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Paleodiet, ecology, and extinction of Pleistocene gomphotheres (Proboscidea) from the Pampean Region (Argentina)

Paleodieta, ecología y extinción de los gonfoterios (Proboscidea) de la Región Pampeana (Argentina)

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Abstract: To reconstruct the paleodiet and habitat preference of gomphotheres, we measured the carbon and oxygen isotope composition of 32 bone and tooth samples of *Stegomastodon platensis* (AMEGHINO, 1888) from 10 different Pleistocene localities in Pampean Region (Argentina). In order to compare the different stratigraphic levels we have divided the samples in two groups: middle and late Pleistocene. Samples from the middle Pleistocene are more homogeneous, with a range of ^{13}C values between –9.0 to –5.9‰. This data indicates a mixed C_3 y C_4 diet. On the contrary, samples from late Pleistocene show a wide range of diet adaptation (with a range ^{13}C values between –12.11 to –6.09 ‰), since specimens that indicate an exclusively C_3 diet from latest Pleistocene, to others with a mixed-feeder diet. Several nutritional hypotheses to explain late Pleistocene extinctions adopt the assumption that extinct taxa had specialized diets. The resource partitioning preference of *Stegomastodon platensis* from latest Pleistocene supports in part this hypothesis.
Key words: Pleistocene, mammals, *Stegomastodon platensis*, paleodiet, ecology, extinction.

Resumen: Se ha realizado el análisis de la composición isotópica del oxígeno y del carbono del carbonato apatítico en 32 restos fósiles de gonfoterios procedentes de 10 localidades del Pleistoceno de la Región Pampeana (Argentina). A partir de los resultados obtenidos se ha inferido la dieta y el hábitat de *Stegomastodon platensis* (AMEGHINO, 1888). Para analizar las variaciones temporales de los resultados isotópicos, las muestras fueron agrupadas según su procedencia estratigráfica (Pleistoceno medio y superior). El análisis indica que las muestras del Pleistoceno medio son más homogéneas, con un rango de variación de los valores de ^{13}C entre -9.06 y -5.9‰. Estos datos sugieren una dieta mixta, compuesta por plantas de tipo C_3 y C_4. Por el contrario, los resultados de las muestras del Pleistoceno superior presentan un mayor rango de variación (–12.11 a –6.09 ‰), desde individuos adaptados a una dieta mixta hasta otros exclusivamente C_3. 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 de fines del Pleistoceno. La especialización en la dieta que se observa en los gonfoterios del Pleistoceno final es una evidencia más en favor de esta teoría.
Palabras clave: Pleistoceno, mamíferos, *Stegomastodon platensis*, paleodieta, ecología, extinción.

INTRODUCTION

The proboscidean gomphotheres have been recorded in South America from the early Pleistocene to the latest Pleistocene (ALBERDI & PRADO, 1995). They were descendants of the gomphothere stock that originated in North America and arrived in South America during the "Great American Biotic Interchange" (WEBB, 1991). Only two genera are recognised: *Cuvieronius*, which has only one species, *Cuvieronius hyodon*, and *Stegomastodon*, which has two species, *Stegomastodon platensis* and *Stegomastodon waringi*.

Stegomastodon platensis was recorded in Argentina from the middle to the late Pleistocene, principally in the Pampean Region, and in Uruguay and Paraguay during the late Pleistocene. *Stegomastodon*

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appears to have predominated at middle and lower latitudes, where it occupied savannas or xerophytic pasture areas, and consequently would have been better adapted to warm or temperate climatic conditions. The presence of gomphotheres diminished from North to South, particularly during the latest Pleistocene, when environmental conditions became colder and drier (PRADO *et al*., *1999*).

Based on dental morphology, gomphotheres groups are considered to have been mixed feeders to browsers (WEBB, 1983). Carbon isotopic data of *Cuvieronius* from Bolivia (MACFADDEN *et al*., 1994; MACFADDEN & SHOCKEY, 1997) suggest a mixed-feed to C_4 grazer adaptation. This paper presents new carbon and oxygen isotopic data from tooth enamel, dentine, and bone of *Stegomastodon platensis* from Pampean Region. These new data are used to evaluate previous hypotheses about the paleoecology and extinction of this species.

ISOTOPIC BACKGROUND

Previous studies have also shown that the carbon isotope ratio (^{13}C) in 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, 2000). This carbon isotope ratio is influenced by that of ingested plant material, which is in turn influenced by the photosynthetic pathway utilized by the plants. 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). As a result, C_3 plants have ^{13}C values of –22 per mil (‰) to –30‰, with an average of about –26‰, whereas C_4 plants have ^{13}C values of –10 to –14‰, with an average of about –12‰ (SMITH & 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 ^{13}C values between about –10 and –16‰, while in contrast, animals that eat C_4 tropical grasses (including blades, seeds, and roots) have ^{13}C values between +2 and -2‰. A mixed-feeders 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 an animal diet can be determined by analysing their tooth and bone ^{13}C.

In recent decades, there has been an increasing use of oxygen isotope analyses to reconstruct paleoclimatic conditions. In the case of homoeothermic animals in general, the oxygen isotope composition of apatite depends primarily on the oxygen balance of the animal (LONGINELLI, 1984; LUZ *et al*., 1984). Large mammals oxygen isotope variations depend largely on external factors such as the ^{18}O of ingested water. Because the oxygen isotopic composition of apatite in mammalian bones and teeth is related to that of ingested water, and ingested water comes ultimately from precipitation, the ^{18}O of teeth and bone can be used to infer climatic conditions in the past (LONGINELLI & NUTI, 1973; KOLODNY *et al*., 1983; D'ANGELA & LONGINELLI, 1990; BRYANT *et al*., 1994; SÁNCHEZ *et al*., 1994; BRYANT & FROELICH, 1995; DELGADO *et al*., 1995).

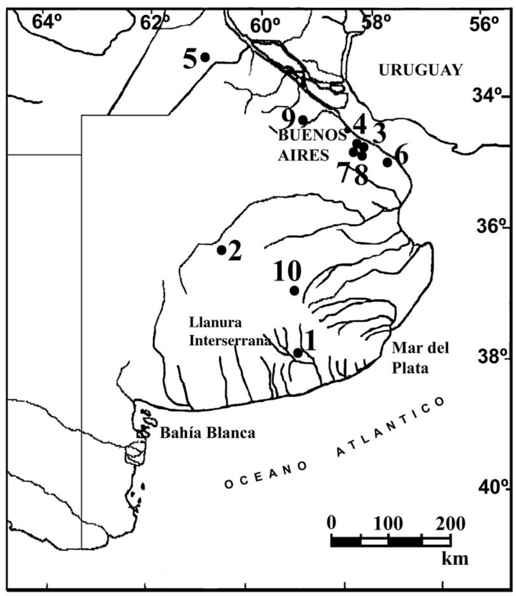

Figure 1.- Geographical distribution of analysed samples of *Stegomastodon platensis* from the Pleistocene of Buenos Aires Province (Argentina). 1: Quequén Grande; 2: Arroyo Tapalqué; 3: Ensenada; 4: La Plata; 5: Arroyo Pavón; 6: Magdalena; 7: Cant. Orazi; 8: Cant. Landa; 9: Mercedes; 10: Ayacucho.
Figura 1.- Distribución geográfica de las muestras de Stegomastodon platensis *analizadas procedentes del Pleistoceno de la Provincia de Buenos Aires (Argentina).*

MATERIAL AND METHODS

Sampled Area

The Pampa plains contain extensive formations of superficial sand and loess that are known as the Pampean Formation (Teruggi, 1957). The palaeomagnetic stratigraphy and radiometric data suggests that most of this formation was deposited over the last 3.3 Ma (Schultz *et al*., 1998). The stratigraphy of the Pampean loess consists typically of superposed beds 1-2 m thick separated by either erosional discontinuities or palaeosols. Most of the *Stegomastodon* remains come from the localities assigned to Ensenadan and Lujanian South American Land Mammal Age. The majority of these palaeo-aeolian features lie in areas presently supporting vegetation communities dominated by Pampean grassland. The Pampa plains at present enjoy a subtropical climate, which varies from humid in the east to arid in the west. This climatic pattern reflects the dominance of the ocean in the southern half of South America (Iriondo & García, 1993). The mean annual temperature is about 17°C and the mean annual precipitation is about 800 mm.

Sample Selection

Thirty-two gomphotheres samples of *Stegomastodon platensis* from 10 different middle and late Pleistocene localities from the Pampean Region were measured to obtain the oxygen and carbon isotopic composition of bone and tooth enamel carbonate (Fig. 1). Fossil samples were collected from specimens stored at the Museo de La Plata (MLP). The museum collection number and the locality of each sample are reported in Table 1.

In order to compare middle and late Pleistocene specimens, we have divided the samples in two groups. In Table 1, we have also included the results of the modern elephant *Loxodonta africana* from the Amboseli Park (Kenya) already published by Bocherens *et al*. (1996). The samples from enamel and dentine from each tooth were drilled, in the majority of specimens, at the basal anterior edge of the first loph of M3. In populations where no M3 was available, samples were extracted from the same location of the M2. Anyway, the gomphothere ontogeny dentition is different that in the almost part of mammals. The Gomphotheriidae teeth are characterized by retardation in dental ontogeny (Roth & Shoshani, 1988; Roth, 1989), an anatomic-temporal ordination, and their teeth are braquidont. The biggest inter- and intra-tooth variation in the oxygen isotope composition of mammalian tooth enamel is in the hypsodont teeth (Fricke & O'Neil, 1996: Fricke *et al*., 1998; Koch *et al*., 1998). For a greater explanation of selected samples see Sánchez *et al.* (in press).

Sample Preparation and Analysis

The samples were finely ground in an agate mortar. The chemical pre-treatment of the samples has been carried out basically as described in Koch *et al*. (1997) in order to eliminate secondary carbonates. About 40-50 mg of powdered dentine and bone samples were soaked in 2% NaOCl during three days at room temperature to oxidize organic matter. Residues were rinsed and centrifuged five times with deionised water, and then treated with 1M acetic acid during one day to remove diagenetic carbonates. Pre-treatment of the enamel was slightly different because samples were soaked in 2% NaOCl only during one day. Carbon dioxide was obtained reacting about 40-50 mg of treated powder with 100% H_3PO_4 during five hours at 50ºC, then carbon dioxide was isolated cryogenically in a vacuum line. The samples were analysed for their carbon and oxygen isotopic compositions using mass spectrometer. Results are reported as δ= ([Rsample/Rstandard]-1) x 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 have applied the data corrections for calcite to calculate the magnitude of the oxygen isotopic fractionation between apatite CO_2 and H_3PO_4 at 50ºC (Koch *et al*., 1989). Analytical precision for repeated analyses was 0,1‰ for ^{13}C and 0,2‰ for ^{18}O.

Statistical Analyses

We performed both parametric (t-test) and nonparametric (Wilcoxon Signed-Rank) statistical tests to evaluate ^{13}C and ^{18}O differences in middle and late Pleistocene populations, accepting the null hypothesis of no difference among means unless $p < 0.05$. SPSS 10.0 software was used for the statistical analysis.

Specimen number	Skeletal tissue	Locality (age)	$\delta^{13}C$ (CO_3) ‰ PDB	$\delta^{18}O$ (CO_3) ‰ V-SMOW
MLP 68-X.31.1	e	Ensenada (mid Pl)	-7,28	28,73
MLP 68-X.31.1	e	Ensenada (mid Pl)	-7,37	28,6
MLP 71-II.14.1	e	La Plata (mid Pl)	-9,06	29,07
MLP 71-II.14.1	e	La Plata (mid Pl)	-8,99	29
MLP 71-II.14.1	e	La Plata (mid Pl)	-9,03	30,25
MZK 288b	e	La Plata (mid Pl)	-5,9	30,6
MZK 1785 30.11	e	Aº Pavón (mid Pl)	-7	29,98
MLP 40-XII-17.1	e	Quequén Grande (latest Pl)	-10,42	29,19
MLP 40-XII-17.1	e	Quequén Grande (latest Pl)	-10,53	28,91
MLP 40-XII.17.1	b	Quequén Grande (latest Pl)	-10,83	29,6
MLP 40-XII.17.1	b	Quequén Grande (latest Pl)	-9,69	28,92
MLP 40-XII.17.1	b	Quequén Grande (latest Pl)	-9,69	28,25
MLP 40-XII.17.3	b	Quequén Grande (latest Pl)	-12,11	33,19
MLP 40-XII.17.3	b	Quequén Grande (latest Pl)	-11,95	30,82
MLP 44-XII.29.1	d	Aº Tapalqué (late Pl)	-8,26	29,15
MLP 44-XII.29.1	e	Aº Tapalqué (late Pl)	-9,02	31,21
MLP 31-VII.16.1	e	Magdalena (late Pl)	-7,4	30,12
MLP 31-VII.16.1	e	Magdalena (late Pl)	-7,46	30,06
MLP 31-VII.16.1	d	Magdalena (late Pl)	-8,1	30,49
MLP 31-VII.16.1	d	Magdalena (late Pl)	-8,25	30,37
MLP 31-VII.16.1	b	Magdalena (late Pl)	-8,02	29,41
MLP 31-VII.16.1	b	Magdalena (late Pl)	-8,26	29,42
MLP 87-XII.35.1	d	Cant. Landa (late Pl)	-6,09	30,31
MLP 87-XII.35.1	e	Cant. Landa (late Pl)	-8	30,72
MLP 87-XII.35.1	e	Cant. Landa (late Pl)	-8,05	30,36
MLP 90-VIII.1.1	d	Cant. Orazi (late Pl)	-9,08	29,99
MLP 90-VIII.1.1	d	Cant. Orazi (late Pl)	-8,65	29,63
MLP 90-VIII.1.1	e	Cant. Orazi (late Pl)	-7,3	30,42
MLP 90-VIII.1.1	e	Cant. Orazi (late Pl)	-7,38	29,76
MLP 8-407	e	Mercedes (late Pl)	-8,74	30,44
MLP 8-407	e	Mercedes (late Pl)	-8,7	30,32
MLP 8-62	d	Ayacucho (late Pl)	-9,56	32,76
L. Africana (extant)	e	Amboseli (Kenya)	-7,3	30,4
L. Africana (extant)	e	Amboseli (Kenya)	-5,7	29,3
L. Africana (extant)	e	Amboseli (Kenya)	-10,2	28,3
L. Africana (extant)	e	Amboseli (Kenya)	-10,7	30
L. Africana (extant)	e	Amboseli (Kenya)	-6,6	31
L. Africana (extant)	e	Amboseli (Kenya)	-10	29,8

Table 1.- Results of ^{18}O and ^{13}C from samples of *Stegomastodon platensis* analysed compared with the distribution obtained for *Loxodonta africana* from Amboseli Park (Kenya) (BOCHERENS *et al.*, 1996). e = enamel; d = dentine; b = bone. Samples with the same "specimen number" belong to the same individual; the bones belong to a mandibular o maxilar fragment of the same tooth.
Tabla 1.- Resultados de ^{18}O y ^{13}C de las muestras analizadas de Stegomastodon platensis *comparados con la distribución obtenida para* Loxodonta africana *del Parque Amboseli (Kenia) (BOCHERENS et al., 1996). e = esmalte; d = dentina; b = hueso. Las muestras con el mismo número de colección pertenecen al mismo individuo, los huesos pertenecen a los fragmentos mandibulares o maxilares del mismo diente.*

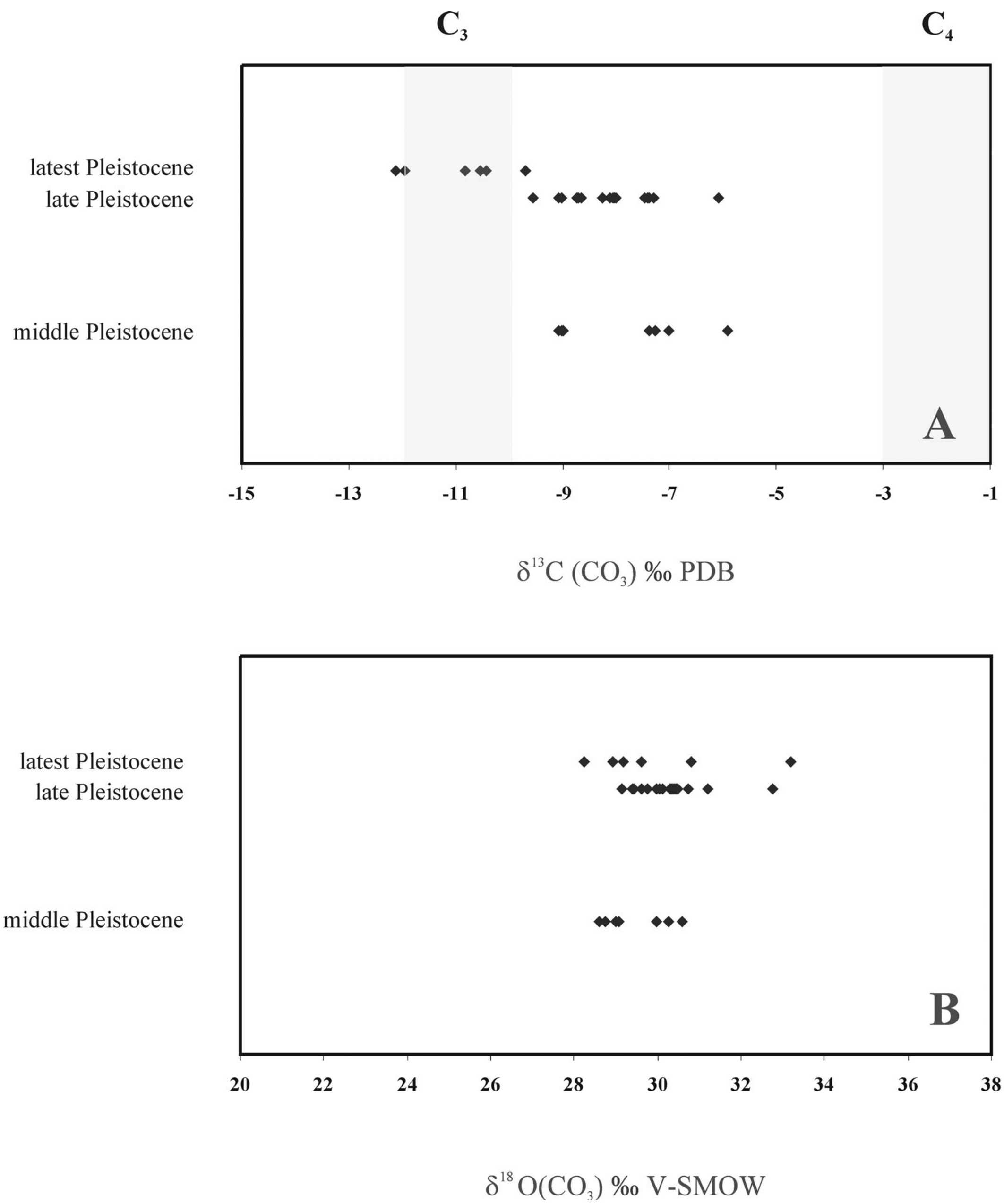

Figure 2.- Results and variation with time in ^{13}C (A) and ^{18}O (B) for *Stegomastodon platensis* of Buenos Aires Province (Argentina).
Figura 2.- Resultados y variación temporal de la composición isotópica del carbono (A) y del oxígeno (B) de Stegomastodon platensis *de la Provincia de Buenos Aires (Argentina).*

Groups	n	Mean $\delta^{13}C$ (‰)PDB	SD (‰)	Range (‰)	Mean $\delta^{18}O$ (‰)V-SMOW	SD (‰)	Range (‰)
late Pleistocene	25	-8,86	1,46	-12.11 to -6.09	30,15	1,1	28.25 to 33.19
middle Pleistocene	7	-7,8	1,24	-9.06 to –5.9	29,46	0,8	28.6 to 30.60

Table 2.- Univariate statistics for the two groups of *Stegomastodon platensis* established.
Tabla 2.- *Análisis estadísticos univariados realizados para los dos grupos de* Stegomastodon platensis *establecidos*.

Variable	Comparison groups	df	*t*-test p	Nonparametric p	Significant difference?
$\delta^{13}C$	middle vs. late Pleistocene	6	0,01	0,018	yes
$\delta^{18}O$	middle vs. late Pleistocene	6	0,487	0,237	no

TABLE 3.- Parametric (*t* - test) and non-parametric (Wilcoxon) significance tests for the ^{13}C and ^{18}O results for the two compared groups.
TABLA 3.- Test de significación paramétrico (*t* - test) y no-paramétrico (Wilcoxon) de los resultados de ^{13}C y ^{18}O en los dos grupos comparados.

ANALYTICAL RESULTS AND DISCUSSION

Feeding Ecology and Habitat Preference

Initial evaluation and analysis of $\delta^{13}C$ showed that *Stegomastodon* developed different feeding patterns over the middle and late Pleistocene. In addition, a relationship between diet change and latitude was observed.

Substantial differences in isotopic composition are observed in this genus as he evolves from the middle to the late Pleistocene (Fig. 2 A). *Stegomastodon platensis* from the middle Pleistocene fed on a mixed diet, as their isotopic values are more homogeneous, ranging from –9.06 to –5.9 ‰. Alternatively, *Stegomastodon platensis* from late Pleistocene exhibit a wider range of diet adaptations (between –12.11 to –6.09 ‰) that includes a mixed C_3-C_4 diet to an exclusively C_3 diet in the latest Pleistocene populations. Parametric (t-test) and non-parametric (Wilcoxon) statistical tests confirm significant differences between these groups (Tables 2 and 3).

The proportion of C_3 and C_4 grasses in modern ecosystems varies with latitude and the crossover between C_3 versus C_4 dominance in grasslands in the northern hemisphere (Ehleringer *et al*., 1997; Epstein *et al*., 1997; Tieszen *et al*., 1997). In Buenos Aires Province we observed the transition to C_3 feeding in the latest Pleistocene of Quequén Grande, showing a $\delta^{13}C$ mean value of –10.75‰.

Pollen records of the central and south-western Pampa grassland during the late glacial suggesting sub-humid-dry to semiarid climatic conditions (Prieto, 2000).

Both samples of *Stegomastodon platensis* from middle and late Pleistocene have similar mean ^{18}O value (Fig 2 B). The mean values for both populations are not significantly different (Table 3). The temperature record established for the Buenos Aires *Stegomastodon* is in agreement with the current temperature record of Amboseli Park (Bocherens *et al*., 1996).

Gomphothere extinction in Pampean Region

Currently, two main theories are accepted as possible explanations for the Quaternary extinction of South American large mammals. One theory attributes their extinction to the direct impact of man through hunting activities (Martin, 1984). For example, the archaeological record from South America shows that gomphotheres were frequent in Paleo-Indian sites (Dillehay & Collins, 1988; Montane, 1968; Correal Urrego, 1981; Bryan *et al*., 1978), but not in Pampean Region.

In contrast to the above, climatic and ecological changes, particularly nutritional stress induced by rapid change in plant communities may be a main cause of extinction (Graham & Lundelius, 1984; King & Saunders, 1984). This model implies that gomphotheres died off because they were specialized feeders, adapted to a kind of plant that may be disappeared during the Holocene times. The specimens from middle Pleistocene exhibit feeding habitat similar to those of modern elephants. They live in a diverse habitat, are opportunists, capable of living on nearly any dietary mixture (Bocherens *et al*., 1996). On the contrary, the latest Pleistocene specimens from the south area of the Province (Quequén Grande) show more focused feeding, exclusively C_3 diet. Our results are in agreement with this extinction hypothesis.

CONCLUSION

The goal of this study was to reconstruct the ancient diet and habitat preference of *Stegomastodon platensis* using the carbon and oxygen isotopic composition of teeth and bone. Carbon isotope analyses reveals that Pleistocene gomphotheres from Pampean Region had a different food adaptation. Specimens from late Pleistocene were principally C_3 plants eater (for example, those from Quequén Grande was full C_3) while the others coming from the middle Pleistocene had a mixed C_3-C_4 diet. Carbon isotopic values showed an adaptive change to C_3 feeding in the latest Pleistocene of Quequén Grande.

The gomphotheres, including *Stegomastodon platensis* and the other species of South America, became extinct abruptly at the end of Pleistocene. This extinction seems to have been a result of diminished specialized food resources.

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