# Isotopic trends in the diets of hunter-gatherers of the lower Paraná wetland, South America

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## ARTICLE INFO

## ABSTRACT

The results of the isotopic analysis of 23 individuals recovered in the lower Paraná wetland, South America, are presented. The samples were recovered from complex hunter-gatherer sites ranging from the years 1800 to 600 BP. Two isotopic trends were identified. The first one is based on depleted proteins with high trophic levels, related to freshwater fish consumption. The second one is similar, but includes a moderate intake of carbohydrates. The regional tendency was focused on fishing resources over time, and not on the alleged importance of cultigens. The data obtained from infants and children suggest an early period of weaning and age-based food allocation for infants based on depleted carbs. The data obtained are compared to other results published for humans recovered from sites of other archaeological units distributed throughout the same region.

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## 1. Introduction

The Parana River basin is the second most important in South America and is the world's fifth largest, covering Paraguay, the northeast of Argentina, East of Uruguay, Bolivia and Southeast of Brazil (see Fig. 1). In its lower section, complex hunter-gatherer societies were developed within a subtropical wetland environment from at least the third millennium BP, according to the archaeological record recovered from the Playa Mansa and Isla Lechiguanas sites (Acosta et al., 2010a; Loponte et al., 2012). During the chronological range between the years 2400–500 BP, local hunter-gatherers based their economy on freshwater fish, especially *Prochilodus lineatus* (shad) and secondary *Pterodoras granulosus* (granulated catfish), complemented with the exploitation of deer (*Blastocerus dichotomus* and *Ozotoceros bezoarticus*), mainly small to medium rodents (*Myocastor coypus*) and freshwater clams (especially *Rhipidodonta variabilis*) (Acosta and Musali, 2002; Acosta et al., 2010a, 2010b; Arrizurieta et al., 2010; Bonomo et al., 2011a; Ceruti and González, 2007; Cione and Tonni, 1978; Loponte, 2008; Loponte and Acosta, 2004, 2015; Loponte et al., 2012; Sartori and Colasurdo, 2011; among others). The largest living rodent in the world (*Hydrochoerus hydrochaeris*) was also exploited, although seemingly only marginally, since its archaeological representation is small, probably due to symbolic restrictions (Loponte, 2008; Salemme, 1987; Ottalagano and Loponte, 2016; see also Cabrera Pérez, 2005 for a similar

situation in the archaeological record in eastern Uruguay). Agroforestry of local palm (*Syagrus romanzzofiana*) and the development of sporadic small gardens have also been postulated based on historical sources and some archaeological features (Acosta and Ríos Román, 2013; Caggiano, 1984; Ceruti, 2000, 2003; Aparicio, 1939; Krapovickas, 1996; Loponte, 2008; Lothrop, 1932; Ottalagano, 2005; Rodríguez, 2001; Serrano, 1972). In fact, the archaeological presence of phytoliths, vegetal tissues and starch grains assignable to species such as *Cucurbita* sp. (squash), *Prosopis* sp. (algarrobo), *Phaseolus* sp. (beans), *Ipomea* sp. (sweet potato), *Zea mays* (maize) and palms (*i.e. S. romanzoffiana*) has been reported (Acosta et al., 2013; Bonomo et al., 2011a, 2011b, 2011c; Caggiano, 1984; Colobig and Ottalagano, 2016; Colobig et al., 2015; Cornero and Rangone, 2015; Sánchez et al., 2013; Torres, 1911; Zucol and Loponte, 2008).

The settlements of these societies were based on a centrally located foraging system, with medium to high residential stability, including true earth mounds built in specific areas in the region (Bonomo et al., 2011c; Loponte and Acosta, in press-a). Large cemeteries have been discovered at many sites (Torres, 1911; Lothrop, 1932), some of them were used over generations (Mazza and Loponte, 2012). Other behaviors detected and/or inferred are food storage, territoriality, ownership of territories and productive patches, intensification of the exploitation of the environment, and the development of a complex trade network (Ceruti, 2003; Loponte, 2008; Loponte and Acosta, 2006; Lothrop, 1932; Torres, 1911). Small to medium-sized pottery vessels were produced to process food and to extract nutrients by boiling (Loponte, 2008). Practically all the vessels show evidence of fatty acids associated
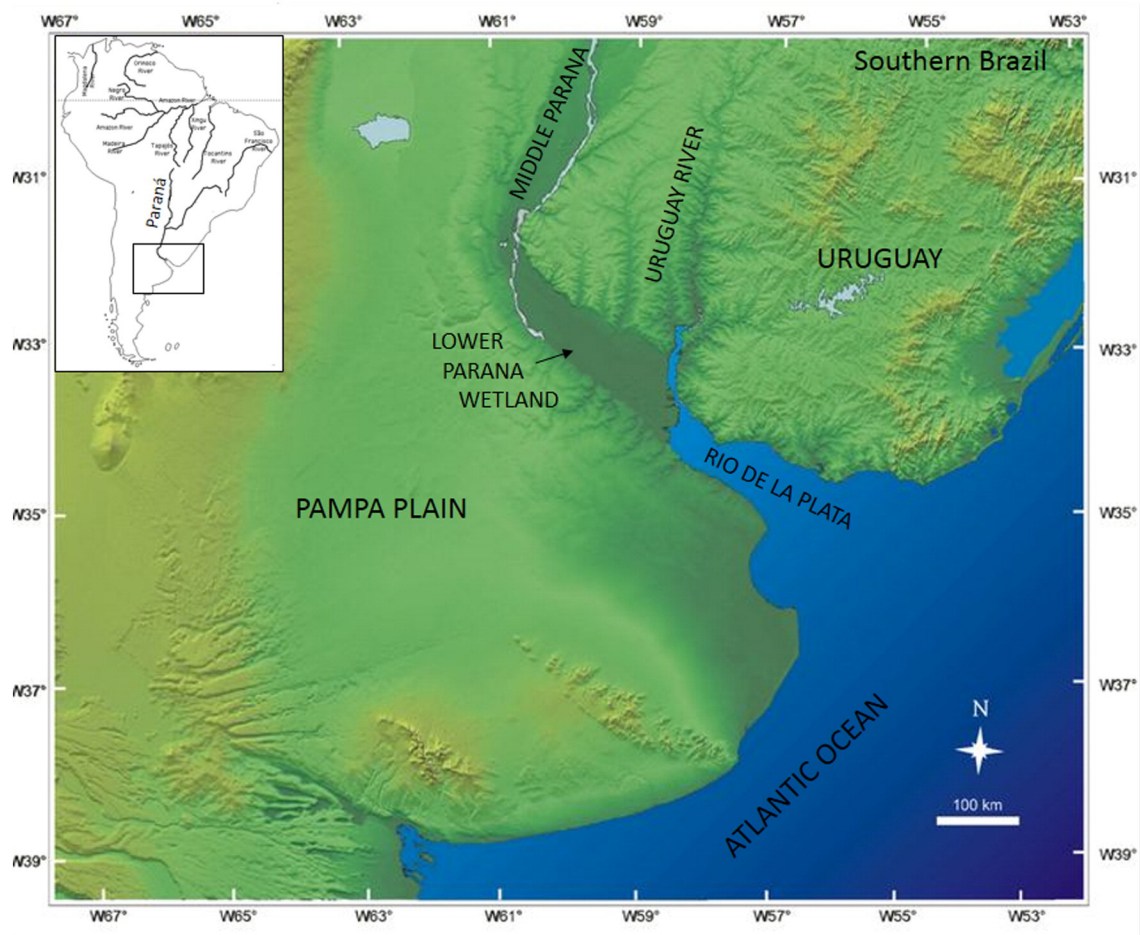
**Fig. 1.** Lower Paraná wetland.

with vegetable and/or animal foods (Naranjo et al., 2010; Ottalagano, 2013; Pérez et al., 2013). Likewise, complex and sophisticated weapons systems was developed, including bows and arrows, hand-held spears, spear throwers, bola stones, detachable harpoons, fishing nets and traps (Buc, 2012; Buc and Silvestre, 2010; Caggiano, 1984; Ceruti, 2003; Loponte, 2008; Loponte and Acosta, 2006; Lothrop, 1932; Serrano, 1972; Silvestre et al., 2010; Torres, 1911). Ornamental artifacts made of metal and green rock allochthonous to the region have been recovered, as well as earrings made from local carnivorous canine teeth and freshwater mollusk shells (Acosta et al., 2015; Loponte, 2008; Lothrop, 1932; Torres, 1911). The buried individuals generally lack ornamental artifacts, including those that are sex markers, such as *tembetás* (an ornamental artifact used under the lip). While there is some weak evidence (from historical sources) suggesting the existence of chiefdoms during times of war, archaeological studies have not yet been able to identify the existence of institutionalized inequality as a system of established social hierarchies (Loponte, 2008; Mazza and Loponte, 2012). Domestic dogs were present in these societies, at least from the years 1594 ± 59 ^{14}C BP, but until today there has been no evidence that they were used in hunting activities (Acosta et al., 2011; Loponte and Acosta, in press-b).

From the beginning of the academic investigations in the area, and based on the stylistic criteria of the pottery, the entire pre-Columbian record was divided into three units by Torres (1911). The first one belongs to Amazonian horticulturalist groups called Guaraní, which are very well defined contexts quite different from those of local hunter-gatherers (Loponte and Acosta, 2013). These groups arrived in the wetland a few centuries before the Europeans. Their economy was based on hunting, fishing and slash-and-burn horticulture. Isotopic analysis of

human bones recovered from these sites shows values according to a mixed diet related to maize consumption and depleted proteins (Loponte et al., in press). In turn, the hunter-gatherer record described above was divided into two different archaeological units. The first has incised pottery with geometric patterns based on lines and dots. The second one has incised pottery also based on lines, but with a different technological style (in the sense of Lechtman, 1977) and zoomorphic figures as handles. These criteria identifying archaeological assemblages were followed, with some variations, by other researchers in the area during the twentieth century. Similarly, the rule of the stylistic and typological criteria of the pottery will remain as a guide to distinguish archaeological units, essentially excluding all other aspects of the record (*i.e.* Caggiano, 1984; Rodríguez, 2001; Aparicio, 1939; Lothrop, 1932; Rodríguez, 2001; Serrano, 1972).

Recent studies that take into account a more complete analysis of the record show that the physical evidence is more complex than that original view. Different "descriptive units" (in the sense of O'Brien and Lyman, 2002) related to the local hunter-gatherers have been detected in the wetland, which can be divided into several clusters (Loponte, 2008). One of them has only plain pottery ("Plain Pottery Cluster" or PPC for short). Ornaments for the lips with "T" shapes (*tembetás*) made from fresh water shells were identified in these assemblages. Faunal remains are composed mainly of freshwater fish, reflecting a narrow diet range. Mammals were also hunted, whose bones were extremely reduced down in order to increase the nutrient extraction through boiling. A second cluster that has been identified has pottery decorated with geometric patterns, such as in Torres (1911), and as other authors later described (Caggiano, 1984; Serrano, 1972). In this Incised Pottery Cluster (IPC from now on), no T-shaped *tembetás* were found, but circular

ones were detected at some sites. Fishing was also important, but mammal exploitation was more significant, indicating a broader diet. The reduction of mammal bones in order to boil them was not as intense. A fraction of the sites assigned to this cluster, especially those located in the southwest of the Paraná River, show a more intensive use of rocks brought into the Pampas, which means the existence of different lithic raw material procurement systems.

Other properties of the archaeological record are homogenous between both clusters. For instance, the bone and stone tool technology and typology are basically the same. While there appear to be a few differences in some typological aspects of the pottery, as well as in a different quality in the walls of the containers, the shapes of all the vessels are basically the same (pots and bowls with open shapes and small to medium in size) (Buc and Silvestre, 2010; Loponte, 2008). So far, differences in mortuary patterns between both clusters have not been identified, although we still lack an adequate record of the death-related behavior (Mazza and Loponte, 2012).

These two archaeological units are contemporaneous with each other, and they are distributed across the southwest area of the wetland, although the former has a greater extent, as recognized in deep areas in the lower Parana region, reaching the shores of the Uruguay River. The sites excavated for both clusters are residential camps, showing the same types of activities. Therefore, the differences cannot be explained by chronological, seasonal or environmental issues, or by distinct activities. At the same time, both clusters have different degrees of internal variability, some of them may have a chronological and/or a geographical component. For instance, the IPC cluster has at least one geographical variation (IbPC from now on), in the area of the Ibicuy grasslands and the southern island area of the wetland, where the pottery decoration was mainly carried out using dots (Caggiano, 1984; Serrano, 1972; Torres, 1911). The archaeological properties of the IbPC are still not well known, and therefore more investigation is required in order to define its characteristics and their relationships with the other clusters, so far it has only been based on the type of pottery decoration.

The other original archaeological unit defined by Torres (1911) and mentioned above, is also basically defined by the pottery, which is decorated by lines and dots using a different technological style compare to the IPC. In addition, the typology of the vessels includes closed profile recipients of larger sizes and animal figures modeled in ceramic as handles. These contexts were described as "Goya-Malabrigo" (Badano, 1940; Ceruti, 2003; Ottalagano, 2013; Rodríguez, 2001; Serrano, 1946, 1972). We call it here G-M for short. Isotopic studies of human bones recovered from classical sites of this unit (Las Mulas 1 and Isla Los Marinos) show a diet based on depleted proteins linked to the $C_3$ photosynthetic pathway, which is in turn consistent with the isotopic values detected in the main food sources of these human groups: freshwater fish and continental mammals. The $\delta^{15}N$ values and the application of linear discriminant functions also indicate a low intake of plant foods (Loponte and Kozameh, 2009; Ottalagano and Loponte, 2016). Although the archaeobotanical information from the G-M sites has reported maize and other potential cultigens (see above), the diet of the individuals studied was based on animal proteins, especially freshwater fish. Moreover, the intake of maize was not isotopically detectable in 23 individuals, except in one of them, which could have had a small potential maize consumption.

On the contrary, isotopic studies in humans recovered from the ICP and PPC sites are scarce. The isotopic values of the diets of 4 individuals were presented elsewhere by Acosta and Loponte (2001), which showed diets based on depleted proteins with a high to moderate direct intake of plants within the $C_3$ photosynthetic pathway. Since then, no new results have been published. In order to equilibrate the available data related to the isotopic values of the diets of past populations of this wetland, we present this study based on human bones recovered from these last two archaeological units. We also compare them with the results previously obtained from the Amazonian horticulturalist and G-M sites. Additionally, we present new isotopic data of prey and other animals in order to expand our knowledge of the local food web, and to get a more accurate picture of the isoscape and past human diets.

## 2. Environmental background

The Paraná basin is an extensive and high-volume South American river that covers 3.5 millions square km, with headwaters above 15° SL, along a vast tropical area. The Paraná watercourse originates from rains associated with the South American Summer Monsoon (MSSA), which is in turn associated with the Inter Tropical Convergence Zone (ITCZ) (Gan et al., 2004; Vuille et al., 2003; Zhou and Lau, 1998). The tropical conditions of its water catchment areas in the center of South America extend along the basin to the Atlantic Ocean at 34° SL, where the wetland of the lower Paraná develops, which is the southernmost subtropical wetland in South America, covering around 17,000–19,000 square km. Here the main course of the Paraná River is divided into two branches (north and south) and in a large number of streams and lakes. Because the region presents a very small slope, the river runoff is very smooth. The environment is characterized by a multilayered riparian forest with a semi-continuous canopy with height of 8 to 15 m, associated with the fluvial banks of the Paraná and Uruguay rivers. However, most of the region is composed of herbaceous communities distributed in prairies, grasslands and reedbeds, interrupted by numerous small streams and lagoons. Most of them are connected or intermittently connected with the main watercourses (Cabrera, 1976; Kalesnik et al., 2008; Roesler and Agostini, 2012). This environment of high primary productivity cuts through the temperate Pampean steppe, facilitating the dispersal of flora, fauna and humid conditions from the northern areas, creating a giant azonal patch of resources. Most of the vegetable cover has a $C_3$ pattern (Madanes et al., 2013) as well as the sources of energy in the fluvial system (Marchese et al., 2014; Saigo et al., 2015).

## 3. Stable isotopes

The success of isotopic studies in the archaeological field is related to their capacity to obtain information about an individual's diet for the last 7–10 years of his/her life, especially when these analyses are carried out on bone tissue (Ambrose, 1993). Several studies have shown that the $\delta^{13}C$ values measured in an individual's collagen ($\delta^{13}Cco$ from here on) are enriched by about 5‰ compared with the diet. Thus, herbivorous diets based on resources with a $C_3$ photosynthetic pathway show values of approximately −21‰, while monoisotopic $C_4$ diets present values of around −7‰ (DeNiro and Epstein, 1978a, 1978b; Koch, 2007; Krueger and Sullivan, 1984; Lee-Thorp et al., 1989; Vogel and van der Merwe, 1977). In the inorganic fraction ($\delta^{13}Cap$ from here on), monoisotopic diets present magnitudes of −13.5 and −3‰ and below, respectively (Kellner and Schoeninger, 2007; Lee-Thorp and van der Merwe, 1987; Sullivan and Krueger, 1981). The carbon values from collagen reflect more closely the content of the protein intake in the diet, while those from apatite have a closer relationship with the overall diet (proteins + fats + carbs) (Ambrose and Norr, 1993; Katzenberg, 2008; Krueger and Sullivan, 1984; Tykot, 2006). Thus, the differences between the two carbon sources ($\delta^{13}Cco-ap$, or $\Delta^{13}C$) largely reflect the plant component of the diet (Krueger and Sullivan, 1984). This "spacing model" is used as an indicator of the trophic level of diets and/or to identify the marine components in them (Ambrose and Norr, 1993; Ambrose et al., 1997, 2003; Ambrose and Krigbaum, 2003; Harrison and Katzenberg, 2003; Lee-Thorp et al., 1989; Loftus and Sealy, 2012; Norr, 1995; Pate, 1994; Rand et al., 2013; Roksandic et al., 1988; Waterman et al., 2015a, 2015b; White et al., 2006). Larger differences are typical of herbivores, with mean values of $6.8 \pm 1.4‰$, while carnivorous diets are below $4.0 \pm 1.0‰$ (Ambrose and Norr, 1993; Ambrose and Krigbaum, 2003; Clementz et al., 2009; Krueger and Sullivan, 1984; Lee-Thorp et al., 1989; Loftus and Sealy, 2012). However, there are no absolute thresholds, and instead these should

be defined empirically, usually as range values more than a specific value, according to the region and to the particular organisms being analyzed (Ambrose and Norr, 1993; Kellner and Schoeninger, 2007). These thresholds also depend on the combination of photosynthetic proteins and carbohydrates ingested (Ambrose and Norr, 1993; Ambrose and Krigbaum, 2003; Ambrose et al., 2003; Cormie and Schwarcz, 1996; Kellner and Schoeninger, 2007; Metges et al., 1990; Stevens et al., 2008; Van Klinken et al., 1994, van Klinken et al., 2000). However, the spacing of the values related to trophic levels has been supported empirically in many studies, and reinforced when the nitrogen values are used in combination. In fact, the $\delta^{15}$N increases at a rate of 3–4‰ as the body incorporates foods with higher trophic levels (Bocherens and Drucker, 2003; Hedges and Reynard, 2007; Schoeninger and DeNiro, 1984). Thus, the combination of both carbon and nitrogen isotopes is used to estimate the trophic positions of the individuals (Ambrose et al., 1997, 2003; Ambrose and Norr, 1993; Froehle et al., 2010, 2012; Loftus and Sealy, 2012; Tykot, 2006; Warinner and Tuross, 2009).

Kellner and Schoeninger (2007) developed a model based on regression lines using both values of $\delta^{13}$Cco and $\delta^{13}$Cap in order to improve the diet analysis related to the differential intake of carbs, fats and proteins. Some authors have suggested that this model is limited due to methodological issues related to the metabolic process, the intake of other nutrients, as well as a lack of consideration of nitrogen values (Froehle et al., 2012; Loftus and Sealy, 2012; Warinner and Tuross, 2009). To overcome some of these problems, Froehle et al. (2012) developed a multivariate model incorporating the $\delta^{15}$N values from the calculation of discriminant functions, which are then plotted in clusters of known diets. This allows a more accurate evaluation of archaeological diets, especially those that incorporate $C_4$ plants such as maize, which has played a significant role in isotopic studies (Ambrose et al., 2003; Balasse et al., 1999; Boyd et al., 2008; Calo and Cortés, 2009; Gheggi and Williams, 2013; Gil et al., 2010; Hart et al., 2011; Froehle et al., 2012; Killian et al., 2012; Laguens et al., 2009; Metcalfe et al., 2009; Rand et al., 2013; Scherer et al., 2007; Slovak and Paytan, 2009; Smalley and Blake, 2003; Staller et al., 2006; Stronge, 2012; Tykot, 2002, 2004, 2006; White et al., 2006). All this background to the isotopic study of maize is particularly important to us due to the archaeological research related to the different kinds of manipulation and adoption of cultivated plants that have been discussed in local archaeology since its beginnings.

## 4. Materials and methods

In this study we present the results obtained from 23 humans (20 adults, two children and one infant) and 70 samples corresponding to the prey consumed by hunter-gatherers and that is representative of animals in the wetland ecosystem, totaling >180 isotopic values related to the local isoscape. Ten humans were recovered from the southwest Paraná riverbank and 13 samples from the flooded prairies in the south and southeast of the wetland. The human bones measured in the adults were selected mostly from ribs and long bones. In the infants and child-juveniles, ribs were selected due to their high turnover process, which fits the discussion of breastfeeding and the weaning process (Richards et al., 2002).

The humans analyzed here are mostly adults. Their stage of maturation was determined following the general criteria described in Buikstra and Ubelaker (1994). The ages of the infants and children were identified following the most reliable measures available in each case. The age of the individual CM-E2 (10 ± 1 months) is based on the femora and tibiae lengths (cf. Fazekas and Kóse in Schaefer et al., 2009). The age of the individual LAN-E4a (2–3 years) is based on humerus and clavicle measurements (cf. Maresh, 1970 in Schaefer et al., 2009), and the bone fusion stage (cf. Scheuer and Black, 2000). The age of the individual LAN-E1 (4–6 years) is based on tooth eruption and dental calcification (Moorrees et al., 1963; Ubelaker, 1989;). All the estimations of the

ages also fall also within the broader age parameters following Buikstra and Ubelaker (1994).

Most of the animal samples included here were recovered from archaeological sites located on the southwest bank of the lower Paraná River (see Fig. 2), except H. hydrochaeris, which was obtained from the Iberá wetland, located 500 km to the north. These bones were collected from animals that had died from natural causes (Corriale and Loponte, 2015). The values of Rhipidodonta variabilis (freshwater clam) were also ascertained from the muscle tissue of modern samples. Due to the "Suess effect" (Francey et al., 1999; Indermühle et al., 1999), we applied to these samples a time-dependent correction of − 0.005‰ per year between 1860 and 1960, and − 0.022‰ per year from 1960 (Chamberlain et al., 2005) until the year when these modern samples were collected. This correction provides an approximate value of $\delta^{13}$C for comparing ancient and modern ecosystems.

The isotopic analyses were performed at the Environmental Isotope Laboratory of the University of Arizona (sample codes EIL),[1] the SIRFER Laboratory at the University of Utah, the Center for Applied Isotope Studies at the University of Georgia (sample codes UGA), and at the Institute of Geochronology Isotope in Buenos Aires city (CONICET) (sample codes AIE). Some values of $\delta^{13}$C were obtained during the AMS dating process, especially in bone animals. These analyses were done in the NSF Arizona AMS Laboratory Department of Physics, University of Arizona (sample codes AA).

All the bone samples selected for this study were fragments of compact bone tissue with acceptable parameters of wt%C and wt%N (>13% and >4.8%, respectively). For the analyses based on collagen, only samples with adequate quantities of this element were retained for analysis (>1%; cf. Van Klinken, 1999) and within a ratio C/N between 2.9 and 3.6 (De Niro, 1985; Ambrose, 1990). The protocol for extracting collagen follows Longin (1971) and Tykot (2004). Some animal bones used in the AMS dating process have no C/N ratio available. However, among these species there are others which do have this ratio, with similar magnitudes. Good preservation of the late Holocene archaeological bones throughout the wetland has been well established until today; only three archaeological samples of almost 100 (~3%) with a known C/N ratio are outside the range 2.9–3.6. Five human values of $\delta^{13}$C were obtained during the AMS dating. Four of them have C/N ratios measured at INQUIMAE (Instituto de Química Física de los Materiales, Medio Ambiente y Energía, Universidad de Buenos Aires), which falls between 2.9/3.6. Only one human sample (Túmulo de Campana site 1, code 402; see Table 3) lacks a C/N ratio.

The removal of diagenetic carbonates followed the pre-treatment methods described in Koch et al. (1997), removing the adsorbed carbonate, which is more soluble than the carbonate structural, and increasing the reliability of the readings for the paleodietary analysis (Ambrose and Krigbaum, 2003; Garvie-Lok et al., 2004; Grimes and Pellegrini, 2013; Krueger, 1991; Lee-Thorp and van der Merwe, 1987, 1991; Tykot, 2004). The values for $\delta^{15}$N and $\delta^{13}$Cco, as well as the carbon and nitrogen content, were measured on a continuous-flow gas-ratio mass spectrometer. The samples were burned using an elemental analyzer coupled to a mass spectrometer. The standardization is based on acetanilide for elemental concentration, NBS-22 and USGS-24 for $\delta^{13}$C, and IAEA-N-1 and IAEA-N-2 for $\delta^{15}$N (EIL). The precision is better than ± 0.08‰ for $\delta^{13}$Cco (except in the INGES samples ± 0.2‰) and ± 0.2‰ for $\delta^{15}$N (± 1σ), based on repeated internal standards. There is a latent problem in isotopic studies when different laboratories are used, which is certainly applicable to comparative analysis of most of the archaeological literature related to this field. However, with the exception of data related to oxygen, a recent study of the variability of results among different labs proved to be insignificant interpretatively, especially when the samples are well preserved (Pestle et al., 2014).

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[1] This laboratory does not provide analysis code numbers, so the numbering in the respective tables correspond to our own internal parameters.
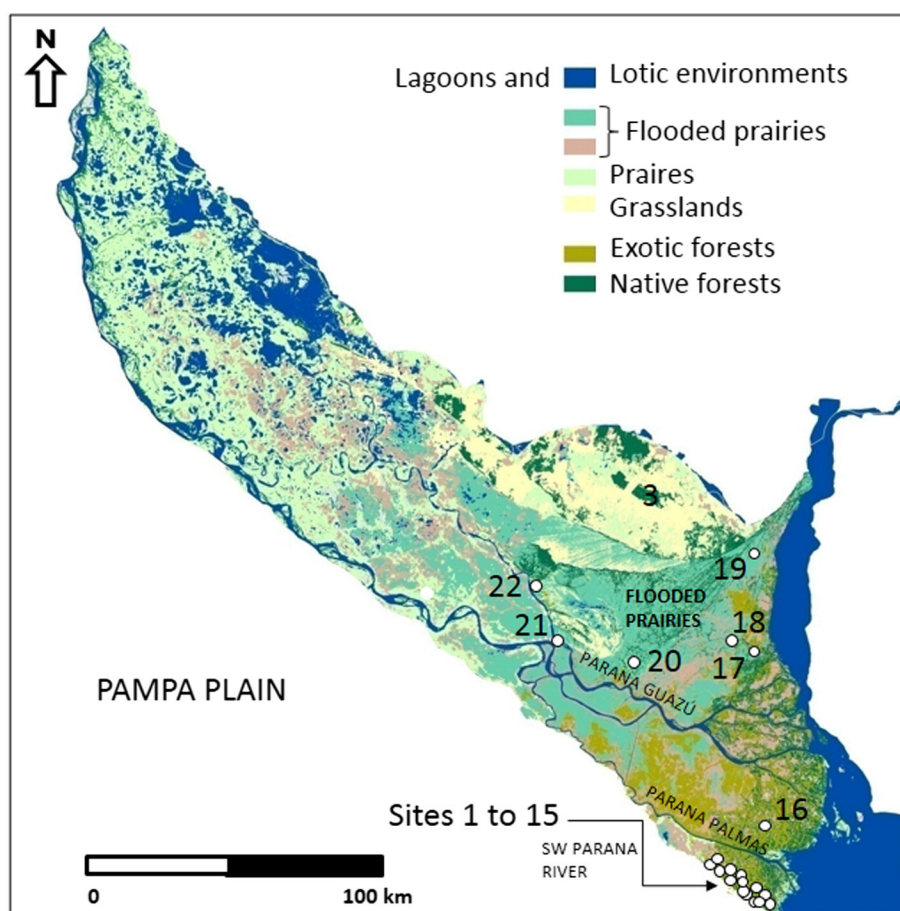
**Fig. 2.** Archaeological site locations included in this study. Sites 1 to 15) Arroyo Guazunambí; El Espinillo; Garín; El Cazador site 3; Túmulo de Campana sites 1 and 2; Las Vizcacheras, Rancho largo; Arroyo Sarandí; Punta Canal; Médanos de Escobar; Anahí; La Bellaca sites 1 and 2; Río Luján site 2. 16) Arroyo Fredes. 17) Cerro Lutz. 18) Las Animas. 19) Cerro Mayor. 20) Escuela 31. 21) Islas Lechiguanas 1. 22) La Argentina.

Multivariate variance analysis (MANOVA) was used to test for differences between the archaeological clusters. The dependent variables taken into account were collagen carbon, apatite carbon and nitrogen. The Pillai's test was selected because it is more robust against violations of assumptions. The Hotelling's test with the Bonferroni correction was used for multiple comparisons (Olson, 1976; Johnson and Field, 1993). When MANOVA showed significant differences, discriminant analysis (DA) was performed to determine which variables better discriminated between the groups.

## 5. Prey

Both species of hunted deer (*B. dichotomous* and *O. bezoarticus*) have an opportunistic dietary strategy (browser-feeder), with some intake of aquatic plants in the case of the first ungulate (Cosse et al., 2009; Tomas and Salis, 2000; Loponte and Corriale, 2012). Exploited semi-aquatic mammals (*M. coypus* and *H. hydrochaeris*) are generalist herbivores that feed on a wide variety of aquatic plants (Borges and Colares, 2007; Barreto and Herrera, 1998; Guichón et al., 2003; Corriale and Loponte, 2015). All of them are 100% herbivorous. The isotopic values of $\delta^{15}$N of all these mammals are typical of continental diets (~5.5‰; cf. Schoeninger and DeNiro, 1984), and the carbon sources are within a $C_3$ photosynthetic pattern except *H. hydrochaeris*, which has an average value of a mixed diet, but with a broad range between individuals, which varies from an almost pure $C_4$ to an almost pure $C_3$ diet (Corriale and Loponte, 2015) (see Tables 1 and 2).

*Didelphis albiventris* (white-eared opossum) was rarely present in the archaeological assemblages, but it is isotopically interesting because is an omnivorous terrestrial mammal. We lack a local analysis of diet, but in southern Brazil it is composed of insects, small vertebrates and large quantities of fruit (Cáceres, 2002) like other species of the genus *Didelphis* (Atramentowicz, 1988; Cajal, 1981; Cordero and Nicolas, 1987, 1992; Santori et al., 1995). The individual analyzed here shows a $C_3$ photosynthetic pathway, with an increased level of nitrogen compared to local herbivores (+1.3‰).

Terrestrial carnivores such as *Panthera onca* (jaguar) were not prey, but their canine teeth were used to make earrings. Their isotopic values are extremely interesting for the local food chain, since they are pure carnivores. The prey selection of this felid depends on local options, including large and small to medium-sized animals. In other regions of the Paraná Forest, its diet is composed mainly of larger terrestrial animals, especially deer, tayasuids and tapirs (Paviolo, 2010). There are no local studies in the lower Paraná wetland since this species has been extinct for a long time there, but both deer appear to be the most likely common prey. Its collagen values also shed a typical $C_3$ pattern, showing that the ecosystem is based mainly on $C_3$ plants. The nitrogen level is enriched +4.4‰ with respect to the average values of terrestrial herbivores (see discussion Section 7).

The other pure carnivore included in this study is *Lontra longicaudis*. The neotropical otter is defined as an ichthyophagus species (Chemes et al., 2010; Espitia et al., 2006; Restrepo and Botero-Botero, 2012). However, in several studies it is also described as opportunistic with high plasticity feeding behaviors related to seasonal changes. Its diet can include large quantities of crustaceans, insects and amphibians, but fish normally constitutes at least 50% of its total food (Chemes et al., 2010; Gori et al., 2003). The isotopic values obtained in L.

**Table 1**
Paraná wetland. Isotopic values of animal bone collagen, except *R. variabilis* (muscle tissue).

| Site | Scientfic name | Common name | Sample code | Lab. code | $\delta^{13}C_{co}$ | $\delta^{13}C_{ap.}$ | $\delta^{15}N$ |
|---|---|---|---|---|---|---|---|
| Arroyo Sarandí | *B. dichotomus* | Marsh deer | AS-102 | AIE 26925/6 | −20.9 | −12.8 | 4.7 |
| Campo Binaghi | *B. dichotomus* | Marsh deer | N/D | AIE 26947/8 | −21.0 | −12.3 | 7.6 |
| Bajada Guereño | *B. dichotomus* | Marsh deer | N/D | AIE26944 | | −12.2 | |
| Playa Mansa | *B. dichotomus* | Marsh deer | N/D | AIE 26946 | | −9.8 | |
| Punta Canal | *B. dichotomus* | Marsh deer | PC-C2-1 | AIE 26931/2 | −17.7 | −8.3 | 8.8 |
| Cerro Lutz | *B. dichotomus* | Marsh deer | CL1-Bd-1 | AIE 26923/4 | −21.6 | −15.5 | 4.7 |
| El Espinillo | *B. dichotomus* | Marsh deer | ES-C6-I-94 | AA103652 | −21.4 | | |
| La Argentina | *B. dichotomus* | Marsh deer | LA/C1-34 | AA97463 | −21.5 | | |
| Médanos Escobar | *B. dichotomus* | Marsh deer | ME-I-101 | AA97465 | −21.9 | | |
| Garín | *B. dichotomus* | Marsh deer | G-66 | AIE 26935/6 | −20.7 | −12.2 | 6.5 |
| Anahí | *B. dichotomus* | Marsh deer | A-700 | UGA 9907 | −20.3 | −10.3 | 6.0 |
| Anahí | *B. dichotomus* | Marsh deer | A-701 | AIE 26937/8 | −20.1 | −12.7 | 4.9 |
| Arroyo Fredes | *B. dichotomus* | Marsh deer | AF93 | AIE 26927/8 | −22.0 | −14.9 | 4.5 |
| Arroyo Guazunambí | *B. dichotomus* | Marsh deer | GZ-M2 | Beta 147109 | −19.0 | | |
| Arroyo Guazunambí | *B. dichotomus* | Marsh deer | GZ-113 | AIE 26929/30 | −21.8 | −12.9 | |
| La Bellaca 2 | *B. dichotomus* | Marsh deer | LBS2-17 | AIE 26941/2 | −17.1 | −10.7 | 5.4 |
| Túmulo Campana 2 | *B. dichotomus* | Marsh deer | TC-100 | Beta 172059 | −21.1 | | |
| Túmulo Campana 2 | *B. dichotomus* | Marsh deer | TC-101 | AIE 26933/4 | −21.5 | −13.8 | 5.4 |
| Cerro Mayor | *B. dichotomus* | Marsh deer | CM 20-30 | AA97469 | −21.7 | | |
| Cerro Mayor | *B. dichotomus* | Marsh deer | CM 160-170 | AA97457 | −21.2 | | |
| Islas Lechiguanas 1 | *B. dichotomus* | Marsh deer | IL 70-80 | AA97467 | −21.4 | | |
| Islas Lechiguanas 1 | *B. dichotomus* | Marsh deer | IL 90-100 | AA97461 | −21.2 | | |
| Río Luján site 2 | *B. dichotomus* | Marsh deer | RL/S1 | AA97458 | −21.3 | | |
| Escuela 31 | *B. dichotomus* | Marsh deer | E31/P/NS | AA103651 | −20.6 | | |
| Escuela 31 | *B. dichotomus* | Marsh deer | E31/P/NM | AA103650 | −21.7 | | |
| Escuela 31 | *B. dichotomus* | Marsh deer | E31/P/NI | AA103649 | −21.8 | | |
| El Cazador site 3 | *B. dichotomus* | Marsh deer | ECS3/64 | AA97470 | −16.8 | | |
| El Cazador site 3 | *B. dichotomus* | Marsh deer | ECS3/212 | AIE 26939 | −22.0 | −12.7 | 6.2 |
| Garín | *O. bezoarticus* | Pampas deer | G389 | EIL 2023 | −22.5 | −12.3 | 5.7 |
| Garín | *O. bezoarticus* | Pampas deer | G397 | EIL 2024 | −21.8 | −11.2 | 4.8 |
| Anahí | *O. bezoarticus* | Pampas deer | A-4317 | AIE20922 | | −12.0 | |
| Guazunambí | *O. bezoarticus* | Pampas deer | Gz-M1 | UGA 9908 | −18.8 | −9.3 | 5.2 |
| Guazunambí | *O. bezoarticus* | Pampas deer | Gz-M3 | AIE20924 | | −13.9 | |
| El Espinillo | *M. coypus* | Coypu | ES-C1-I-93 | AA103655 | −19.6 | | |
| Arroyo Sarandí | *M. coypus* | Coypu | AS 101 | AA103654 | −20.8 | | |
| Garín | *M. coypus* | Coypu | G227 | UGA 9905 | −17.9 | −6.9 | 4.3 |
| Anahí | *M. coypus* | Coypu | A-1370 | Beta 147108 | −19.0 | | |
| Cerro Mayor | *M. coypus* | Coypu | CM 220-230 | AA97466 | −19.3 | | |
| Río Luján site 2 | *M. coypus* | Coypu | RL/S2 | EIL 1006 | −21.6 | −11.3 | 6.5 |
| Islas Lechiguanas 1 | *M.coypus* | Coypu | 20-30 | AA97462 | −21.2 | | |
| Rancho largo | *M.coypus* | Coypu | RL 50-60 | AA97459 | −22.4 | | |
| Arroyo Fredes | *H. hydrochaeris* | Capibara | AF1000 | AA77309 | −12.0 | | |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh1 | AIE 24832 | −14.2 | | |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh2 | AIE 24833 | −19.0 | | |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh3 | AIE 24835 | −16.1 | | |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh4 | AIE 24837 | −20.2 | | |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh5 | AIE 24838 | −18.8 | | |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh6 | AIE 24839 | −15.3 | | |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh7 | AIE 24840 | −14.2 | | |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh8 | AIE 24841 | −11.7 | | |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh9 | Sirfer 12-7783 | −20.0 | | 5.0 |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh10 | Sirfer 12-7784 | −15.9 | | 4.4 |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh11 | Sirfer 12-7785 | −13.4 | | 4.6 |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh12 | Sirfer 12-7786 | −13.5 | | 4.2 |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh13 | Sirfer 12-7787 | −14.7 | | 4.6 |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh14 | Sirfer 12-7788 | −11.9 | | 3.9 |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh15 | Sirfer 12-7789 | −16.7 | | 5.5 |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh16 | Sirfer 12-7790 | −13.7 | | 5.1 |
| Esteros del Iberá | *H. hydrochaeris* | Capibara | Hh17 | Sirfer 12-7791 | −17.2 | | 5.9 |
| Islas Lechiguanas 1 | *Tayassu sp.* | Peccary | IL1/NS-1 | AA103659 | −20.5 | | |
| Anahí | *P. onca* | Jaguar | A-79 | EIL 1028 | −19.3 | −14.3 | 9.7 |
| La Bellaca site 1 | *L. longicaudis* | Otter | LBS1/11 | EIL 2060 | −21.6 | −13.1 | 10.1 |
| La Bellaca site 1 | *D. albiventris* | Opossum | LBS1/12 | EIL 2061 | −19.3 | −11.9 | 6.6 |
| Anahí | *P. granulosus* | Granulated catfish | A-600 | UGA 9906 | −17.6 | −10.2 | 5.5 |
| Garín | *Pimelodidae sp.* | Catfish | G228 | UGA 9909 | −18.1 | −9.4 | 6.1 |
| San Nicolas | *R. variabilis* | Freshwater clam | SN16 | AIE-25410 | −24.7 | | |
| San Nicolas | *R. variabilis* | Freshwater clam | SN17 | AIE-25411 | −23.8 | | |
| San Nicolas | *R. variabilis* | Freshwater clam | SN18 | AIE-25412 | −24.0 | | |
| San Nicolas | *R. variabilis* | Freshwater clam | SN19 | AIE-25413 | −23.5 | | |
| San Nicolas | *R. variabilis* | Freshwater clam | SN20 | AIE-25414 | −24.0 | | |

*longicaudis* show more depleted carbon sources and a higher nitrogen content than *P. onca*, related to the influence of its ichthyophagus diet (see Table 1, and Section 6).

All the fish exploited by humans are within a C₃ photosynthetic pathway. *Prochilodus lineatus* (shad) represents >50% of the fish biomass of the Paraná River (Tablado et al., 1988), and was probably the

**Table 2**

Isotopic values of the most common prey of hunter-gatherers in the Paraná wetland, late Holocene. The "N" column refers to the sample size for $\delta^{13}Cco$ and $\delta^{15}N$. For the $\delta^{13}Cap$ sample sizes, see Table 1. (*) Values corrected by the Suess effect following Chamberlain et al. (2005). (**) *Leporinus obtusidens, Pimelodus maculatus, Hoplias malabaricus, Salminus brasiliensis, Ageneiosus brevifilis, Pterodoras granulosus* and *Pseudoplatystoma reticulatum*.
(") Average based on the values published by Saigo et al. (2015), corrected by the Suess effect, and Loponte (2008). (+) Bulk value. (++) Values on muscle tissue. Sources: (1) This work. (2) Corriale and Loponte (2015). (3) Ottalagano and Loponte (2016). (4) Loponte et al. (in press).

| Scientific name | Common name | N | $\delta^{13}Cco$ (‰) | $\delta^{13}Cap$ (‰) | N | $\delta^{15}N$ (‰) | Weight (kg) | Source |
|---|---|---|---|---|---|---|---|---|
| *B. dichotomus* | Marsh deer | 26 | −20.7 ± 1.5 | −12.2 ± 1.9 | 11 | 5.9 ± 1.3 | 90–150 | (1) |
| *O. bezoarticus* | Pampas deer | 3 | −21.1 ± 1.9 | −11.7 ± 1.7 | 3 | 5.2 ± 0.5 | 18–25 | (1) |
| *H. hydrochaeris* | Capibara (*) | 18 | −14.0 ± 2.7 | | 9 | 4.8 ± 0.6 | 30–60 | (2) |
| *M. coypus* | Coipo | 7 | −20.2 ± 1.5 | −9.1 ± 3.1 | 2 | 5.4 ± 1.5 | 4–8 | (1) |
| *P. lineatus* | Shad (*) | 112 | −24.5 ± 3.0 | | 17 | 8.3 ± 1.2 | 0.5–5 | (3) |
| *P. granulosus* | Granulated catfish (") | 2 | −20.8 ± 4.5 | | 2 | 7.2 | 0.5–6.5 | (4) |
| Other fish (+) | (*) (**) | 14 | −23.7 ± 3.0 | | 14 | 8.0 ± 1.4 | 1–60 | (3) |
| *R. variabilis* | Freshwater clam (*) (++) | 5 | −22.3 ± 0.4 | | | | 0.02 | (1) |
| Mean (mammals) | | | −19.0 ± 3.3 | −10.7 ± 1.5 | | 5.3 ± 0.4 | | |
| Mean (fish) | | | −23.0 ± 1.9 | | | 7.8 ± 0.5 | | |

most fished species in the wetland (Loponte, 2008). It is a detritivorous bottom-feeder, which ingests large amounts of particulate organic carbon in bulk, epiphyton, zooplankton and phytoplanktonic and periphytic algae (Bayo and Cordiviola de Yuan, 1996; Marchese et al., 2014). Therefore, it can be classified as an omnivorous fish from the nitrogen sources point of view. *Pterodoras granulosus* (granulated catfish), another omnivorous species, is together with the shad, the best represented species in the archaeological assemblages (Acosta and Musali, 2002; Arrizurieta et al., 2010; Loponte, 2008; Sartori and Colasurdo). Other less abundant fish in archaeofaunal collections, but representative of the Paraná system, are *Leporinus obtusidens, Pimelodus maculatus, Hoplias malabaricus, Salminus brasiliensis, Ageneiosus brevifilis, Pseudoplatystoma reticulatum, Cyphocharax platanus, Schizodon borellii* and *Brycon orbignanus*. All of them show more negative values in carbon sources and a higher nitrogen level than local terrestrial mammals, as in many examples in freshwater ecosystems throughout the world (*i.e.* Hedges et al., 2006; Katzenberg and Weber, 1999; Tykot, 2002, 2004). Within the fish ensemble, there are some differences in nitrogen content (SD = ±1.4‰), since some are omnivorous and others carnivorous (Saigo et al., 2015). We present these magnitudes as bulk values, except for shad, due to its economic significance for past populations.

Finally, freshwater clams (*Rhipidodonta variabilis and Diplodon* sp.) are filterer mollusks, and also shed typical $C_3$ values (see tables 1 and 2). There is no information on the nitrogen content of this species in the area, but some values obtained from the related taxon *Diplodon parellelopipedum* in the middle Paraná demonstrate high magnitudes close to omnivorous fish (Marchese et al., 2014). Clams seem to have played a marginal role in the human diet in the past, although there are important middens at a few sites. Exploitation seems to have been more opportunistic and/or as an alternative to specific situations of an irregular food supply, rather than strategies developed steadily over time, although this topic requires more research.

The isotopic magnitudes obtained from different components of the local fauna used in this study are listed in Table 1; meanwhile, Table 2 summarizes the values of the main prey selected by hunter-gatherers, including the results published by other authors.

## 6. Wild and cultivated plants

In the southern lower Paraná wetland, 261 wild native plant species have been recorded, 90% of them are within a $C_3$ pattern. In turn, 63 species have been classified as potentially edible. Only 10% have a $C_4$ photosynthetic pattern, the rest are $C_3$ plants (Madanes et al., 2013). The wild plant most commonly recovered from archaeological sites, and which is one of the few identified unambiguously, corresponds to the seeds of the Pindó palm (Acosta and Ríos Román, 2013; Loponte, 2008). Starch grains were also identified in small grinding artifacts, which probably correspond to *Prosopis* spp., a genus of legumes that produces edible seeds ($C_3$) (Acosta et al., 2013).

The remainder of the plants that have been reported as being associated with archaeological occupation along the entire wetland, and which would have been cultivated by local groups, all have a $C_3$ photosynthetic pattern, except maize[2] (see Table 3). The values of this crop obtained from different parts of American humid and subtropical lowlands as well as from temperate lowlands show similar magnitudes, averaging −9.7‰ (Coltrain and Janetski, 2013; Warinner et al., 2013). This is probably the only significant $C_4$ plant that could have been included in a past diet. All these cultivated plants have a low nitrogen level (~+3‰), except *Ipomea batatas* and the legumes (*e.g. phaseolus vulgaris*), which show lower values (close to 0–1‰), due to their different nitrogen fixation (Coltrain and Janetski, 2013; Hart et al., 2002, 2007; Pennycock, 2013; Szpak et al., 2014; White et al., 2001) (see Table 3). Cucurbits have many closely related species (*Cucurbita pepo, C. moschata, C. maxima* and *C. argyrosperma;* cf. *C. mixta*), which are widely distributed throughout South America, whose carbon and nitrogen values are similar between them (Reed, 1998).[3]

## 7. Humans

The bulk carbon values obtained for local hunter-gatherers from both archaeological clusters (PPC + IPC) show a $C_3$ monoisotopic trend, with a depleted $\delta^{13}Cco$ mean of −20.0 ± 1.0‰. Similarly, the average $\delta^{13}Cap$ of −12.1 ± 1.5‰ reflects an almost purely monoisotopic diet (cf. Kellner and Schoeninger, 2007; Lee-Thorp and van der Merwe, 1987; Sullivan and Krueger, 1981). There is scant variability within the sample related to both collagen and apatite carbon sources (CV = 5% and 12.4%, respectively). The infant CM-E2 (Cerro Mayor) has a more negative value, probably due to the intake of different foods (see the discussion below in this section) and the individual GI (Garín) has the most enriched one, except in this last individual perhaps, no maize intake has been isotopically detected. Also, there is no influence of prey with mixed diets or closer to the $C_4$ photosynthetic pattern such as the capybara, which is consistent with its low incidence in the faunal assemblages. It is quite clear that all the proteins, fats and carbs were derived from $C_3$ sources (see Table 4 and Fig. 3).

If we compare the carbon sources in the humans recovered from the ICP sites to those from the PPC sites, there are no statistically significant differences (IPC $\delta^{13}Cco$ −19.4 ± 1.5‰; PPC $\delta^{13}Cco$ −20.2 ± 1.3‰; $T = 0.94$; $p = 0.36$) nor in apatite (IPC $\delta^{13}Cap$ −11.1 ± 1.37‰; PPC $\delta^{13}Cap$ −12.3 ± 1.45‰; confidence interval (CI) of PPC sites = −12.9‰/−11.7‰). However, there are differences in nitrogen.

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[2] There are some few references to *Chenopodium* sp., *Amaranthus* sp. and *Manihot* sp. ($C_4$), which have wild representatives in the area. No reliable information was provided about if they are cultivated nor the association between them and humans.

[3] Different and highly variable are the values in several samples of archaeological *Cucurbita spp.*, recovered at arid lowlands, whose nitrogen cycles are linked to water stress (*e.g.* Gil et al., 2010).

**Table 3**

Carbon and nitrogen values of plants reported from archaeological sites. Sources: (1) Coltrain and Janetski (2013). (2) based on Hart et al. (2002, table 2). (3) Nitrogen value after Pennycock (2013). (4) Loponte et al. (in press).

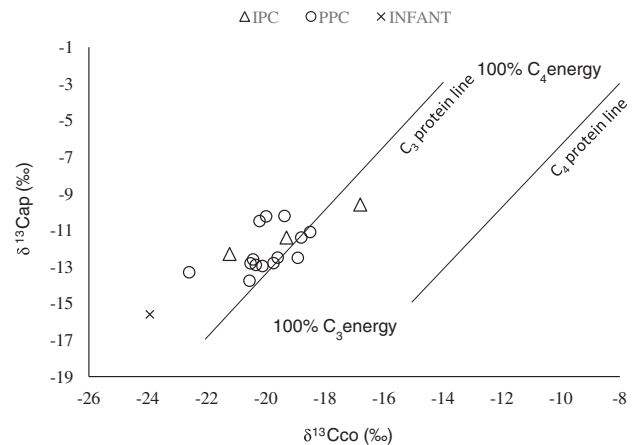| Scientific name | Common name | N | $\delta^{13}Cco$ (‰) | $\delta^{15}N$ (‰) | Source |
|---|---|---|---|---|---|
| *Zea mays* | Maize | 32 | −9.7 ± 0.8 | 3.0 ± 1 | (1) |
| *Cucurbita pepo* | Squash | 6 | −22.8 ± 0.7 | 3.2 ± 0.7 | (1) |
| *Phaseolus vulgaris* | Beans | 24 | −26.6 ± 1.1 | 1.1 | (2–3) |
| *Ipomea batatas* | Sweet potato | 1 | −25.5 | 0.3 | (3) |
| *Syagrus romanzoffiana* | Pindo Palm | 3 | −25.1 ± 0.8 | 3.8 ± 0.3 | (4) |

In fact, the humans recovered from the IPC sites show lower values than those from the PPC sites ($\delta^{15}N$ 8.9 ± 0.8‰ vs. 10.5 ± 0.8‰; confidence interval of PPC sites = 9.8/11.1). Infants and children were excluded from the latter due to the influence of breastfeeding. The higher levels of nitrogen in the PPC humans should be related to increased fish consumption, since fish have higher nitrogen values than terrestrial mammals (7.8 ± 0.5‰ vs. 5.3 ± 0.4‰, see Table 2). Indeed, between the human and fish mean values there is a fractionation average of ~3‰, which reflects a diet preponderantly influenced by fish consumption, which can concurrently explain the trophic position of humans in the local food web (see Fig. 4). On the contrary, plants had a very limited impact on the hunter-gatherers, as can be seen in Fig. 4, with almost no possibility of having made a significant contribution to the diet, except in two individuals recovered from the IPC sites.

The importance of fishing is visible not only for the nitrogen values, but also carbon. Comparing the average collagen values of the three main mammals consumed (marsh deer, pampas deer and coypu; $\delta^{13}Cco$ −20.0 ± 4.5‰) with the human bones recovered from the PPC sites (adults and juveniles only, $\delta^{13}Cco$ $x_{14}$ = −20.0 ± 1‰) there is no fractionation. The expected difference between the isotopic values of the prey and predator collagen ranges from 0.8 to 3‰ (Bocherens and Drucker, 2003; Schwarcz, 1991; Szepanski et al., 1999; Topalov et al., 2012; van der Merwe, 1989). Freshwater fish have a depleted value in collagen carbon, which can explain the fractionation between humans and their carbon sources.



**Fig. 3.** Biplot of the values for $\delta^{13}Cco$ and $\delta^{13}Cap$ for individuals recovered from the ICP and PPC sites following the linear model proposed by Kellner and Schoeninger (2007).

The values obtained from both carnivores are consistent with this interpretation. Between the jaguar and terrestrial prey there is a typical fractionation rate in collagen carbon and nitrogen (+1.4‰ and +4.4‰ respectively). In turn, the ichthyophagous otter (*L. longicaudis*) has a higher level of nitrogen than the jaguar, due to more intake of fish, but it is lower than humans, because the otter has a broader diet that includes crustaceans, insects and amphibians. Thus, humans had a more ichthyophagus diet than *L. longicaudis*. Although metabolic differences could exist between different species, the results obtained are consistent throughout the nitrogen fractionation, where humans are indisputably at the top of the nitrogen chain.

In both the humans recovered from the IPC sites located on the southwest bank of the Paraná River, the values are slightly different. In one of them (G1, see Table 4), the carbon sources are enriched close to a mixed diet, with a lower level of nitrogen. The other individual (A-121, see Table 4) has a negative value in carbon as the others belong
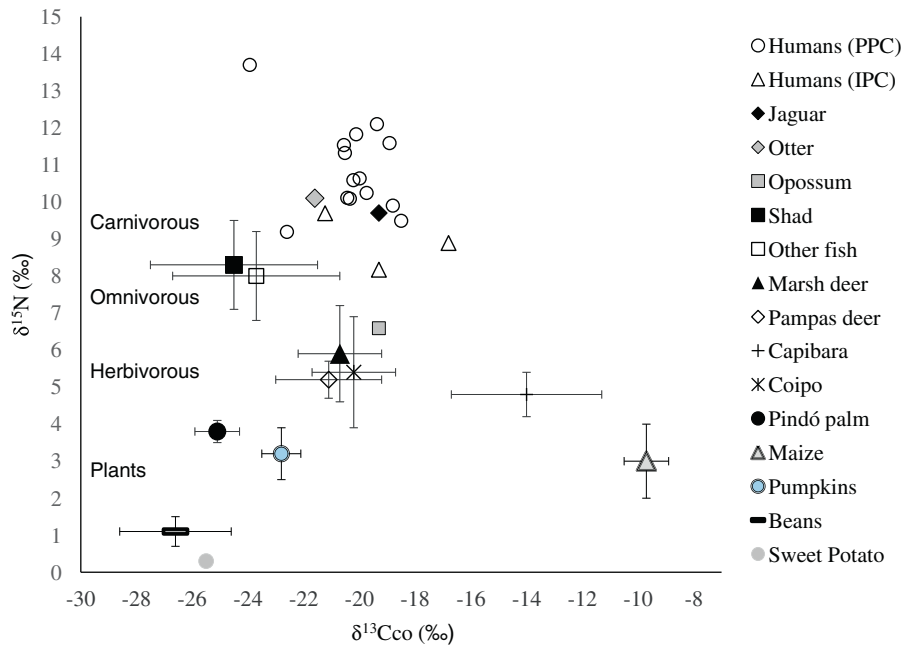
**Table 4**

Isotopic values of the human bones included in this study.

| Sites | Cluster | Sample code | Lab. code | Sex/age | $\delta^{13}Cco$ (‰) | $\delta^{13}Cap$ (‰) | $\delta^{15}N$ (‰) | $^{14}C$ | $^{14}C$ Code |
|---|---|---|---|---|---|---|---|---|---|
| Túmulo de Campana 1 | IPC | 402 | AA100007 | Fem./adult | −18.7 | | | 1754 ± 49 | AA100007 |
| Arroyo Sarandí | IPC | 6477-23-14 | UGA 10788 | -/adult | −20.2 | | | 1290 ± 40 | UGA 10788 |
| Arroyo Sarandí | IPC | 6478-24-18 | AIE 12366 | -/adult | −20.3 | | | | |
| Garín | IPC | G1 | UGA 8783 | Masc./adult | −16.8 | −9.6 | 8.9 | 1360 ± 70 | LP -3082 |
| Anahí | IPC | A-121 | UGA 8782 | Male/adult | −19.3 | −11.4 | 8.2 | | |
| La Bellaca site 1 | PPC | LBS1-33 | UGA 8780 | Fem./adult | −18.8 | −11.4 | 9.9 | | |
| La Bellaca site 2 | PPC | LBS2-12 | UGA 8781 | -/>13 years | −18.5 | −11.1 | 9.5 | | |
| El Cazador site 3 | PPC | EC-E1 | EIL-2050 | Male/adult | −20.3 | −12.9 | 10.1 | | |
| El Cazador site 3 | PPC | EC-E2 | EIL-2051 | Male/adult | −20.4 | −12.6 | 10.1 | 1031 ± 36 | AA97464 |
| El Cazador site 3 | PPC | EC-E3 | EIL-2052 | Male/adult | −22.6 | −13.3 | 9.2 | | |
| La Argentina | IbPC | LA-E2 | EIL-2040 | Male/adult | −21.2 | −12.3 | 9.7 | 979 ± 44 | AA103642 |
| Cerro Lutz | PPC | CL1-E3 | AA77310 | Fem./adult | −20.3 | | | 976 ± 42 | AA77310 |
| Cerro Lutz | PPC | CL1-E9 | AA77311 | Male/adult | −19.7 | | | 795 ± 42 | AA77311 |
| Cerro Lutz | PPC | CL-RS1 | AIE 15193 | -/adult | −19.6 | −12.5 | | | |
| Cerro Lutz | PPC | CL1 E1 | EIL-2041 | Male/adult | −20.1 | −13.0 | 11.8 | 1116 ± 45 | AA103643 |
| Cerro Lutz | PPC | CL1-E10 | EIL-2042 | Male/adult | −20.2 | −10.5 | 10.5 | 730 ± 70 | LP-1711 |
| Cerro Lutz | PPC | CL1-E14 | EIL-2043 | Male/adult | −18.9 | −12.5 | 11.5 | | |
| Cerro Lutz | PPC | CL1- E20 | EIL-2044 | Fem./adult | −19.7 | −12.8 | 10.2 | | |
| Cerro Lutz | PPC | CL1-E6 | EIL-2045 | Male/adult | −20.5 | −12.8 | 11.3 | | |
| Cerro Mayor | PPC | CM-E1 | EIL 2046 | Male/juvenile | −20.0 | −10.2 | 10.6 | 1665 ± 45 | AA97468 |
| Cerro Mayor | PPC | CM-E2 | EIL-2047 | -/10 months | −23.9 | −15.6 | 13.7 | | |
| Las Animas | PPC | LAN-E4a | EIL-2048 | Fem./2–3 years | −19.3 | −10.2 | 12.1 | | |
| Las Animas | PPC | LAN-E1 | EIL-2049 | Male/4–6 years | −20.5 | −13.7 | 11.5 | 1121 ± 315 | AA97460 |
| N | | | | | 23 | 18 | 17 | | |
| Mean | | | | | −20.0 | −12.1 | 9.9 | | |
| S.D. | | | | | 1.0 | 1.5 | 1.9 | | |
| Max. | | | | | −23.9 | −15.6 | 12.1 | | |
| Min. | | | | | −16.8 | −9.6 | 3.7 | | |
| Percentile 25% | | | | | −20.4 | −12.9 | 9.5 | | |
| Percentile 75% | | | | | −19.3 | −11.1 | 11.3 | | |

**Fig. 4.** Values of $\delta^{13}Cco$ and $\delta^{15}N$. Humans and food sources based on Tables 1 and 2.

to the PPC sites, but with a low nitrogen level close to the G1 individual. These data imply a moderate intake of plants, with a significant decrease in fish consumption. Thus, the isotopic data constitute an independent source that reinforces the results obtained from the faunal analysis, where an increased emphasis on fishing at the PPC sites was noted compare to the IPC sites (Loponte, 2008).

While we still have only a few individuals that are directly dated, the tendency shows an increase in carbon depleted foods over time. Although here the results are affected if the measured individuals come from one cluster or another, it is useful to rule out the alleged importance of maize in the diet (see Fig. 5). A similar trend was observed in individuals recovered from the G-M sites, where there is no progressive enrichment of carbon sources. On the contrary, the nitrogen levels are higher when the samples are more recent, showing an increase in fish dependence (Ottalagano and Loponte, 2016).

Within the sample there is one infant (10 months), one infant-child (2–3 years) and one child (4–6 years) recovered from two different PPC sites. This is an opportunity to discuss breast-feeding and weaning, a

topic without any background in the archaeological literature of the region. Infant feeding practices influence the demographic structure of a population due to its close relation to the mean interbirth interval, and are thus a key to understanding other organizational components of a society (Kachel et al., 2011; Kelly, 1995; Konner, 2005; Lee, 1996; Waters-Rist et al., 2011). To discuss this issue properly from an archaeological point of view, an adequate record of infants and women is essential (Katzenberg and Pfeiffer, 1995; Herring et al., 1998; Dupras et al., 2001; Herrscher, 2003; Schurr and Powell, 2005; Richards et al., 2006; Jay et al., 2008; Waters-Rist et al., 2011; Eerkens and Bartelink, 2013). Unfortunately, infants recovered from the region are rare in museum collections, probably due to a biased methodology of recovery and analysis, and modern excavations in large cemeteries have only been conducted recently. In turn, the individuals listed in Table 2 are sex biased because there are only two adult females with nitrogen values recovered from the PPC sites. So, the quantity and quality of the samples available is quite small and partial to discussing such complex topics such as breastfeeding and weaning, particularly when this behavior has many sources of variation, and thus a high level of heterogeneity (cf. Waters-Rist et al., 2011). However, the analysis of these three individuals below 6 years old is a start in exploring these topics in the area, especially when the values obtained are significantly different from adults.

The infant CM-E2 recovered at Cerro Mayor was buried with the juvenile male CM-E1. He was 10 months old at death. The high level of nitrogen ($\delta^{15}N$ 13.7 ± 0.2‰), probably due to breastfeeding, makes him seem like an outlier in Figs. 3 and 4, quite different from the average nitrogen level of the adults of this cluster recovered from the sites located in the same area (flooded prairies) ($\delta^{15}N$ $x_6 = 11.0 \pm 0.6$‰). The sources of carbon in this infant ($\delta^{13}Cco$ −23.9‰) are depleted compared with any of these two subsamples of adults ($\delta^{13}Cco$ $x_{10} = -20.0 \pm 0.6$‰ in flooded prairies and $x_{10} = -20.1 \pm 1.6$‰ the southwest bank, see Table 4). So, there is a "carnivore effect" (cf. Dupras et al., 2001; Richards et al., 2002) in the nitrogen values, probably due to a milky diet, but not in carbon sources, whose magnitude could be a reflection of the intake of soft and moist foods such as porridge derived from $C_3$ plants. The practice of incorporating solid foods while breastfeeding is continuing is well known in the archaeological literature (Wright and Schwarcz, 1998). The other individuals (LAN-E4a, 2–3 years and LAN-E1, 4–6 years) show lower nitrogen levels
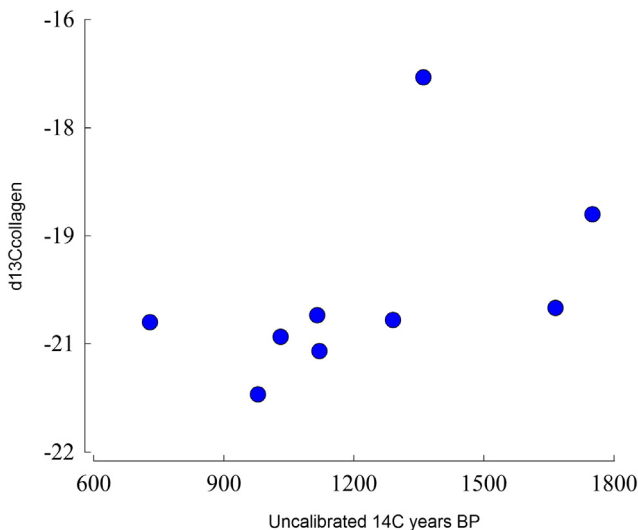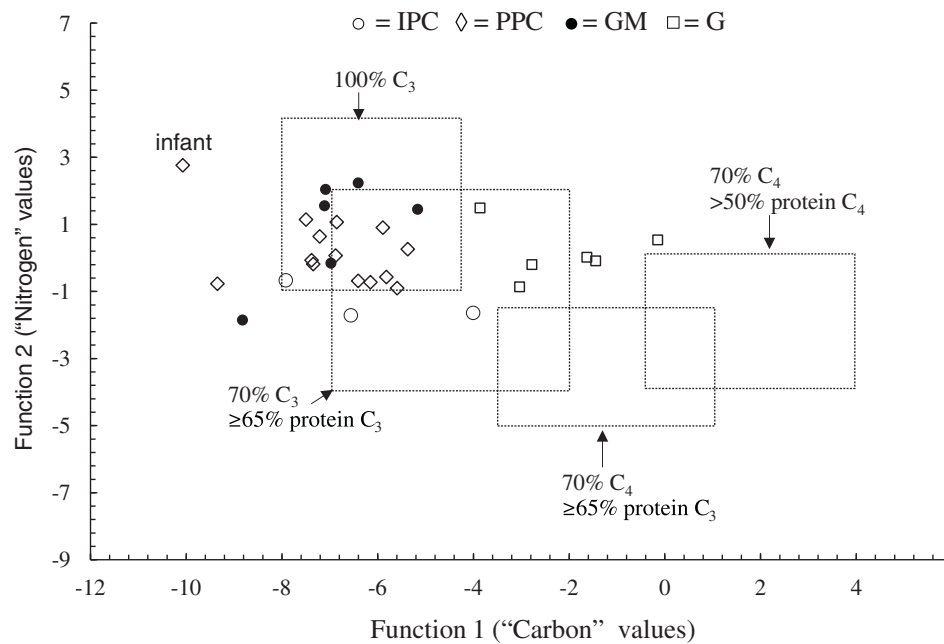


**Fig. 5.** Isotopic trend in the values of $\delta^{13}Cco$ (‰) over time (infants excluded).

**Fig. 6.** F1 and F2 discriminant function values from individuals recovered from the sites of the archaeological units mentioned in the text, plotted against previously generated dietary clusters (see Froehle et al., 2012). IPC = Incised Potter cluster (IbPC included). PPC = Plain Pottery cluster. GM = Goya-Malabrigo. G = Guaraní.

($\delta^{15}$N 11.4 ± 0.2‰ and 11.5 ± 0.2‰, respectively), already similar to the adult values in this cluster recovered from the same area (flooded prairies; $\delta^{15}$N $x_6$ = 11.0 ± 0.6‰), suggesting an early weaning process and a dietary shift at or before the age of 2–3 years, which is typical in other hunter-gatherer societies (Kelly, 1995:248).

## 8. A regional overview

Humans with mixed diets show bone collagen values ranging between −17.0‰ and −14.0‰, which could have been made up of 25–50% $C_4$ plants and/or $C_4$ plant-based animal protein (Coltrain and Leavitt, 2002). Only one sample (G1 from Garín site; $\delta^{13}$Cco −16.8‰) falls (marginally) within these parameters, close to those observed in Amazonian horticulturalists (see Fig. 6). More samples are needed to determine if he represents an extreme of the variability observed in local hunter-gatherers, or integrates a population with an enriched diet. In order to explore this topic from a regional point of view, we applied the discriminant functions developed by Froehle et al. (2012), and we included in the analysis the values obtained in the human bones of hunter-gatherers recovered from the classical G-M site (Los Marinos) and another recently discovered (Escuela 31). We also included the Guaraní values, already published and discussed (Loponte et al., in press; Ottalagano and Loponte, 2016). As can be seen in Fig. 6, only the Guaraní, who were true horticulturalists of maize, present a mixed diet with a significant intake of $C_4$ carbs. It is also quite clear that complex hunter-gatherers recovered from the PPC and G-M sites show a $C_3$ photosynthetic pattern concurrently with the most carnivorous intake (see also Fig. 7). We already see that both individuals recovered from the ICP sites located on the southwest bank of the Paraná River show a moderate intake of plants. One of them is more related to a $C_3$ intake, while the other shows some intake of $C_4$ carbs (G1 individual). It is important to recognize that in between this fluvial bank and the adjacent Pampa plain, an important xeromorphic forest with species with edible seeds developed. In fact, this availability of plant foods could be the source of the slightly lower nitrogen level in the individuals recovered from the PPC sites located here, compared to those recovered from the flooded prairies ($\delta^{15}$N $x_5$ = 9.8 ± 0.9‰ vs. $\delta^{15}$N $x_6$ = 11.0 ± 0.6‰ respectively).

Using centroids, the humans recovered from G-M and PPC show similar diets, close to purely carnivorous animals from the wetland. The carbon sources in the humans from the IPC sites, although slightly enriched, are similar, but values of Function 2 are clearly below. Between all of them and the Guaraní samples, there is a significant isotopic silence in Function 1 (Fig. 7). We also included here a centroid for the most common herbivorous prey since the new data obtained are listed in Table 1. Taking into account the three isotopic values (collagen and apatite carbon and nitrogen) the PPC and G-M archaeological clusters show no difference, but between them and the Guaraní there is a significant one (Pillai's trace = 3.5, $p$ < 0.0015).[4]

## 9. Complementary data

The limited importance of carbs in the diet of hunter-gatherers in the Paraná wetland is also evidenced by the low level of caries and other oral pathologies, since plant consumption, and especially cultivated ones, has a multiplying effect on their occurrence (Cohen and Armelagos, 1984; Buikstra and Ubelaker, 1994; Larsen, 1984; Larsen et al., 1991; Larson, 1995; Rose et al., 1984; Turner, 1979). Many hunter-gatherer societies show a caries rate lower than 7% prior to the adoption of maize (Larsen 1997; Turner, 1978, 1979), but many wild plants also have a high carbohydrate content, so that they are also a source of cariogenic foods (Hart et al., 2011). Thus, the incidence of caries is an indicator used in dietary reconstruction in archaeological studies.

In the middle and lower Paraná basin a previous study with 623 teeth corresponding to 39 individuals recovered from eight G-M sites showed a caries rate of 4.9%, a typical value for hunter-gatherers (Cornero and Puche, 2000).[5] A more detailed analysis with samples recovered from Los Marinos (G-M site), also shows representative values of non-agricultural populations (0.03 caries per tooth and 0.3 caries per

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[4] IPC was not considered in this test due to the small simple size.
[5] At the Nicanor Molinas site, the caries rate increased to 11%, but this higher value is very sensitive to the small sample available in this collection (nine teeth). At the Isla Barranquita site, a sample of 49 teeth shows 13% caries, which is clearly a higher value than the rest of the samples analyzed in that study, but again, quite small compare with Arroyo Aguilar and Arroyo Arena, with the largest samples (Cornero y Puche 2000).
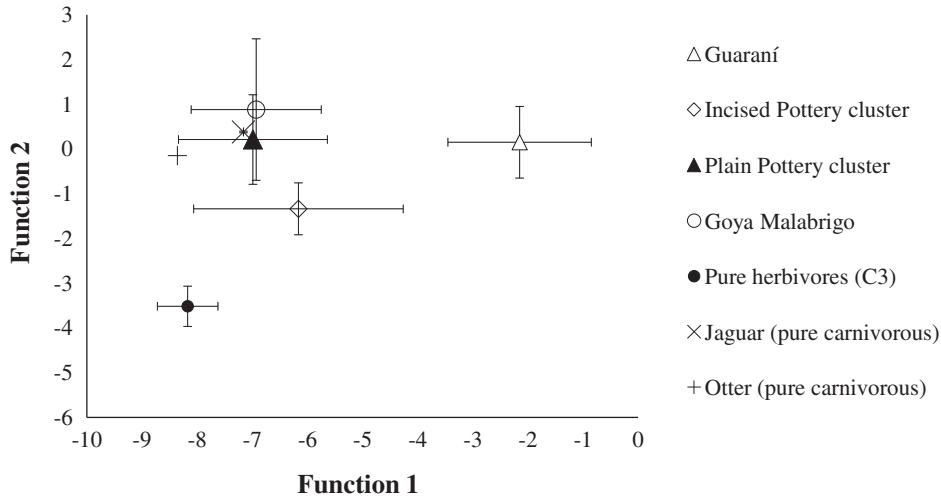
**Fig. 7.** Centroids of discriminant function values (after Froehle et al., 2012) from individuals recovered from the different archaeological units in the Paraná wetland. The pure herbivore group includes *B. dichotomus, O. bezoarticus* and *M. coypus*.

individual) (Kozameh and Barbosa, 1996; L'Heureux, 2000). A recent study was done with 2100 teeth belonging to almost 300 individuals recovered from complex hunter-gatherer sites located in the wetland (Mazza and Barrientos, 2012). Most of them were obtained during the excavations between the end of the XIX century to the early beginning of the XX century by the pioneers of local archaeology, as well as the first technicians from the La Plata Museum (University of La Plata), where this huge collection is curated. All these samples were collected at sites more modern than 2000 years BP, since they are located in young geomorphological areas in the wetland. We also included most of the humans recovered from the sites listed in Table 3. Because not all those contexts curated in La Plata Museum are clearly identified in terms of the archaeological units currently used, the results are presented as a bulk value for hunter-gatherers. The results show a low caries rate per tooth (0.013) and per individual (0.079). Although there is a high variability in the incidence of the cariogenic process in the populations that prevents establishing a strict threshold for determining diets

(*cf.* Lanfranco and Eggers, 2012), the caries rate as well as premorten tooth loss and pathological dentoalveolar lesions are low and consistent with values reported in other hunter-gatherer societies in America (Mazza and Barrientos, 2012; see Fig. 8).

Other indirect data that are consistent not only with proteins as a source of food, but fishing as the main subsistence activity, are the identification of auditory exostoses among past populations in the region. This pathology is caused by prolonged exposure to cold water rather than genetic disorders (Kennedy, 1986; Kuzminsky et al., 2016; Okumura et al., 2007; Standen et al., 1985, 1997). An analysis of 176 crania recovered from 21 archaeological sites of hunter-gatherers in the region (listed in Table 3 and curated in the La Plata Museum collection), detected this pathology in 6.25% of the individuals. All of them are adult males. This moderate prevalence, sex-based and age-based, agrees with the expected levels for populations related to systematic fishing activities with immersion (Mazza, 2015). Precisely speaking, one the most common fishing techniques during historical times in the Paraná
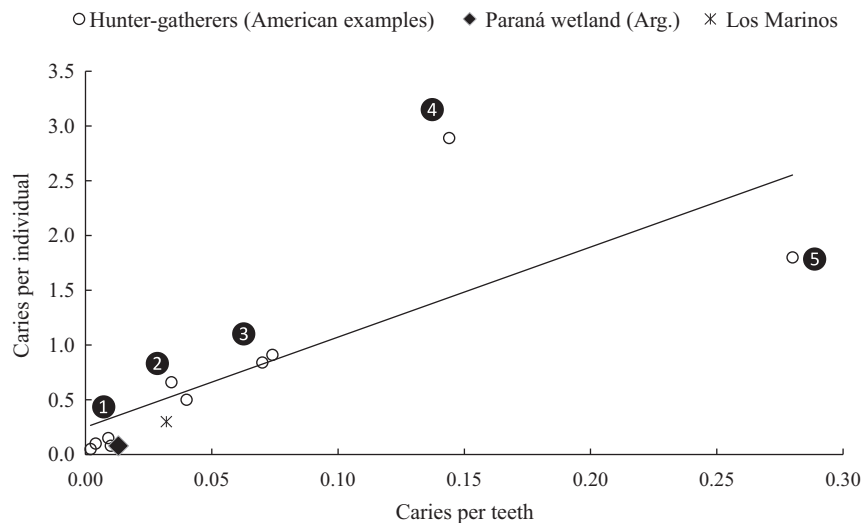


**Fig. 8.** Caries rate in several archaeological populations. Group 1 = Paleo Americans (USA); hunter-gatherers from the Pampean region (Early Holocene); Pre-farmers from Georgia and Florida (USA) and hunter-gatherers from Tierra del Fuego (Argentina). Group 2 = hunter-gatherers from the Pampean region (Late Holocene); Indian Knoll (USA). Group 3 = Fourche Maline (USA) and other hunter-gatherers from Tierra del Fuego (Argentina). 4 = Ipiutak (Eskimo; USA). 5 = Seminole Sink (Archaic; USA). *Paraná wetland*, sites included: Paraná Ibicuy 1; Mazaruca; Escuela 31; Las Ánimas; Cerro Lutz; Paranacito; Túmulo Brazo Gutiérrez; Túmulo I Brazo Largo; Túmulo II Brazo Largo; Arroyo Los Tigres; Túmulo I del Paraná Guazú; Túmulo 2 del Paraná Guazú; Túmulo de Campana sites 1 and 2; Anahí; El Cazador site 3; Garín; La Bellaca sites 1, 2 and 3 (after Mazza and Barrientos, 2012). Los Marinos sites taken from L'Heureux (2000).

basin, and probably in the Late Holocene, was immersion related, with a type of net used by the local populations (Arenas, 2003; Nordenskiöld, 1912; Scarpa, 2007).

## 10. Final remarks and future directions

Between the hunter-gatherers and Amazonian horticulturalists who colonized the lower Paraná wetland, there are 56 individuals available with known isotopic diets, within a chronological range from the years 1800 to 400 BP. Also, between the modern and archaeological samples, the isotopic database of faunal resources includes >200 animals targeted as prey, as well as those representative of the trophic chain. Therefore, it is possible to characterize trends and discuss future directions in the local isotopic analysis for the studied area.

It is quite clear that there are two marked tendencies in the past populations in the lower Paraná wetland. The first one constitutes the mixed diet of the Amazonian horticulturalist groups, historically known as the Guaraní, based on depleted proteins obtained from the local prey, and enriched carbohydrates related with maize intake. This population also exhibits an increased level of $\delta^{15}$N, indicating significant fish consumption.

The second one belongs to complex hunter-gatherers based on depleted proteins derived from a monoisotopic $C_3$ diet. In turn, two tendencies could be distinguished here. One of them is a more carnivorous diet, based on the fishing resources of the Paraná system, with depleted proteins and high nitrogen levels (the Plain Pottery cluster and Goya Malabrigo contexts; in this case the samples also include sites located in the Middle Paraná). There was no maize intake isotopically detected. Likewise, a moderate consumption of vegetables was not detected, although this should have been modest. The other isotopic trend also shows no isotopic evidence of maize consumption, except maybe in one individual (the IPC of the southwest bank of the Paraná River). It is difficult to continue with the analysis here since only the complete values of two individuals are available. However, it is quite clear that both have lower levels of nitrogen, probably due to lower fish consumption and moderate plant intake.

We cannot leave aside the possibility that some of the plants consumed by humans in the wetland correspond to cultivated vegetables. However, again, this intake must have been small compared to the average diet. This scenario is not surprising in complex hunter-gatherers, who often incorporate a few cultivated products (Ames, 2004, 2005; Barnes, 1993; Finlayson, 2009; Smith, 2001, among others). In turn, these data are consistent with the historical sources, which indicate that some groups from the wetland manipulate cultivated plants (see Section 1), but essentially they are described by chroniclers as hunters, and especially as fishermen. The caries rate and other pathologies are according to the isotopic and historical data.

It is also quite clear that, although there is a substantial sample available for the lower Paraná wetland, we still need to add new data to understand the regional and chronological variability, as well as other sources of bias such as age, gender and eventually social status. The study of breastfeeding and weaning behavior is another topic to explore since the data available are too small, but again consistent with hunter-gatherers patterns. Progress in the excavations in the various sectors of the lower Paraná wetland, as well as in the Middle Paraná River, is ongoing every new season, providing new data that will be integrated in the short term to test the results so far obtained here, which are basically a state of the current data available.

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