-0,65	30,2
H. principale (latest Pl)	MACN 10441	d	Río Luján	35	-12,06	20,86	-0,22	30,7
H. principale (latest Pl)	MLP 6-364	b	Río Luján	35	-11,28	19,52	-0,34	30,6
H. principale (latest Pl)	MACN 6092	b	Río Luján	35	-11,16	21,67	-0,41	30,5

1 taken from MacFadden *et al.* (1994)
2 taken from MacFadden and Shockey (1997)
3 taken from MacFadden *et al.* (1996)
* taken from MacFadden *et al.* (1999)

principale and *Stegomastodon platensis* (t-test = -2.61, p = 0.80; Wilcoxon, Z=-1.83, p = 0.068; and between *Equus* (*Amerhippus*) *neogeus* and *Stegomastodon platensis* (t-test =-0.82, p = 0.437; Wilcoxon, Z=-0.84, p =0.401). These results indicate that the three species were mostly C_3 grazers.

Table 2. Descriptive statistics for twelve compared groups of pampean horses and gomphotheres. **A, *Equus* (*Amerhippus*)**, all specimens. **B, *Hippidion*,** all specimens. **C, *Hippidion devillei*,** all specimens. **D, *Hippidion principale*,** all specimens. **E, *Hippidion principale*** from middle-late Pleistocene. **F, *Hippidion principale*** from latest Pleistocene. **G, *Equus* (*Amerhippus*) *neogeus*** from middle-late Pleistocene. **H, *Equus* (*Amerhippus*) *neogeus*** from latest Pleistocene. **I, *Stegomastodon platensis*,** all specimens. **J, *Stegomastodon platensis*** from lower Pleistocene. **K, *Stegomastodon platensis*** from middle-late Pleistocene. **L, *Stegomastodon platensis*** from latest Pleistocene / *Análisis estadísticos realizados para la comparación de doce grupos de caballos y gonfoterios pampeanos. A,* **Equus (Amerhippus)**, *todos los ejemplares. B,* **Hippidion**, *todos los ejemplares. C,* **Hippidion devillei**, *todos los ejemplares. D,* **Hippidion principale**, *todos los ejemplares. E,* **Hippidion principale** *del Pleistoceno medio y superior. F:* **Hippidion principale** *del Pleistoceno final. G,* **Equus (Amerhippus) neogeus** *del Pleistoceno medio y superior. H,* **Equus (Amerhippus) neogeus** *del Pleistoceno final. I,* **Stegomastodon platensis**, *todos los ejemplares. J,* **Stegomastodon platensis** *del Pleistoceno inferior. K,* **Stegomastodon platensis** *del Pleistoceno medio y superior. L,* **Stegomastodon platensis** *del Pleistoceno final.*

	Groups	n	Mean $\delta^{13}C$ (‰) PDB	SD ‰	Min ‰	Max ‰	Mean $\delta^{18}O$ (‰)V-SMOW	SD ‰	Min ‰	Max ‰
Equus total	A	26	-9,68	1,40	-11,70	-7,20	30,36	0,69	29,11	32,14
Hippidion total	B	15	-10,37	1,28	-12,06	-8,08	29,75	1,05	27,66	31,55
H. devillei	C	3	-10,56	1,03	-11,73	-9,79	28,80	1,10	27,66	29,85
H. principale	D	12	-10,32	1,38	-12,06	-8,08	29,98	0,94	28,33	31,55
H.p. middle-late	E	8	-9,85	1,43	-12,05	-8,08	29,73	1,07	28,33	31,55
H.p. latest	F	4	-11,27	0,60	-12,06	-10,60	30,49	0,19	30,24	30,68
E.n. middle-late	G	17	-9,04	1,31	-11,50	-7,20	30,51	0,63	29,69	32,14
E.n. latest	H	9	-10,88	0,48	-11,66	-10,20	30,07	0,72	29,11	31,32
Stegomastodon total	I	32	-8,63	1,47	-12,11	-5,90	30,00	1,07	28,25	33,19
St. early	J	7	-7,80	1,24	-9,06	-5,90	29,46	0,80	28,60	30,60
St. middle-late	K	17	-8,04	0,75	-9,08	-6,09	30,13	0,52	29,15	31,21
St. latest	L	8	-10,60	1,00	-12,11	-9,56	30,21	1,87	28,25	33,19

Mean $\delta^{18}O$ results range between 28.8‰ and 30.5‰, but there are no significant differences among the mean $\delta^{18}O$ values for the stratigraphical intervals considered. The overall range of the total mean isotopic values for equids is approximately 1.7‰. Based on the equation for living horses (Delgado *et al.*, 1995), the isotopic values indicate a total range of the environmental water isotopic composition is this area to be approximately 2.9‰. If we translate the data into temperatures, bearing in mind that the Dansgaard equation is calculated for northern Europe (Dansgaard, 1964), we obtain approximate temperature values and are able to compare them with current temperatures. So, the range of $\delta^{18}O$ (H_2O) calculated for the equids of the Pampean Region would correspond to a variation of 4.2°C in annual mean temperatures from early to latest Pleistocene. For example, current annual mean temperature range from 13.4° in Mar del Plata city (38° S), 16.4°C for Buenos Aires city (34°S), to 19.2°C in Santa Fé city (32°S). Our results indicate that the interval of mean temperature variation inferred for the Pleistocene is in the same order of variation as current temperature variation (at 6° of latitude). Sánchez and Alberdi (1996) report similar results for pampean gomphotheres.

Our results indicate that a relationship exists between the extinction of large mammals and their dietary preferences. Currently, Quaternary extinction of large mammals is explained by two main groups of accepted theories. One group of theories attributes large mammal extinction to climatic and ecological changes, while the other group holds man's hunting activities responsible.

The most widely accepted hypothesis related to climatic and ecological factors postulates that nutritional stress induced by rapid changes in plant communities may have been a primary cause of extinction (Graham and Lundelius, 1984; King and Saunders, 1984). This model implies that large mammals died off because they were specialized feeders, adapted to certain kinds of plants that may have disappeared during the Holocene. With this in mind, Guthrie (1984) hypothesized that plant diversity was greater, and the growing season longer, in the Pleistocene than in the Holocene. These changes in plant diversity and growing season may have affected the large mammal populations that were specialist feeders. In addition, Vrba (1993) suggests that herbivores might be more vulnerable to changes in climate that affect vegetation structure, while omnivores would be less affected as they are more able to adapt to different types of food and habitats.

The Pleistocene was characterized by rapid and repeated climatic fluctuations that caused the formation and retreat of massive continental glaciers in southern South America. The fact that large mammal extinctions in this region occurred at the same time as

Table 3. Results of parametric (t - Test) and non-parametric (Wilcoxon Signed Rank) test performed on 13 paired comparisons between horse and gomphothere groups from Pampean Region. For definition of groups see table 2 / *test de significación paramétrico (t - Test) y no-paramétrico (Wilcoxon Signed Rank) de los resultados obtenidos de las comparaciones entre los grupos de caballos y gonfoterios de la Región Pampeana tomados dos a dos.*

Variable	Comparison groups	t-test *p*	Nonparametric *p*
$\delta^{13}C$	A *vs.* B	0,022	0,036
$\delta^{13}C$	A *vs.* I	0,051	0,064
$\delta^{13}C$	B *vs.* I	0,796	0,099
$\delta^{13}C$	C *vs.* J	0,106	0,109
$\delta^{13}C$	G *vs.* E	0,383	0,575
$\delta^{13}C$	G *vs.* K	0,011	0,010
$\delta^{13}C$	E *vs.* K	0,019	0,025
$\delta^{13}C$	H *vs.* F	0,752	0,715
$\delta^{13}C$	H *vs.* L	0,437	0,401
$\delta^{13}C$	F *vs.* L	0,080	0,068
$\delta^{13}C$	E *vs.* F	0,168	0,114
$\delta^{13}C$	C *vs.* F	0,083	0,109
$\delta^{13}C$	E *vs.* C	0,257	0,180
$\delta^{18}O$	A *vs.* B	0,058	0,078
$\delta^{18}O$	A *vs.* I	0,389	0,209
$\delta^{18}O$	B *vs.* I	0,083	0,570
$\delta^{18}O$	C *vs.* J	0,998	1,000
$\delta^{18}O$	G *vs.* E	0,218	0,263
$\delta^{18}O$	G *vs.* K	0,038	0,076
$\delta^{18}O$	E *vs.* K	0,565	0,674
$\delta^{18}O$	H *vs.* F	0,221	0,273
$\delta^{18}O$	H *vs.* L	0,921	0,889
$\delta^{18}O$	F *vs.* L	0,007	0,068
$\delta^{18}O$	E *vs.* F	0,606	0,465
$\delta^{18}O$	C *vs.* F	0,145	0,109
$\delta^{18}O$	E *vs.* C	0,498	0,593

the major climatic deterioration associated with the last glacial cycle, has prompted considerable speculation about the extent to which these events are causally related (Borrero, 1984; Politis and Prado, 1990). During the latest Pleistocene to earliest Holocene in the Pampean Region, all megamammals (over 1 t) and a majority of large mammals (over 44 kg) suffered massive extinctions. Recent studies (Lessa and Fariñas, 1996; Lessa *et al.*, 1997) based on late mammals from America, corroborate the idea that large body mass is the only factor strongly associated with the probability of extinction. Based on late mammals from the Pampean Region, Prado *et al.* (2001a, 2001b) analyzed the quantitative relationship between climatic changes and mammal diversity, and corroborated the vulnerability of large mammals to extinction.

The second group of theories hypothesises that large mammal extinction was a direct result of man and his hunting activities. Among this group, Politis and Gutiérrez (1998) identified three main models: the first postulated by Martin (1967, 1973, 1984), proposed that the extinction of large mammals from North America, South America and Australia was related to sudden human expansion into these continents. This "overkill" hypothesis is supported by the synchronism of extinction with the arrival of large numbers of humans to these continents and by mathematical simulation (Alroy, 2001). Recently, Cione *et al.* (2003) suggested that the main cause of the extinction in South America was due to human overhunting but was also influenced by climatic changes and reduction of open areas. Large mammals were adapted to the dry and cold climate and open areas that predominated in South America during Pleistocene. The periodic interglacial increases in temperature and humidity may have provoked shrinking of open areas and reduction of the biomass of mammals adapted to these habitats. The authors refer to this alternation of low and high biomass of animals from opened and closed areas as the "Broken Zig-Zag".

The archaeological record from the Pampean Region shows that Pleistocene mammals were common in Paleo-Indian sites (Miotti and Salemme, 1999). There are several archaeological sites where extinct mammals were recorded: La Moderna, Cerro La China 1, Zanjon Seco 2, Laguna Tres Reyes, Campo Laborde, Arroyo Seco 2 and Paso Otero 5. Each of these sites has special characteristics and different kinds of associations. In particular, the last two sites contain horse remains. Among the nine extinct species found in Arroyo Seco 2, only horses [*Hippidion* and *Equus (Amerhippus)*] and the giant sloth (*Megatherium*) are numerically significant (Politis *et al.*, 1987, 1995). For the early component of this site, three radiocarbon dates were obtained on *Equus* (*Amerhippus*) *neogeus* (AA-7964, with AMS 11250±105 yrs BP; OXA-4590, with AMS 11000 ± 100 yrs BP and TO-1504, with AMS 8890±90 yrs BP). Tonni *et al.* (2003) also present radiocarbon data on *Equus* (*Amerhippus*) *neogeus* from Quequén Grande (the upper part of Guerrero member, Luján Formation) with values of 10290±130 yrs BP (LP-1235). In addition, the datum of 8890 yrs BP provides exact chronological information with regard to the latest record, or taxon-data (Grayson, 1987) of *Equus* (*Amerhippus*) *neogeus*.

The influence of early hunter-gatherers on horses is difficult to quantify. Not enough information is available to evaluate the extent to which the pressure caused by hunting affected the late populations of these species. There is evidence that verifies that humans were present in the Pampean Region around 11,500 yrs B P and that they coexisted with the extinct large mammals for three thousand years or more. Politis *et al.* (1995) suggest that humans played a secondary role in the extinction of the native South American fauna, but had a greater effect on immigrant fauna such as horses and mastodons. Miotti and Salemme (1999) were able to verify evidence of the consumption of horses by the cut marks they found in fossil bone.

It has been difficult for proponents of the climatic hypothesis to isolate a single climatic cause for the extinctions. Climate may have provoked changes in flora communities and as consequence altered herbivores diets and caused heightened periods of competition (Graham and Lundelius, 1984). Also, a shortened growing season at the end of the Pleistocene would have created environmental stress for large mammals (Guthrie, 1984). Although horses may have been able to adapt to any one of these environmental perturbations, the combination of all of them at the same time may have been devastating for species that showed more selective dietary adaptations. Undoubtedly, pressures exerted by hunter-gatherers may have also added to the environmental stresses.

Conclusion

The objective of this study was to reconstruct the ancient diet and habitat preference of *Hippidion devillei*, *Hippidion principale* and *Equus* (*Amerhippus*) *neogeus* from the Pampean Region using carbon and oxygen isotopic composition of teeth and bones. Carbon isotope analyses reveal that these horses had different food adaptations. Due to their high crowned teeth, it has traditionally been thought that horses fed on abrasive grasses. However, carbon isotopic data from the Pampean Region indicate that these horses ranged from mixed feeders to more specialized C_3 grazers. *Hippidion devillei* from lower Pleistocene were principally C_3 grazers. Specimens of *Hippidion principale* and *Equus* (*Amerhippus*) *neogeus* from the middle Pleistocene had a C_3 to mixed C_3-C_4 diet, while specimens from latest Pleistocene were primarily C_3 grazers. These results are partially corroborated by data from the lower to middle Pleistocene from Bolivia (MacFadden and Shockey, 1997; MacFadden, 2000). These authors indicate that horses from Tarija ranged from largely C_4 grazers (*Equus insulatus*) to principally mixed-feeders (*Hippidion principale* and *Hippidion devillei*) which suggests that they may have partitioned their available food resources across a broad spectrum of pastures.

We believe that horses from middle Pleistocene exhibited opportunistic feeding strategies and consequently may have been adapted to diverse habitats, even though the majority of equids from the middle Pleistocene showed a preference for mixed-feeding. In contrast, populations from late Pleistocene appear to have adapted to a more selective diet, which restricted their habitat preference. A similar isotopic pattern was found for *Stegomastodon platensis* from the Pampean Region (Sánchez *et al.*, 2003). The authors propose that gomphotheres were driven to extinction because they were specialized feeders, adapted to a kind of plant that may have disappeared during the Holocene (Sánchez *et al.*, 2004).

Several nutritional hypotheses postulated for latest Pleistocene megamammal extinctions operate under the assumption that extinct taxa had specialized diets. The resource partitioning preference of *Hippidion principale* and *Equus* (*Amerhippus*) *neogeus* from latest Pleistocene in Pampean Region supports these hypotheses.

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