The extinction of Equidae and Proboscidea in South America. A test using Carbon isotope data

Extinción de Equidae y Proboscidea en América del Sur. Un test usando datos de isótopos de carbono

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ABSTRACT

Carbon isotopes, preserved in 166 samples of fossil teeth and bone, provide key data for understanding the ecology of extinct horses and gomphotheres during the Plio-Pleistocene in South America. To analyze the patterns of dietary partitioning throughout this time we divided the samples into 19 groups, taking into account the genus and the age of the corresponding localities. In this study, the diets of both groups are assessed to test extinction hypotheses. The strong resource partitioning among herbivores assumed under Co-evolutionary disequilibrium hypothesis is supported by isotopic data of horses from latest Pleistocene. *Hippidon* and *Equus* had very different diets. In contrast, species of gomphotheres from late Pleistocene in South America seem to have had less specialized diets containing a broad mix of both C_3 and C_4 plants, which is in line with the dietary assumptions of the mosaic-nutrient hypothesis, but does not support the assumptions of Co-evolutionary disequilibrium hypothesis.

Keywords: Late Pleistocene extinction, South America, Proboscidea, Perissodactyla, stable isotope.

RESUMEN

Los isótopos del carbono preservados en 166 muestras de dientes y huesos fósiles son un dato clave para entender la ecología de los de caballos y gonfoterios durante el Plio-Pleistoceno en América del Sur. Para analizar los cambios en las reconstrucciones de la dieta durante este lapso temporal hemos dividido las muestras en 19 grupos, teniendo en cuenta la sistemática y la cronología de cada localidad. En este estudio, las dietas de ambos grupos son evaluadas para probar las hipótesis sobre su extinción. El alto fraccionamiento en el uso de los recursos entre los herbívoros que asume la hipótesis del desequilibrio co-evolutivo es sustentada por los datos isotópicos de los caballos del Pleistoceno tardío. *Hippidion* y *Equus* tenían una dieta muy diferente. En contraste, las especies de gonfoterios de finales del Pleistoceno parecen tener una dieta menos especializada con una combinación de plantas C_3 y C_4, que está en consonancia con los supuestos de la hipótesis del mosaico de nutrientes, pero no admite los supuestos de la hipótesis de desequilibrio Co-evolutivo.

Palabras clave: Extinciones del Pleistoceno tardío, América del Sur, Proboscidea, Perissodactyla, isótopos estables.

Introduction

Gomphothere and horse species arrived in South America during the Great American Biotic Interchange around 3 Ma (Webb, 1991). During this time, two main corridors developed in South America that shaped the biogeography of both groups (Alberdi *et al*., 2011). The model with the greatest support of dispersal and diversification processes postulated seem to indicate that the small forms of both gomphotheres and horses (*Cuvieronius hyodon, Equus andium, Equus insulatus* and *Hippidion*

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saldiasi) utilized the Andes corridor, whereas the large forms of these groups (*Stegomastodon waringi, Stegomastodon platensis, Equus neogeus and Hippidion principale*) utilized the Eastern route and some coastal areas. The route of each form seems to reflect an adaptive shift in their ecology (Alberdi & Prado, 1992; Sánchez *et al*., 2004; Prado *et al*., 2011).

Despite their wide distribution and abundance for most of the Pleistocene, gomphotheres and horses had disappeared from South America, along with many other large animals by the end of this epoch (Barnosky *et al*., 2004). Two types of theories have been offered for this extinction. One of these groups of theories attributes the extinction of large mammals to climatic and ecological changes, while the other holds human hunting activities responsible. Martin (1984) proposed that the extinction of large mammals from North America, South America and Australia is related to various, sudden impacts resulting from human activity. This "overkill" hypothesis is supported by the synchronism of extinction with the arrival of large numbers of humans to these continents. For North America, some authors (Haynes, 2002; Fiedel, 2009) argue that large mammals, especially mastodons and mammoths, were exterminated by Clovis hunters at c. 11 000 years BP. Conversely, the survival of megamammals and large mammals till c. 7000 ^{14}C BP in South America indicate that extinctions would have occurred throughout an extended period (c. 6000-4000 ^{14}C BP) considering the timing of human dispersal in the southern cone of South America (Steele & Politis, 2009). This situation does not provide any support for the *Overkill* and *Blitzkried* models in South America (Gutierrez & Martinez, 2008; Politis & Messineo, 2008; Borrero, 2009; Cione *et al*., 2009).

The archaeological record from South America shows that both gomphotheres and horses were present in Paleo-Indian sites (Borrero, 2008). Gomphotheres appear to have been a human food resource in two areas in central and southern Chile (Dillehay & Collins, 1988; Montane, 1968), and in Venezuela (Bryan *et al*., 1978) they do not appear to have been important for human subsistence. However, bone dates suggest that in many regions of South America, gomphotheres were already gone when the first humans arrived and their continued presence in some areas, especially the Pampean region of Argentina and Uruguay (≈18.5 to ≈22.2 kyr), suggests that these were relict populations

(Alberdi & Prado, 2008; Alberdi *et al*., 2007, 2008; Gutiérrez *et al*., 2005; Prado & Alberdi, 2010). The case for horses is quite different. The archaeological record from South America shows that horses were common in paleoindian sites and some bone remains show cut-marks and helical fractures that indicate human processing (Mengoni Goñalons, 1983; Miotti & Salemme 1999). In fact, horses appear to have been a human food resource in Colombia (Correal Urrego, 1982), Venezuela (Bryan *et al*., 1978), Ecuador (Ficcarelli *et al*., 2003), Brazil (Guérin, 1991), central and southern Chile (Dillehay & Collins, 1988; Montane, 1968; Núñez *et al*., 1994) and southern Patagonia (Alberdi & Prieto, 2000; Alberdi *et al*., 2001; Bird, 1988; Borrero, 2003; Mengoni Goñalons, 1987; Martinic, 1992; Miotti & Salemme, 1999; Nami & Menegaz, 1991).

Authors who doubt the role of human hunting activities often attribute the extinctions to climatic and ecological changes, particularly to nutritional stress induced by rapid changes in plant communities. Climate may have provoked changes in communities of flora and as a result the diets of herbivores were altered, causing heightened periods of competition. Although gomphotheres and 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. The "mosaic-nutrient hypothesis" argues that climate change reduced the growing season and local plant diversity, and also increased plant antiherbivore defenses, all of which reduced the carrying capacity of the environment for herbivores (Guthrie, 1984). A more general hypothesis (the coevolutionary disequilibrium hypothesis) was postulated by Graham & Lundelius (1984) who suggested that the high herbivore diversity of Pleistocene ecosystems was maintained by extensive resource partitioning, analogous to the grazing succession of modern African savannas, and that an extremely rapid glacial-interglacial transition reorganized floras, disrupting this tightly co-evolved system.

Dietary assumptions about Pleistocene herbivores being used in environmental hypotheses it can be tested with stable isotope data (Koch *et al*., 1994). Isotopic analyses can reveal information about resource use and resource partitioning among species and is also able to determine diet and habitat use (Tütken & Vennemann, 2009; Feranec *et al*., 2009). In this study, the diets of gomphotheres and

horses from South America are assessed using carbon isotope analysis to test both hypotheses for extinction.

Isotopic paleoecology in South America

Previous studies have shown that the carbon isotope ratio (δ^{13}C) of fossil teeth and bones can be used to obtain dietary information about extinct herbivores (De Niro & Epstein, 1978; Vogel, 1978; Sullivan & Krueger, 1981; Lee-Thorp *et al*., 1989, 1994; Koch *et al*., 1990, 1994; Quade *et al*., 1992; Cerling *et al*., 1997; MacFadden, 2000a).

Stable carbon and oxygen isotopes are incorporated into the tooth and bone apatite of fossil specimen and are representative, respectively, of the food and water consumed while alive. The 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 altitude and high latitude grasses) discriminate more markedly against the heavy ^{13}C isotope during fixation of CO_2 than C_4 plants (tropical grasses and sedges). Thus C_3 and C_4 plants have distinct δ^{13}C values. C_3 plants usually have δ^{13}C values of -30 per mil (‰) to -22‰, with an average of approximately -26‰, whereas C_4 plants have δ^{13}C values of -14 to -10‰, with an average of about -12‰ (Smith & Epstein, 1971; Vogel *et al*., 1978; Ehleringer *et al*., 1986, 1991; Cerling *et al*., 1993). Animals incorporate carbon isotopes from food into their teeth and bone with an additional fractionation of ~12 to 14‰ (Cerling & Harris, 1999; Passey *et al*., 2005). Mammals feeding on C_3 plants characteristically have δ^{13}C values between -14 and -8‰, while animals that eat C_4 tropical grasses have δ^{13}C values between +2 and -2‰. A mixed-feeder would fall somewhere in between these two extremes (Lee-Thorp & van der Merwe, 1987; Quade *et al*., 1992). Hence, the relative proportions of C_3 and C_4 vegetation in the diet of an animal can be determined by analyzing the δ^{13} C value of its teeth and bones. A number of previous studies have used the carbon and oxygen isotopic abundance of fossils and paleosols from South America to reconstruct the diets of extinct herbivores and the paleoenvironmental parameters of ancient terrestrial communities and ecosystems (Latorre *et al*., 1997; MacFadden, 2000a, 2005; MacFadden & Higgins, 2004; MacFadden *et al*., 1996; Sánchez *et al*., 2004).

Carbon isotopic data for horses from South America have been presented in several papers (MacFadden *et al*., 1994; MacFadden & Shockey, 1997; MacFadden, 2000b; Sánchez *et al*., 2006). MacFadden *et al*. (1999) interpreted the ancient distributions and latitudinal gradients of C_3 and C_4 grasses in North and South America from the stable isotopes preserved in the teeth of Pleistocene New World horses. In addition, some papers investigated the application of geochemical techniques in conjunction with morphological data to characterize and reconstruct the feeding ecology and niche characterization of individual species (MacFadden & Shockey, 1997; MacFadden, 1998).

Materials and methods

Here, we use stable carbon isotopes preserved in 166 fossil teeth and bone samples for 29 localities where horses have been recorded and 23 localities where gomphotheres have been recorded, published in Sánchez *et al*. (2004); MacFadden *et al*. (1994, 1996) and Prado *et al*. (in press). We have also included results previously published by Bocherens *et al*. (1996) for the modern elephant *Loxodonta africana* from the Amboseli Park (Kenya) to compare the dietary partitioning in the South American fossil taxa with that in an extant analogue (Table 1).

To analyze the patterns of dietary partitioning throughout the Plio-Pleistocene we divided the samples into 19 groups, taking into account the genera as well as the age of the corresponding localities. The nineteen groups are listed in Table 2: (Hi) *Hippidion*; (Eq) *Equus* (*Amerhippus*); (Cu) *Cuvieronius*; (St) *Stegomastodon*; (Hi1) *Hippidion* from the Late Pliocene; (Hi2) *Hippidion* from the Early-Middle Pleistocene; (Hi3) *Hippidion* from the Middle Pleistocene; (Hi4) *Hippidion* from the Late Pleistocene; (Hi5) *Hippidion* from the latest Pleistocene; (Eq2) *Equus* from the Early-Middle Pleistocene; (Eq3) *Equus* from the Middle Pleistocene; (Eq4) *Equus* from the Late Pleistocene; (Eq5) *Equus* from the latest Pleistocene; (Cu3) *Cuvieronius* from the Middle Pleistocene; (Cu4) *Cuvieronius* from the Late Pleistocene; (Cu5) *Cuvieronius* from the latest Pleistocene; (St2) *Stegomastodon* from the Early-Middle Pleistocene; (St4) *Stegomastodon* from the Late Pleistocene and (St5) *Stegomastodon* from the latest Pleistocene.

We performed both parametric (*t*-test) and non-parametric (Wilcoxon Signed-Rank) statistical

Table 1.—**Isotopic carbon values and descriptive statistics obtained from the enamel, dentine and bone of horse and gomphothere fossils from various South American localities. Results are given in ‰ versus PDB for carbon**

Taxa	Localities	Ages	Altitude	n	Mean δ¹³C (‰)PDB	SD (‰)	Min (‰)	Max (‰)
Hippidion	Tarija (Bo)	middle Pleistocene	22S	5	-9,05	1,468	-10,8	-6,6
	Mina Aguilar (Ar)	latest Pleistocene	23S	2	-9,90	0,095	-9,98	-9,79
	Uquía (Ar)	late Pliocene	23S	4	-10,13	0,121	-10,26	-9,94
	Paraná (Ar)	late Pleistocene	32S	2	-8,52	0,155	-8,67	-8,36
	Olivos (Ar)	early-middle Pleistocene	35S	3	-10,56	0,841	-11,73	-9,79
	Buenos Aires (Ar)	early-middle Pleistocene	35S	2	-11,55	1,350	-12,9	-10,2
	Luján (Ar)	latest Pleistocene	35S	4	-11,30	0,519	-12,1	-10,6
	Rio Salado (Ar)	latest Pleistocene	36S	3	-10,10	1,586	-12,05	-8,16
	Arroyo Tapalqué (Ar)	latest Pleistocene	38S	4	-10,10	0,901	-11,6	-9,365
	Quequén Salado (Ar)	latest Pleistocene	38S	1	-8,08			
	U. Esperanza (Ch)	latest Pleistocene	52S	1	-12,22			
Equus (Amerhippus)	La Venta (Co)	late Pleistocene	3N	2	-1,50	0,750	-2,2	-0,7
	Rio Chiche (Ec)	middle Pleistocene	0	4	-4,88	1,052	-5,8	-3,18
	Alangasi (Ec)	latest Pleistocene	0	3	-6,21	0,565	-6,87	-5,49
	Quebrada Colorada (Ec)	latest Pleistocene	2S	3	-6,21	0,393	-6,71	-5,75
	Punín (Ec)	latest Pleistocene	2S	3	-7,24	1,855	-9,86	-5,77
	La Carolina (Ec)	latest Pleistocene	2S	6	3,76	3,513	-1,45	9,21
	Salinas Oil Field (Ec)	latest Pleistocene	3S	2	1,10	1,900	-0,8	3
	Talara Tar Pit (Perú)	latest Pleistocene	5S	1	2,10			
	Ourolandia (Br)	latest Pleistocene	12S	2	1,40	0,300	1,1	1,7
	Naupua (Bo)	latest Pleistocene	21S	2	0,11	0,095	0,01	0,2
	Tarija (Bo)	middle Pleistocene	22S	12	-4,08	1,648	-8,31	-2,3
	La Banda (Ar)	latest Pleistocene	28S	1	-0,96			
	Esperanza, Santa Fé (Ar)	latest Pleistocene	32S	1	-0,80			
	Buenos Aires (Ar)	early-middle Pleistocene	35S	2	-10,50	0,200	-10,7	-10,3
	Magdalena (Ar)	late Pleistocene	35S	1	-10,60			
	Luján (Ar)	latest Pleistocene	35S	2	-11,43	0,230	-11,66	-11,2
	Cant.Vial Prov. (Ar)	late Pleistocene	35S	2	-9,48	1,978	-11,46	-7,51
	Arroyo Tapalqué (Ar)	latest Pleistocene	36S	2	-8,23	0,290	-8,52	-7,94
	Quequén Salado (Ar)	latest Pleistocene	38S	8	-8,69	0,863	-10,13	-7,8
	P. Hermengo (Ar)	late Pleistocene	38S	1	-7,21	0,327		
	Paso Otero (Ar)	latest Pleistocene	38S	3	-10,62		-11	-10,2
	Centinela del Mar (Ar)	late Pleistocene	38S	1	-9,99			
	Zanjón Seco (Ar)	latest Pleistocene	38S	4	-10,81	0,391	-11,39	-10,4
Cuvieronius	Alangasi (Ec)	late Pleistocene	0	4	-8,60	0,923	-9,59	-7,38
	Quebrada Colorada (Ec)	late Pleistocene	2S	1	-7,32			
	Punín (Ec)	late Pleistocene	2S	7	-7,48	1,696	-9,71	-5,1
	Ulloma (Bo)	middle Pleistocene	18S	1	-9,40			
	Tarija (Bo)	middle Pleistocene	22S	8	-7,22	1,879	-9,9	-4
	Limahuida (Ch)	late Pleistocene	32S	1	-11,30			
	El Parral (Ch)	late Pleistocene	36S	2	-12,30	0,250	-12,5	-12
	Rio Bueno (Ch)	late Pleistocene	40S	1	-13,10			
	Tralmahué (Ch)	late Pleistocene	40S	1	-13,90			
Stegomastodon	La Carolina (Ec)	latest Pleistocene	2S	4	-3,49	2,368	-5,97	-0,78
	Toca dos Ossos (Br)	late Pleistocene	15S	2	-6,60	1,600	-8,2	-5
	Tierras Blancas (Ch)	late Pleistocene	33S	1	-12,10			
	Tagua-tagua (Ch)	latest Pleistocene	34S	2	-12,20	0,600	-12,8	-11,6
	Ensenada (Ar)	early-middle Pleistocene	34S	2	-7,33	0,045	-7,37	-7,28
	La Plata (Ar)	early-middle Pleistocene	34S	4	-8,25	1,354	-9,06	-5,9
	Arroyo Pavón (Ar)	early-middle Pleistocene	34S	1	-7,00	0,353		
	Cant. Sr. Landa (Ar)	late Pleistocene	34S	3	-7,38	0,912	-8,05	-6,09
	Cant. Hdez. Orazi (Ar)	late Pleistocene	34S	4	-8,10	0,778	-9,08	-7,3
	Mercedes (Ar)	late Pleistocene	34S	2	-8,72	0,020	-8,74	-8,7
	Magdalena (Ar)	late Pleistocene	35s	6	-7,92		-8,26	-7,4
	Arroyo Tapalqué (Ar)	latest Pleistocene	36S	2	-8,64	0,380	-9,02	-8,26
	Ayacucho (Ar)	late Pleistocene	37S	1	-9,56			
	Quequén Grande (Ar)	latest Pleistocene	38S	7	-10,75	0,902	-12,11	-9,69
Loxodonta africana	Amboseli (K)	Recent	3S	6	-8,42	1,951	-10,7	-5,7

Table 2.—**Descriptive statistics for the 19 groups of horses and gomphotheres that were compared. *n*: number of samples. SD: standard deviation**

Groups	n	Mean δ^{13}C (‰) PDB	SD (‰)	Min (‰)	Max (‰)
Hippidion	31	-10,11	1,39	-12,9	-6,6
Hippidion late Pliocene	4	-10,13	0,14	-10,26	-9,94
Hippidion early-middle Pleistocene	3	-10,56	1,03	-11,73	-9,79
Hippidion middle Pleistocene	5	-9,05	1,64	-10,8	-6,6
Hippidion late Pleistocene	2	-8,52	0,22	-8,67	-8,36
Hippidion latest Pleistocene	15	-10,39	1,33	-12,22	-8,08
Equus (Amerhippus)	68	-5,21	4,83	-11,66	9,21
Equus (A) early-middle Pleistocene	2	-10,50	0,28	-10,7	-10,3
Equus (A) middle Pleistocene	16	-4,28	1,61	-8,31	-2,3
Equus (A) late Pleistocene	7	-7,10	4,18	-11,46	-0,7
Equus (A) latest Pleistocene	43	-5,00	5,61	-11,66	9,21
Cuvieronius	30	-9,08	2,64	-13,9	-4
Stegomastodon	38	-7,98	2,28	-12,11	-0,78
Cuvieronius middle Pleistocene	9	-7,46	2,01	-9,9	-4
Cuvieronius late Pleistocene	19	-9,51	2,61	-13,9	-5,1
Cuvieronius latest Pleistocene	2	-12,20	0,85	-12,8	-11,6
Stegomastodon early-middle Pleistocene	7	-7,80	1,24	-9,06	-5,9
Stegomastodon late Pleistocene	18	-7,90	1,06	-9,56	-5
Stegomastodon latest Pleistocene	13	-8,19	3,68	-12,11	-0,78

Table 3.—**Results of parametric (t-test) and non-parametric (Wilcoxon Signed-Rank) tests performed on 34 possible paired comparisons between the 19 groups of horses and gomphotheres. The definitions of the groups are the same as for table 2. *p*: significance level. Abbreviations in text**

Comparison groups	*t*-test p	Nonparametric p	Comparison groups	*t*-test p	Nonparametric p
Hi vs. Eq	0,000	0,000	Cu3 vs. Cu4	0,924	0,767
Hi vs. St	0,000	0,000	Cu3 vs. Cu5	0,166	0,180
Hi vs. Cu	0,086	0,063	Cu4 vs. Cu5	0,074	0,180
Eq vs. St	0,000	0,000	St2 vs. St4	0,754	0,499
Eq vs. Cu	0,000	0,000	St2 vs. St5	0,513	0,499
St vs. Cu	0,139	0,136	St4 vs. St5	0,742	0,507
			Eq5 vs. Hi5	0,000	0,001
			Cu5 vs. Hi5	0,137	0,180
Hi1 vs. Hi2	0,477	0,593	St5 vs Hi5	0,068	0,087
Hi1 vs. Hi3	0,332	0,465	Cu5 vs. Eq5	0,010	0,180
Hi1 vs. Hi4	0,043	0,180	St5 vs. Eq5	0,042	0,075
Hi1 vs. Hi5	0,401	0,465	St5 vs. Cu5	0,111	0,180
Hi2 vs. Hi3	0,166	0,109	Eq2 vs. Eq3	0,029	0,180
Hi2 vs. Hi4	0,222	0,180	Eq2 vs. Eq4	0,067	0,180
Hi2 vs. Hi5	0,581	0,655	Eq2 vs. Eq5	0,129	0,180
Hi3 vs. Hi4	0,382	0,180	Eq3 vs. Eq4	0,372	0,398
Hi3 vs. Hi5	0,101	0,080	Eq3 vs. Eq5	0,119	0,326
Hi4 vs. Hi5	0,03	0,180	Eq4 vs. Eq5	0,811	0,735

tests to evaluate δ^{13}C differences between each of the groups (Table 3), accepting the null hypothesis of no differences among means unless $p < 0.05$. We use SPSS 11.5 software for the statistical analysis.

Analytical results and discussion

The carbon isotopic ratio of gomphothere and horse samples provides significant ecological results. Between horses, the *Hippidion* samples are

more homogeneous than the *Equus* (*Amerhippus*) one (Table 1 and Figure 1).

All the species of *Hippidion* were almost exclusively C_3 feeders but some individuals from Bolivia and Argentina fall at the lower end of the mixed C_3/C_4 range. For instance, *Hippidion principale* from the Eastern corridor (at sea level) and *Hippidion devillei* from the Andes corridor yield similar $\delta^{13}C$ values suggesting that they ate mainly C_3 plants. The same pattern of dietary partitioning was obtained when comparisons were made between the same taxa at different latitudes (between 22°S and 52°S). From the upper Pliocene (*Hippidion devillei* from Uquía locality) to the lower Pleistocene (*Hippidion principale*, from the province of Buenos Aires and *Hippidion devillei* from the Tarija locality) the dietary partitioning remains similar. The same pattern in dietary partitioning is observed throughout the Middle to Late Pleistocene (Figure 1) showing a predominance of C_3 plants. Also, we did not find differences between *Hippidion saldiasi* from the Ultima Esperanza in southern Patagonia and the other *Hippidion* species present at different localities across South America. *Equus* species have predominantly been grazers, and as such, carbon isotopic values provide evidence of the C_3 and C_4 grasses. The carbon isotope data indicates that *Equus* (*Amerhippus*) shows three different patterns of dietary partitioning. Samples of *Equus* (*Amerhippus*) *neogeus* from the province of Buenos Aires indicate a preference for C_3 plants in the diet. The samples from Ecuador and Bolivia [*Equus* (*Amerhippus*) *andium* and *Equus* (*Amerhippus*) *insulatus*] show a preference for a diet of mixed C_3-C_4 plants, while those from La Carolina (sea level of Ecuador), Bolivia, and Brazil are mostly C_4 feeders. A few outliers (e.g. $\delta^{13}C$ values of 9,2; 6,1 and 5,4‰ from La Carolina) cannot be easily explained. These extremely high $\delta^{13}C$ values (above 3‰) cannot be explained by consumption of C_4 vegetation, which should impart an upper limit of about 3‰. These outliers could be the result from one of several possibilities, such as individuals living in costal peninsula areas of Ecuador during the time in which C_4 grasses were abundant and may have produced δ13C values not observed in the modern ecosystem, or the sample presents taphonomic alteration.

For gomphotheres, the $\delta^{13}C$ values of *Cuvieronius* samples indicate mixed feeding (Table 1 and Figure 2). Carbon isotopic data from *Cuvieronius* from Bolivia (MacFadden *et al.*, 1994; MacFadden & Shockey, 1997) suggests an adaptation from mixed feeding to grazing. One notable exception was *Cuvieronius* from Chile. Specimens of this group indicate that they were exclusively C_3 feeders (Figure 2). *Stegomastodon* shows two different adaptations. Samples from Buenos Aires Province (except for Quequén Salado samples) and Brazil indicate that these species were mixed-feeders whereas those from La Carolina (Ecuador) were mostly C_4 feeders. Substantial differences in isotopic composition are also observed between these two genera as they evolved from the Middle to the Late Pleistocene (Figure 2). *Stegomastodon* from the Middle Pleistocene of Buenos Aires fed on a mixed diet, as their isotopic values are more homogeneous. Alternatively, *Stegomastodon* from the Late Pleistocene exhibit a wider range of dietary adaptations. These include an exclusively C_3 diet (Quequén Salado), a mixed C_3-C_4 diet (Buenos Aires), and a diet completely composed of C_4 plants (Ecuador). The dietary regimes of *Cuvieronius* samples from the Middle and Late Pleistocene, on the other hand, show less variation. With the exception of the strictly C_3 feeding *Cuvieronius* of the Late Pleistocene in Chile, mixed feeding predominated in both the Middle Pleistocene (Bolivia) and the Late Pleistocene (Ecuador). A trend from a mixed C_3-C_4 diet in the middle Pleistocene to a more strictly C_3 diet in the upper Pleistocene can be more clearly observed in the Buenos Aires remains.

Both parametric (t-test) and non-parametric (Wilcoxon) statistical tests (Table 3) confirm significant differences between *Equus* (*Amerhippus*) and *Hippidion* $\delta^{13}C$ values (t-test = -8.88; p = <0.01 and Wilcoxon Z = -4.86, p = <0.01). Between gomphotheres, *Cuvieronius* have $\delta^{13}C$ values between about -13.9 and -4‰ while *Stegomastodon* have $\delta^{13}C$ values between about -12.1 and -0.7‰. Parametric and non-parametric statistical tests show that there are no significant differences between both groups (t-test= -1.52; p=0.139 and Wilcoxon Z=-1.49, p=0.136). There are significant $\delta^{13}C$ differences between *Equus* (*Amerhippus*) and both genera of gomphotheres; and *Hippidion* and *Stegomastodon*. There are also no significant $\delta^{13}C$ differences between the *Hippidion* and *Cuvieronius* samples (Table 3).

Concluding Remarks

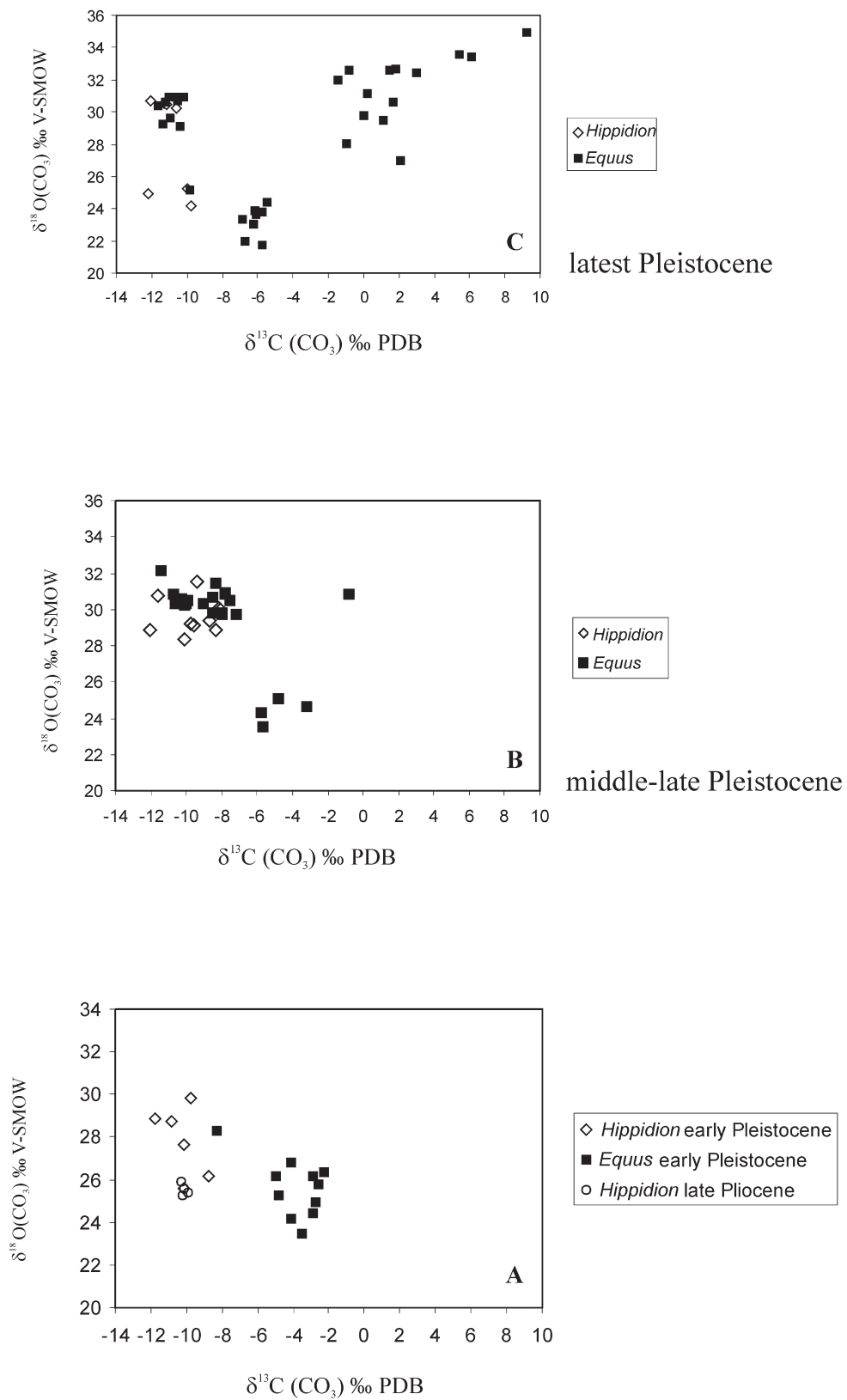The Late Quaternary Extinction roughly coincided with the most recent glacial-interglacial transi-

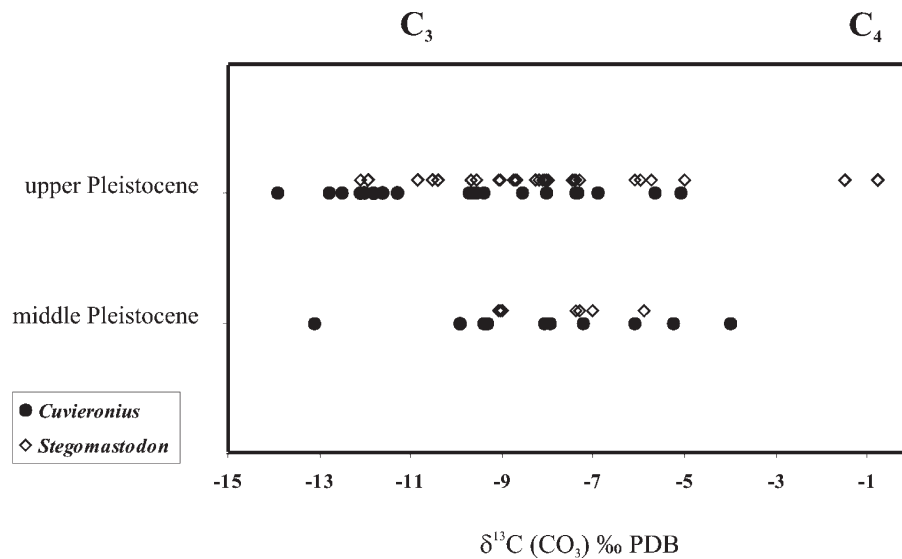Fig. 1.—Patterns of dietary partitioning through time for South American horses.

Fig. 2.—Patterns of dietary partitioning through time for South American gomphotheres.

tion, leading some to conclude that megafauna extinction was due to environmental change. Habitat loss hypotheses argue that as climate changed, areas with adequate conditions to maintain large mammals either disappeared entirely or became too small and fragmented to support viable populations (Koch & Barnosky, 2006). The mosaic-nutrient hypothesis is a special case of habitat loss. It argues that climate change reduced the growing season and local plant diversity, and also increased plant anti-herbivore defenses, all of which reduced the carrying capacity for herbivores (Guthrie, 1984). On the other hand, the Co-evolutionary disequilibrium is a more general hypothesis. It posits that the high herbivore diversity of Pleistocene ecosystems was maintained by extensive resource partitioning and that an extremely rapid glacial-interglacial transition reorganized floras, disrupting this tightly coevolved system (Graham & Lundelius, 1984). The premise under these entire hypotheses is the claim that the last glacial-interglacial transition was unusually large and unusually rapid relative to earlier glacial-interglacial transitions, too fast for animal adaptation or redistribution in the new climate space. In this study, the diets of gomphotheres and horses from South America are assessed using carbon isotope analysis to test principally the mosaic-nutrient and Co-evolutionary disequilibrium.

Based on modern analogues, Pleistocene horses are inferred to be grazers but none of the grazing horses were interpreted as consumers of only C_4

grasses. Our data shows that *Equus* (*Amerhippus*) had three different patterns of dietary partitioning. *Equus* (*Amerhippus*) *neogeus* from the province Buenos Aires indicates a preference for C_3 plants. *Equus* (*Amerhippus*) *andium* from Ecuador and *Equus* (*Amerhippus*) *insulates* from Bolivia show a preference in a mixed diet of C_3-C_4 plants, while *Equus* (*Amerhippus*) *santaeelenae* from La Carolina (sea level of Ecuador) and Brazil are mostly C_4 feeders (Prado *et al*., 2011). In particularly, the specimen from the latest Pleistocene shows a more focused dietary adaptation that suggests that they were specialized feeders.

Specimens of gomphotheres from the Middle and upper Pleistocene in South America exhibit feeding strategies similar to those of modern elephants, which live in diverse habitats, are opportunists, and therefore are capable of living on nearly any dietary mixture. Same specimen of *Cuvieronius* from Chile fed on C_3 plants exclusively, whereas other specimens of the genus had a mixed C_3-C_4 diet. The genus *Stegomastodon* showed a broader range of dietary adaptations, including predominantly C_3 feeders (in Buenos Aires Province), exclusively C_4 feeders (in La Carolina Peninsula, Ecuador), and mixed C_3-C_4 feeders (from several localities form Brazil and Argentina).

In sum, the strong resource partitioning among herbivores assumed under Co-evolutionary disequilibrium hypothesis is supported by isotopic data of horses from latest Pleistocene. *Hippidon* and *Equus*

had very different diets. In contrast, species of gomphotheres from late Pleistocene in South America seem to have had less specialized diets containing a broad mix of both C_3 and C_4 plants, which is in line with the dietary assumptions of the mosaic-nutrient hypothesis, but does not support the assumptions of Co-evolutionary disequilibrium hypothesis.

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