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Was there a population replacement during the Late mid-Holocene in the southeastern Pampas of Argentina? Archaeological evidence and Paleoecological basis

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Abstract

Based on radiocarbon and craniofacial morphological evidence, we propose that a population replacement took place in the southeastern Pampas of Argentina sometime between 6000 and 3500 years BP. The analysis of the available radiocarbon database shows that there is a significant gap between 5960 and 5060 ^{14}C years BP. The morphometric analyses of samples of human crania corresponding to the early mid-Holocene (ca. 8000–6000 ^{14}C years BP) and to the early late-Holocene (ca. 3500–2000 ^{14}C years BP) strongly suggest that they probably belonged to at least two different biological populations. We contend that this population event must be considered the outcome of a local population contraction/extinction process, followed by the later expansion/dispersal of a new population into the area. This is consistent with the expectations of metapopulation ecology and evolutionary geography, which predict that increasing extinction risks select for higher dispersal rates, since local population contraction or extinction often result in empty or thinly populated patches, whose existence makes dispersal both feasible and profitable. A slightly corrected version of the model advanced by Politis (1984), that establishes a linkage between the climatic induced demographic and range contraction of critical mammalian resources (e.g., guanaco) and those of human populations, is still useful to explain situations such as the alleged mid-Holocene population replacement event.
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1. Introduction

The archaeological models and hypotheses about the local evolution of hunter–gatherer populations in the Pampas of Argentina formulated in the last 20 years (e.g., Politis, 1984; Martínez, 1999) were proposed assuming that it was a rather continuous and transformative process. To a great extent, this view can be considered as an enduring legacy of the early processual archaeology, especially of its concern with the study of sub-system interactions within individual culture units. Since this required that cultural evolution be viewed as a process of internal, adaptive adjustment, archaeologists tended to focus on the study of local system transformations, particularly when hunter–gatherers were involved (Bettinger and Baumhoff, 1982). However, local population history almost never is the result of a gradual, continuous process, but in many cases it involves marked disruptions and discontinuities. This is the case because human populations, like any other biological populations, are subjected to dynamical and largely stochastic processes alternatively leading to its expansion or contraction, growth or decline, diversification or homogenization, isolation or continuity.

Our main argument here is that the aboriginal population history of the southeastern Pampas was not a continuous process that somehow started in the late Pleistocene and finished in recent times, but a punctuated one in which depopulation and colonization events may have occurred more than once during the

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last 12,000 years (Barrientos, 1997; 2001; Barrientos and Perez, 2002). In this paper we will present the archaeological evidence supporting the claim that a population replacement occurred in the area during the mid-Holocene. This evidence is the existence of a significant gap in the local series of ^{14}C dates observed between ca. 6000 and 5000 ^{14}C years BP, and the existence of significant morphological differences in the facial shape between samples of human crania corresponding to the early mid-Holocene (ca. 8000–6000 years BP) and to the early late-Holocene (ca. 3300–2000 years BP). This evidence will be discussed from the theoretical perspective of population ecology, particularly from the principles of metapopulation theory (Levins, 1969; Hanski, 1999), and evolutionary geography (Lahr and Foley, 1998), in order to obtain a better understanding of the conditions, causes and outcomes of the proposed regional population replacement.

2. The study area and its paleoenvironmental evolution during the mid-Holocene

The southeastern Pampas is the part of the Humid Pampas situated between the Salado River basin to the north, the Colorado River basin to the south, the Radial Depressed Area to the west, and the Atlantic Ocean to the east (Barrientos, 1997) (Fig. 1). It comprises approximately 180,000 km^2 of grassland plains with extremely low gradients, and two low-altitude mountain ranges, Tandilia and Ventania. There are few rivers, but a great number of both fresh and saline lagoons. Thick late Pleistocene and Holocene loess deposits cover most of the territory, acting as the parent material for relatively poorly developed soils (Fidalgo, 1992; Zárate, 1998). The predominant vegetation is herbaceous steppe or pseudo-steppe, although there are other communities including gramineous prairies and psammophytic and halophytic steppes (Cabrera, 1976). It has been proposed that the current herbaceous communities may correspond to different stages of an ancient succession (León et al., 1984).

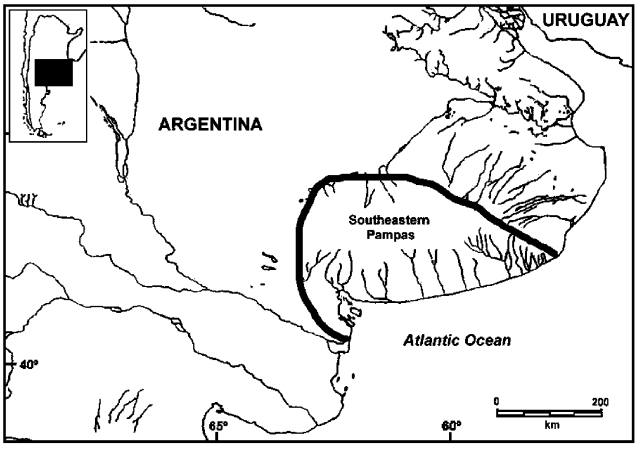

Fig. 1. Geographic localization of the southeastern Pampas.

The available regional paleoenvironmental reconstructions are mostly coarse-grained (sensu Tankersley and Isaac, 1990). They are based on geomorphologic, biostratigraphic and, more recently, palynological and geochemical data (e.g., Tonni and Fidalgo, 1978; Prieto and Páez, 1990; Tonni, 1992; Iriondo and García, 1993; Páez and Prieto, 1993; Zárate and Blassi, 1993; Bonadonna et al., 1995; Quatrocchio et al., 1995; Prieto, 1996; Zárate, 1998; Zárate et al., 1998; Tonni et al., 1999). The calibration of the regional paleoenvironmental record with fine-grained palaeoarchives with absolute or synchronized timescales that can provide high-resolution climatic information at a global or hemispheric scale (e.g., ice cores) remains to be done. Recent data about the occurrence of melt-layers in the Siple Dome ice core in West Antarctica (Das and Alley, 2002) permits to reconstruct changes in the Southern Hemisphere summer temperatures for the last 10,000 years. Melting, which occurs when summer air temperatures reach at least 0°C, was at a minimum from 6500 to 7500 years ago (0 events in 2000 years), representing an extended mid-Holocene cool period for this hemisphere. Remarkably, the age of this minimum in melt events at Siple Dome corresponds to the maximum amount of melting at GISP2 ice core in central Greenland (Alley and Anandakrishnan, 1995), constituting another clue about the asynchrony of both hemispheres during major Quaternary climatic events (e.g. Blunier et al., 1998; Vidal et al., 1999; Raynaud et al., 2000; Alley et al., 2002). From a global perspective, it can be said that data from several sources suggest an increased regionalization of climate from the early to the late Holocene. This may be considered as the manifestation of the varying influences of a variety of climate forcings such as changes in total and season-to-season insolation, ice sheet and sea ice extent, solar variability and volcanism (O'Brien et al., 1995).

Regarding the climatic evolution in the Pampas during the Holocene in general, and during the mid-Holocene in particular, the different nature, degree of resolution and scale of the paleoenvironmental records make difficult both to synthesize all the available information, and to overcome the danger of oversimplifying paleoenvironmental and paleoecological reconstructions. Remarkably, scholars based on different sources of data tend to strongly disagree in some fundamental ways (Fig. 2). For instance Tonni et al. (1999), mainly based on biostratigraphic information (e.g., mammalian associations), stated that during most of the late Pleistocene and Holocene, the climate of the Pampas was arid and cold, with probably very short wetter and warmer periods (e.g., during the mid-Holocene marginal marine ingression of ca. 7000

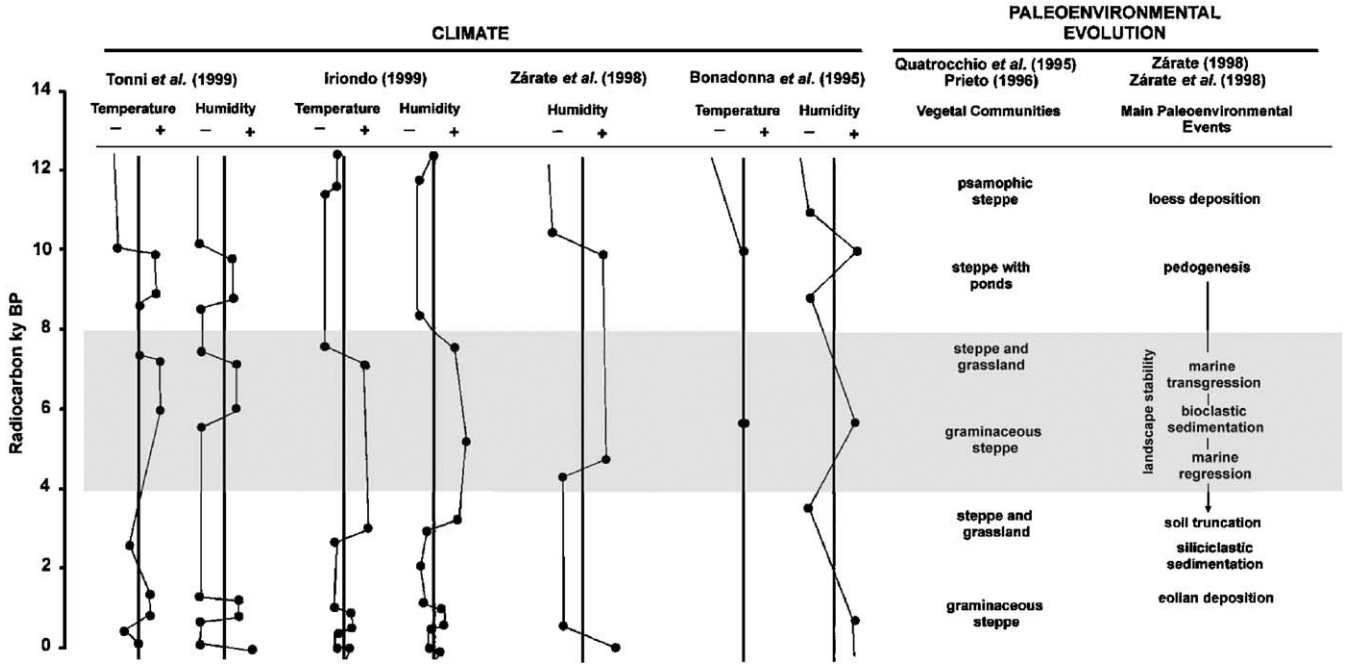

Fig. 2. Paleoenvironmental chart for the southeastern Pampas.

to 6000 ^{14}C years BP; Tonni et al., 1999). On the other hand, Iriondo and García (1993) and Iriondo (1999), based on geomorphologic data, proposed that during the period 8500–3500 ^{14}C years BP the continental Pampean climate was wet and subtropical to tropical. In particular, it is argued that the Hypsithermal period might have been especially warm and humid in the Pampas (Iriondo, 1999).

Geologists also have controversy concerning the Holocene pedo-sedimentary history of the Pampas. Fidalgo and Tonni (1981) and Fidalgo (1992) consider that the aeolian sediments that form the La Postrera Formation were deposited in the interfluvial areas and range from the latest Pleistocene to the most recent beds, under arid to semiarid climatic conditions. During that period, at least two relatively short pedogenetic episodes took place, giving origin to the Puesto Callejón Viejo and Puesto Berrondo paleosols. Zárate (1998), based on stratigraphic sequences from archaeological sites and key stratigraphic localities, stated that in the southeastern Pampas loess deposition ended sometime between 11,000 and 10,000 ^{14}C years BP, followed by the formation of present soil profiles. This pedogenetic process would indicate a prolonged interval of landscape stability at the regional level, locally interrupted around 5000 ^{14}C years BP by partial truncation of soils in upslope areas of the ranges, followed by eolian redeposition, an increase of siliciclastic alluviation in fluvial valleys, and marine regression in the coastal area (Zárate, 1998; Zárate et al., 1998).

The date of the beginning and ending of the *Optimum Climaticum* or Hypsithermal, and the mid-Holocene marine transgression associated with it, is also currently under debate. Based on isotopic evidence, Aguirre and Whatley (1995) point out that marine superficial temperatures higher than the current ones were recorded between 8000 and 4500 years BP, thus indicating the lapse corresponding to the Hypsithermal (Aguirre and Whatley, 1995. p. 250; cf. Clapperton, 1993). According to Isla (1989), the sea reached its current level at ca. 8000 years BP, with peaks of around 2.2—2.5 m above the current sea level between 6000 and 7000 years BP, under predominantly sub-humid to humid conditions. Aguirre and Whatley (1995) established the age of this transgressive event between 8000 and 6000 years BP, whereas Bonadonna et al. (1995) and Zárate and Flegenheimer (1991) placed it between 6000 and 5000 years BP (see discussion in Bayón and Politis, 1996). According to Aguirre and Whatley (1995) and Isla (1989), around 5000 to 4500 years BP, a marine regression period began, coincidental with the post-Hypsithermal climatic worsening. This event may be considered as a major ecosystem regulator, affecting both the marine and terrestrial biota of this region (Aguirre and Whatley, 1995).

Concerning the vegetation, palynological information indicates a change from a psammophytic and halophytic steppe with shrubby elements (Quatrocchio et al., 1995; Prieto, 1996) to a humid prairie between 11,000 and 10,000 ^{14}C years BP. According to Prieto (1996), from about 10,500 years BP, vegetation typical of lagoons, marshes and floodplains became established, indicating environments with a higher local effective humidity. In the central part of the southeastern Pampas, this

hydrophytic vegetation subsisted until 8000 years BP, then being replaced by a humid and herbaceous prairie firmly established at around 7000 years BP (Prieto, 1996). A return to subhumid-arid conditions since at least 5000 ^{14}C years BP is inferable from the palynological analysis of sequences from several localities of Ventania and Tandilia (Heusser n.d.; Nieto and Prieto, 1987; Madrid and Politis, 1991; Prieto, 1996). However, those arid conditions appear not to have been as severe as those during the late Pleistocene (Zárate and Blassi, 1993).

Regarding the faunal composition, it is important to take into account that the level of resolution of Pampean biostratigraphy is not very high, thus creating the conditions for the recovering of time-averaged or non-analogue assemblages (Tonni et al., 1999). Since the southeastern Pampas may be considered an ecotone between two major current zoogeographic areas, i.e., the Brazilian and Patagonian sub-regions, past faunal associations included shifting admixtures of taxa from both areas at different times during the late Pleistocene and Holocene. The main faunal event that occurred during the early/mid-Holocene transition was the local extinction of the last representatives of the large South American mammals. Bones of the giant groundsloth *Megatherium americanum* were dated at 8390 ± 140 and 7320 ± 50 years BP (Fidalgo et al., 1986; Politis and Madrid, 2001), whereas bones of the glyptodon *Doedicurus clavicaudatus* were dated between ca. 7500 and 6500 ^{14}C years BP (Politis and Beukens, 1990; Politis and Gutiérrez, 1998).

3. The archaeological evidence for population replacement

3.1. The spatio-temporal distribution of ^{14}C dates

The radiocarbon data sets available for any given region can be used, if properly treated and discussed, to assess population demographic processes through time (Housley et al., 1997, 2000; Anderson and Faught, 2000; Bocquet-Appel and Demars, 2000; see however Pettitt, 1999, 2000; Pettitt and Pike, 2001). In this paper, we will use the available ^{14}C dates for the southeastern Pampas to search for clues of significant discontinuities, interpretable in terms of human population processes at the regional level.

The current radiocarbon database is composed by a reported minimum of 107 uncalibrated and two calibrated dates (Politis and Madrid, 2001). Sixty-two of these (57%) were obtained through the AMS technique at different laboratories. From a geographical standpoint, they come from 30 archaeological sites unevenly distributed in terms of density across the entire study area. However, they fall in at least 14 complete or fractionated squares of an orthogonal grid of $50\,\text{km} \times 50\,\text{km}$ superimposed onto the map of Fig. 1. This distribution accounts for about one third of the total regional area, thus providing an incomplete but still fairly good coverage of it. The materials used for radiocarbon dating were diverse. Fifty one percent of the dates were obtained from bone collagen samples, 25% from charcoal, 15% from sediments, 5% from other kind of materials (fresh water snail shell and macro-botanical remains), and the remaining 4% from unreported materials. There are important differences in the kind of samples used for dating the archaeological occupations from each period. The late Pleistocene and the early Holocene occupations were dated using exclusively bone collagen and charcoal, whereas the mid and late Holocene occupations were dated using a broader spectrum of sample types. The extent to which this situation affects the degree of comparability between time periods is currently unknown, but there could be important variations in the strength and relevance of the sample/events associations. Although a proper evaluation of this kind of relationship should necessarily be carried out on a case by case basis, the a priori expectation is that bone collagen samples will tend to be more strongly associated with human occupation events than other kind of materials used for dating. However, problems related to the assemblage contamination with younger bones due to vertical migration cannot be discarded in the potentially bioturbated deposits in which most of the Pampean archaeological sites occur. Since in this region charcoal samples rarely come from conspicuous hearth structures, the strict degree of association between most of them and the occupational events targeted for dating is uncertain in many cases. In the case of radiocarbon age determinations made on sediments, shells and macro-botanical remains, the degree of uncertainty related to the sample/event association may increase to even higher levels. However, for the purpose of this research we took all the dates at face value, since to perform an in-depth analysis of the entire data set would be an extremely time consuming task, with no guaranteed results. This is mainly due to the lack of information in most of the original reports about some relevant issues, like sample pretreatment protocols, correction for isotopic fractionation and reservoir effect. Notwithstanding the acknowledgement of the many known and unknown factors that may impinge over the pattern of distribution of radiocarbon dates, we consider the available data set as an appropriate proxy for measuring the main trends in the population process at the regional level.

In order to search for significant discontinuities in the uncalibrated data series, we first proceeded to filter the total database by eliminating all those determinations indicated by Politis and Madrid (2001) as dubious or rejected in the original reports on a context-specific

basis. In all those cases in which more than one determination was made on a single sample, we arbitrarily retained the oldest one, deleting the rest. We also eliminated those dates not directly related to any particular archaeological assemblage (i.e., those corresponding to soil profiles not associated with archaeological materials). As a result of this first screening process, a second data set composed of 81 dates was generated. A further filtering process performed on this second data set consisted of eliminating all those dates with significantly high values of σ. Since there is a direct empirical correlation between the conventional radiocarbon age of a sample and the σ value associated with it, we proceeded to plot the values of σ against the mean value of each radiocarbon date, and then to eliminate those cases that fell outside the 95% of confidence area ellipse. This second screening process yielded a final data set composed of 72 radiocarbon dates, with a mean σ value of 77 ± 22 ^{14}C years, and a highly significant positive mean-σ correlation of 0.48 (Spearman R, $p < 0.001$). In Fig. 3, six clusters of dates (mean $\pm 3\sigma$) can be identified, separated by five temporal gaps of different length. In order to assess which of these gaps have a higher potential to carry some information interpretable in terms of population events or processes due to its significance, we performed a somewhat *sui generis* analysis that followed some principles of an autocorrelation analysis (i.e., the correlation of a series with itself, shifted by a particular lag of k observations; Box and Jenkins, 1990). The radiocarbon sequence of Fig. 3 is a composite of overlapping and non-overlapping segments of different length, interleaved in descending time. These properties make some pre-processing of the data necessary: prior to analysis, we proceeded to convert each segment representing an individual radiocarbon determination into two point values consisting on the mean $\pm 3\sigma$. These two values set the limits of the 99% of probability distribution of the age of each sample. The resulting series of 144 point values was plotted against itself with a lag of 1, in order to search for significant separations between pairs of successive point values. Since our objective was to identify all those points in a successive pair that significantly separated one from the other, thus revealing a major or significant discontinuity in the series, we used the limits of the 99% confidence area ellipse around the point distribution as the rejection line. Clearly, Fig. 4 shows that the only three cases that fall outside of the ellipse correspond to both values of the third cluster and to the last value of the fourth cluster of Fig. 3. These results indicate that, on a statistical basis, we can identify only two major significant gaps in our temporal series. These gaps are situated in the early Holocene, between 8620 and 8060 ^{14}C years BP, and in the second half of the mid-Holocene, between 5960 and 5060 ^{14}C years BP (Fig. 4). The plotting of the point values corresponding to the mean minus 3σ against those corresponding to the mean plus 3σ shifted by a lag of 1, yielded the same results.

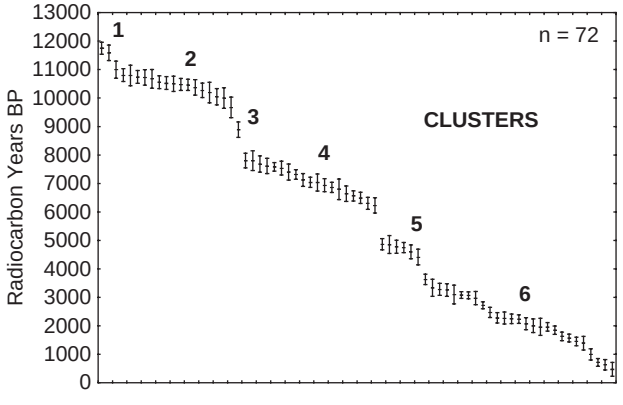

Fig. 3. Temporal distribution of ^{14}C dates.

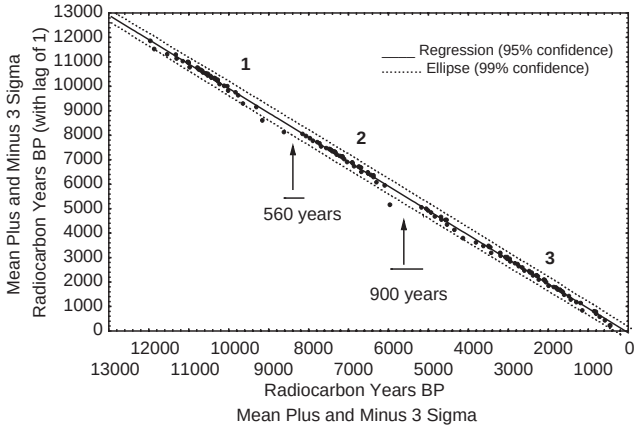

Fig. 4. Scatterplot of 144 point values corresponding to 72 ^{14}C dates plotted against itself with a lag of 1.

3.2. The morphological differences between diachronic human skeletal samples

In the southeastern Pampas at least 49 archaeological sites and localities with human burials have been recorded, with an estimated minimal number of 215 individuals. The average density of burials per site is low (<10 individuals per site), mainly due to the infrequent and discontinuous use of formal burial grounds. This pattern is consistent with that expected for hunter–gatherer populations with a relatively high degree of mobility, a low degree of redundancy in the occupation of places, and a relatively low demography at the regional level (for a more extensive review and discussion, see Barrientos, 1997, 2001). There are six skeletal series radiocarbon-dated using human bone collagen as sample (Barrientos and Perez, 2002). The series from Arroyo Seco 2 mainly corresponds to the early

mid-Holocene (ca. 8000–6000 ^{14}C years BP); those from Laguna de Puán 1, Laguna Tres Reyes 1, El Guanaco and La Toma to the early late-Holocene (ca. 3500–2000 ^{14}C years BP), and that of Laguna Los Chilenos 1 to the early late-Holocene (ca. 500–400 ^{14}C years BP) (Oliva et al., 1991; Madrid and Politis, 1991; Barrientos, 1997, 2001; Barrientos et al., 1997; Flegenheimer et al., 2000; Madrid and Barrientos, 2000). On the basis of various lines of evidence (form of artificial cranial deformation, secondary burials, and funerary goods), Barrientos (1997, 2001) and Madrid and Barrientos (2000) established a link between these skeletal series and those undated that share some similar formal traits with them. The radiocarbon and contextual information show that the available skeletal samples are very discontinuously distributed through time. This distribution tends to coincide with those periods in which an effective and stable occupation of the region can be postulated (Barrientos, 2001).

In order to assess the degree of morphological affinity between the three diachronic skeletal series from the southeastern Pampas, three samples composed of adult individuals of both sexes were analyzed: (a) early mid-Holocene (EMH), (b) early-late Holocene (ELH), and (c) late-late Holocene (LLH). For the sake of comparison, six undated but probably late Holocene series from northeastern Patagonia and one from northeastern Pampas were also incorporated into the analysis (Table 1). Twelve craneofacial metric variables were analyzed: OBH (orbital height), OBB (orbital breadth), DKB (interorbital breadth); FMB (bifrontal breadth), ZMB (bizigomaxillary breadth), NLB (nasal breadth), NLH (nasal height), NPH (nasion-prosthion height), ZYB (bizygomatic breadth), WMH (cheek height), MAB (palate breadth, external) (Howells, 1973), and MAL (maxillo-alveolar length) (Buikstra and Ubelaker, 1994). Neurocranial variables were omitted in this analysis because the cranial vault of most of the specimens was modified, either postdepositionally or culturally. Instead, the facial skeleton, notwithstanding having experienced fractures and some degree of bone loss, did not suffer plastic alteration or any other significant modification of form.

Table 1
Samples of human cranial remains analyzed

Region	Sample	Male *n*	Female *n*
Southeastern Pampas	Early Mid-Holocene (EMH)	4	4
	Early Late-Holocene (ELH)	9	2
	Late Late-Holocene (LLH)	8	4
Northeastern Pampas	Paraná Delta (NPD)	8	8
Northeastern Patagonia	San Blas (NP1)	10	11
	Isla Gama (NP2)	6	6
	Río Negro (tabular erect deformation) (NP3)	32	14
	Río Negro (tabular oblique deformation) (NP4)	11	17
	Río Negro (annular deformation) (NP5)	18	25
	Río Chubut (NP6)	25	22
Total		131	113

In the present study, the analysis of the variation in shape was considered relevant for assessing the degree of differentiation among and between samples. In order to isolate the shape factor, the raw standardization of Darroch and Mosiman (1985) was performed. It is the ratio formed by dividing each variable by the geometric mean (GM) of all variables for each individual (i.e., Y/GM; Jungers et al., 1995, p. 145). The variations in shape were analyzed by means of a standard discriminant analysis. Prior to the analysis, the samples were tested for normality (Shapiro-Wiks test, $p > 0.05$), and homogeneity of variance-covariance (Levene test, $p > 0.05$). Although samples of both sexes were analyzed in all cases, only the results corresponding to the male series will be discussed here.

The results of the discriminant analysis using metric variables indicate the existence of significant differences between all samples (Wilks' lambda = 0.068; $F = 3.361$; d.f. = 108, 813; $p < 0.001$). In Fig. 5 are plotted the first three canonical variables. It clearly shows that the sample that differs the most not only from the other two regional series, but also from most of the other extra-regional ones, is that corresponding to the ELH from the southeastern Pampas. The calculation of the Mahalanobis' D^2 distances between pairs of southeastern Pampas samples indicates that the maximal significant separation occur between the early mid-Holocene and the ELH (22.23; $p < 0.001$). It is followed by those between the early mid-Holocene and LLH (15.7; $p < 0.01$), and between the ELH and LLH (11.02; $p < 0.001$).

In order to obtain a better description of the shape differences between the two most distant samples in the multivariate space (i.e., EMH and ELH), a thin plate spline analysis (Bookstein, 1991) was carried out. It was performed on two-dimensional configurations of landmarks and semi-landmarks (i.e., interpolations between true landmarks; see Bookstein, 1997) taken from images of each crania posited in frontal norm. Fig. 6 exhibits the configuration of points corresponding to the consensus (i.e., sets of landmarks intended to represent the central tendency of an observed sample; Slice et al., 1998) of the EMH sample against that of the ELH. Comparatively, the individuals of the ELH have higher and narrower faces, higher orbits, lesser cheek height and narrower inter-orbital breadth relative to those of the EMH.

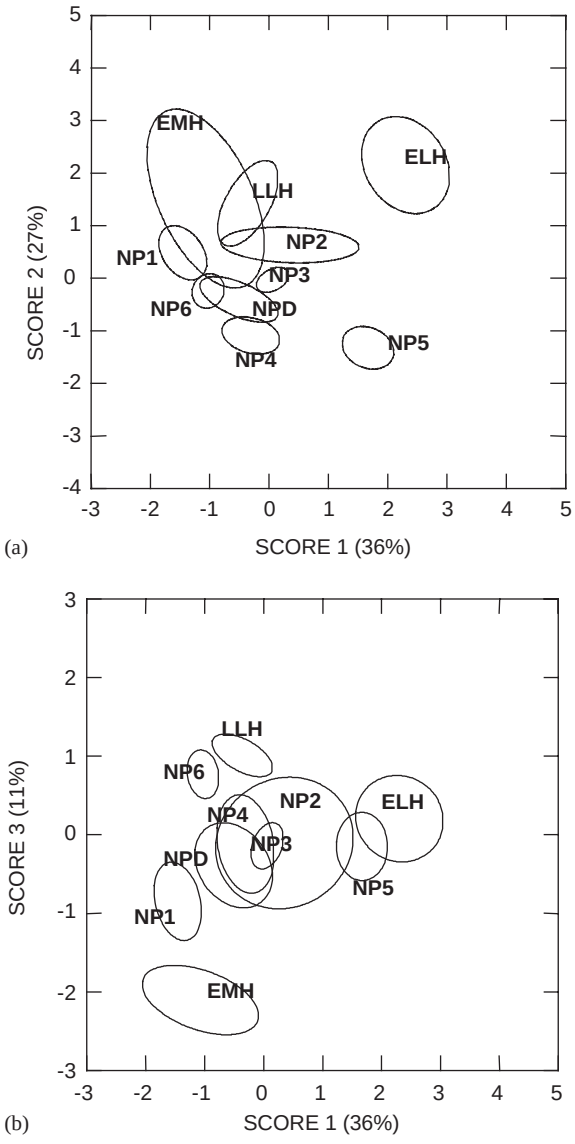

Fig. 5. Scatterplots of the first canonical variable against the second (a) and the third (b) ones, resulting from the discriminant analysis of 12 facial variables (nine samples from the Pampas and northern Patagonia).

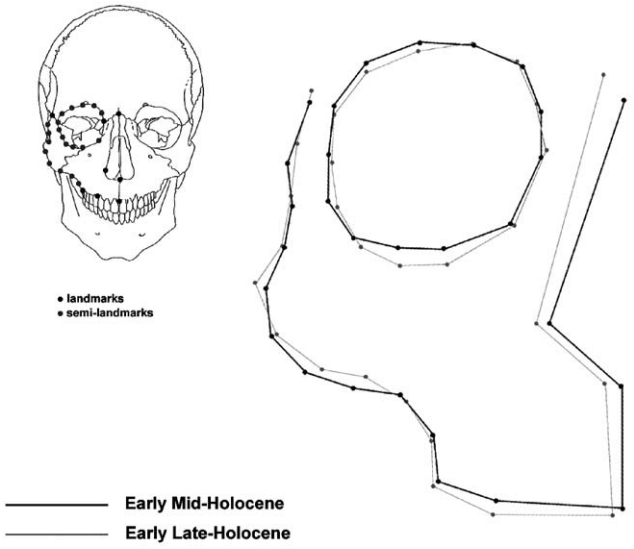

Fig. 6. Comparison between the consensus of the early mid-Holocene and early late-Holocene samples. Thin plate spline analysis.

In summary, we can say that the bulk of the morphological information strongly indicates significant facial differentiation between all the diachronic regional samples, being the differences between the early mid-Holocene and early-late Holocene the greatest. This finding seems to support very well the claim that both samples may derive from at least two different biological populations.

4. Three questions about the population replacement in the southeastern Pampas: when, how, and why?

The evidence presented in the preceding paragraphs strongly suggests that a population replacement effectively took place in the southeastern Pampas of Argentina sometime between ca. 6000 and 3500 ^{14}C years BP. The three relevant questions that immediately arise are: when it exactly occurred?; how this process could have happened?; and, more importantly, why? A great deal of research remains to be done in order to answer these questions properly. However, the first two can be partially approached using the radiocarbon evidence previously discussed. This indicates that in the second half of the mid-Holocene, between 5960 and 5060 ^{14}C years BP, some phenomena implying a significant reduction in the archaeological visibility of the Pampean population occurred. If the latter was caused by a demographic decline leading to a geographic population contraction or by a local extinction event, it remains unclear. This is because the archaeological criteria to distinguish between a wholesale depopulation—whatever its cause—from a population contraction or shrinkage, are not yet fully developed. In a previous paper (Barrientos and Perez, 2002) we proposed that the hunter–gatherers groups that inhabited the southeastern Pampas during the Holocene were members of local populations belonging to geographically extended metapopulations. A metapopulation can be defined as a group of local populations or demes, characterized by a relatively asynchronous and independent dynamic resulting from their geographic separation, but ultimately linked to each other by the migration of individuals (Levins, 1969; Hanski, 1999). Since the Pampas never had significant ecological or physical barriers promoting population isolation, gene flow due to migration from and to neighboring areas may have been an effective mechanism enabling the formation of metapopulations at the supra-regional level. The hypothesized geographic range of such

metapopulations includes the north of Patagonia, the Dry Pampas, southern Cuyo, the northeastern Pampas and, probably, Sierras Centrales. These metapopulations may have been sensitive to the selective conditions imposed by the environmental (e.g., climatic, faunal, vegetational, etc.) and ecological (e.g., habitat reduction or extension, competition, etc.) variations that occurred during the Holocene. As a response, they may have changed by means of demographic regulations that resulted in their contraction or expansion and, eventually, in their local extinction or replacement.

From the theoretical perspective of evolutionary geography (Lahr and Foley, 1998) and metapopulational theory (Hanski, 1999), the evolution of diversity within any one lineage is shaped by both expansion/dispersal and contraction/extinction processes. One of the most important determinants for the evolution of dispersal rates is the extinction risk to which local populations are exposed (Lahr, 2002). They result in empty or thinly populated patches, the existence of which makes dispersal both feasible and profitable. For these reasons, increasing extinction risks are expected to select for higher dispersal rates (Parvinen et al., 2000).

From ca. 7000 to 4000 ^{14}C years BP, gaps in the local sequences of ^{14}C dates are frequent in the latitudinal strip situated between 34°S and 42°S (Orquera, 1987; Berón, 1995; Sanguinetti de Bórmida and Curzio, 1996; Gil, 2000). This geographically extended pattern was probably caused by a metapopulation demographic and spatial contraction process occurring during the second half of the mid-Holocene. Such a contraction, which may have eventually caused local extinctions or marked regional depopulation and social reorganization among the hunter–gatherers groups inhabiting those regions, could create the conditions for a later expansion and dispersal of a new population/metapopulation. At the present time, we cannot establish the exact date of entry of this new population into the southeastern Pampas. All that we know is that about 2500 years BP it was firmly established in the area. The main distinctive and regionally extended cultural trait shared by many individuals dated between 2500 and 2000 ^{14}C years BP, is the tabular oblique deformation of the cranial vault (Barrientos, 1997, 2001; Madrid and Barrientos, 2000). For the period between 5000 and 2500 years BP, there is a remarkable scarcity of bioarchaeological evidence. It consists of only two partial skeletons from Laguna de Puán, one of them radiocarbon-dated at 3330±100 years BP (Oliva et al., 1991). Their crania are artificially deformed, falling into the annular category, like many of the early mid-Holocene specimens from Arroyo Seco 2 (Barrientos 1997, 2001). However, the only single individual from Laguna de Puán with a well-preserved facial skeleton shows no morphological similarity to any of them, being more closely related to the rest of the early late-Holocene specimens (Barrientos and Perez, 2002).

If this new biological population entered the region sometime between 6000 and 5000 years BP, then the archaeological record of the period 5000–4000 years BP can be considered as representing the colonization phase of an empty or thinly populated territory. The two more conspicuous sites from this period, Paso Otero 1 (lower component) and Paso Otero 3, are the first-recorded guanaco (Lama guanicoe) kill/butchering loci for the Pampas, radiocarbon-dated between 4855±105 and 4414±92 years BP (Politis and Madrid, 2001). The archaeological evidence from these sites located at a very short distance from each other and on a similar floodplain environment at the middle reach of Río Quequén Grande, shows a rather "wasteful" behavior put in practice by the prehistoric hunters. At Paso Otero 1 for instance, a minimal number of 30 mature and immature guanaco specimens (NISP = 2198) were killed, being discarded on the spot almost all their skeletal elements, with no evident signs of intensive processing (2.2% of elements with helicoidal fracture planes, and 8.8% of elements with cut marks; Martínez, 1999, p. 247). This situation seems analogous to that of the North American plains, where the under-utilization of prey is a common feature of Paleoindian bison kill sites (Todd, 1987). It is clear that many factors impinge upon the individual and social decision-making involved in prey exploitation in each particular situation, and each ecological context (for an extensive review, see Martínez, 1999, pp. 266–270). However, there is a greater chance that a pattern of recurrent underutilization of prey carcasses be more frequent among small-scale hunter–gatherer groups living under conditions of low global population density—both absolute and relative to their resource base—and no spatial circumscription (i.e., with low levels of population pressure over the specific resource). These are, precisely, the expected conditions during a phase of exploration and colonization of a new environment (Borrero, 1994/95).

The third question, relative to the causes of the alleged process of metapopulation contraction followed by an expansion/dispersal of another (meta) population, which, in the case the southeastern Pampas, plausibly resulted in a population replacement, needs to be approached from a paleoecological perspective. Unfortunately, due to the coarse-grained nature of the available paleoecological reconstructions and to the many discrepancies in the literature about the more probable date of the main paleoenvironmental events, any attempt to correlate human population dynamics with local environmental evolution is a very risky business. Moreover, the time-transgressive nature of many physical, geological, climatic, and biological

processes also contributes to mask a number of significant relationships.

Certainly, a process of population contraction and expansion must be the outcome of multiple factors that operate at different temporal and spatial scales, affecting the distribution, organization and demography of human groups. However, one or a limited number of proximal causes sometimes are equally efficient to explain certain phenomena.

From a regional viewpoint, a very tight relationship has been established between the population density of humans and that of the guanaco, the principal animal resource from late Pleistocene times onwards (Tonni and Politis, 1980; Politis, 1984). In general, it is believed that the guanaco was very sensitive to climatic variations that involved increase in environmental humidity, seemingly due to sanitary reasons (Tonni and Politis, 1980, p. 56; cf. Loponte, 1996/98. pp. 52–54). According to Politis (1984, pp. 39–40), the human population density in the Pampa Interserrana could diminish during humid climatic cycles (e.g., during the Hypsithermal) and rise during the arid-semiarid ones (from a figure of 0.001 to one of 0.05 inhabitants/km^2) in response to the alternate absence or presence in the area of the guanaco and some other secondary resources. However, there seems to be little empirical basis to support the view that the climate during the entire lapse of the Hypsithermal was humid (Tonni et al., 1999; cf. Iriondo and García, 1993 and Iriondo, 1999). However, it seems that it was certainly warmer than today (Tonni et al., 1999; cf. Das and Alley, 2002). Quantitative estimates of mid-Holocene warmth (COHMAP, 1988) suggest that the Earth was perhaps 1 or 2 °C warmer than today. Most of this warmth may primarily represented seasonal (i.e., summer) warmth rather than year-round warmth. It has been demonstrated that climatic warming and cooling beyond the optimum temperature range for conceptions and estrual activity can reduce mammalian fertility, leading to reduction in population numbers and, in abrupt climatic changes, collapse and extinction of mammalian populations (McLean, 1991). In fact, modern summer heat is already killing mammalian embryos on a vast scale prior to the onset of any potential significant global warming (McLean, 1991, p. 93). It is very possible that guanacos, and many other local mammalian prey species, were more sensitive to post Pleistocene changes in temperatures than in humidity. This environmental factor may have been a major ecosystem regulator, alternatively promoting cycles of prey population contraction and expansion, thus affecting the local carrying capacity and human demography. The post Hypsithermal climatic deterioration, beginning after 5000–4500 years BP could create the conditions for an increase in the regional ungulate biomass, and hence of the carrying capacity, allowing the dispersal of a new human population into the area.

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