

Early Holocene Human Remains From the Argentinean Pampas: Additional Evidence for Distinctive Cranial Morphology of Early South Americans

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ABSTRACT The cranial morphology of Early Holocene American human samples is characterized by a long and narrow cranial vault, whereas more recent samples exhibit a shorter and wider cranial vault. Two hypotheses have been proposed to account for the morphological differences between early and late-American samples: (a) the migratory hypothesis that suggests that the morphological variation between early and late American samples was the result of a variable number of migratory waves; and (b) the local diversification hypothesis, that is, the morphological differences between early and late American samples were mainly generated by local, random (genetic drift), and nonrandom factors (selection and phenotypic plasticity). We present the first craniometric study of three early skulls from the Argentinean Pampas, dated ~8,000 cal. years BP (Arroyo Seco

2, Chocorí, and La Tigra), and one associated with megafaunal remains (Fontezuelas skull). In addition, we studied several Late Holocene samples. We show that the skulls from the Argentinean Pampas are morphologically similar to other Early Holocene American skulls (i.e., Lagoa Santa from Brazil, Tequendama, Checua, and Aguazuque from Colombia, Lauricocha from Peru, and early Mexicans) that exhibit long and narrow cranial vaults. These samples differ from the Late Holocene American samples that exhibit a shorter and wider cranial vault. Our results underscore the important differences in cranial morphology between early and late-American samples. However, we emphasize the need for further studies to discuss alternative hypotheses regarding such differences. *Am J Phys Anthropol* 143:298–305, 2010. © 2010 Wiley-Liss, Inc.

Cranial variation of Pleistocene and Holocene human populations seen throughout the world has been widely studied (Howells, 1973, 1995; Gunz et al., 2009). Many of the studies done to date demonstrated that while early human skulls have a relatively long and low vault, the modern ones are relatively short and high (Stringer et al., 1984; Stringer and Andrews, 1988; Stringer, 1992; Lahr, 1996, among others). A similar pattern is found in the Americas (particularly in South America), where early skulls (i.e., Late Pleistocene and Early Holocene samples) are characterized by a long and narrow cranial vault (i.e., dolichocephalic morphology), while more recent populations exhibit a shorter and wider cranial vault, that is, a brachycephalic morphology (Neves and Pucciarelli, 1989; Powell and Neves, 1999; Neves et al., 2003). Specifically, these studies have pointed out that the general morphology of early American skulls does not correspond with the classical Amerindian model—a morphology similar to those of later Northeast Asian samples (Hrdlička, 1912)—but resembles that of Australo-Melanesian and early Southeast Asian samples (Neves and Pucciarelli, 1991; Neves et al., 2003). The dolichocephalic American morphology was observed, among others, in the early archaeological sites at Tequendama (Neves et al., 2007) and Lagoa Santa (Neves et al., 2003) as well as in some Late Holocene samples such as the Pericues from Baja California (González-José et al., 2003; Pucciarelli et al., 2003).

One of the main problems faced when studying American cranial variation is the fact that the extent of the available evidence of early and recent skeletal samples is profoundly different. Although there are numerous samples from the Late Holocene period (e.g., Pucciarelli et al., 2006, 2008), few areas could provide human remains with ¹⁴C dates going back to the Early Holocene period (Neves and Hubbe, 2005; Neves et al., 2007; Perez et al., 2009). Until recently, the oldest samples frequently studied came from East Central Brazil (Lagoa Santa, ~9,000–5,000 years ¹⁴C BP; Dillehay, 2000; Neves and Hubbe, 2005) and the Bogota savannah in Colombia (Tequendama, ~7,300–5,800 years ¹⁴C BP; Correal

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TABLE 1. Sample composition

Sample	Code	Country	N	Period	Main Museum ^a
Aguazuque	Agu	Colombia	10	Early Holocene	ICN
Algonkin	Alg	Canada	11	Late Holocene	Peabody
Amazonas	Ama	Peru	18	Late Holocene	MDH
Ancon	Anc	Peru	26	Late Holocene	MNAAHP
Araucanian	Ara	Argentina	28	Late Holocene	MLP
Botocudo	Bot	Brazil	29	Late Holocene	MMG
Center-Chile	CCh	Chile	10	Late Holocene	MDH
Chequa	Che	Colombia	7	Early Holocene	ICN
Deltaic	Del	Argentina	28	Late Holocene	MLP
Guajajara	Guj	Brazil	12	Late Holocene	MNUFRJ
Koniag	Kon	Alaska	12	Late Holocene	NMNH
Las Pirguas	LPr	Argentina	15	Late Holocene	MLP
Lagoa Santa	LSa	Brazil	29	Early Holocene	MMG
Lauricocha	Lau	Peru	6	Early Holocene	MNAAHP
Maipure	Mai	Venezuela	29	Late Holocene	MDH
Muisca	Mui	Colombia	37	Late Holocene	MDH
North-Chile	NCh	Chile	18	Late Holocene	MDH
North-East	NEa	Argentina	44	Late Holocene	MLP
North-Tehuelche	NTe	Argentina	44	Late Holocene	MLP
North-West	NWe	Argentina	14	Late Holocene	MLP
Paleomexican	PMe	Mexico	5	Early Holocene	INAH
Paltacalo	Pat	Ecuador	43	Late Holocene	MDH
Pampa	Pam	Argentina	4	Early Holocene	MLP
Pericu	Pei	Mexico	20	Late Holocene	MAM
Sambaqui	SRJ	Brazil	12	Late Holocene	MNUFRJ
San Blas	SBl	Argentina	12	Late Holocene	MLP
Santa Cruz Island	SCI	USA	21	Late Holocene	NMNH
Selknam	Sel	Argentina	17	Late Holocene	IP
South-Mendoza	SMe	Argentina	31	Late Holocene	MSR
South-Chile	SCh	Chile	17	Late Holocene	MDH
South-Tehuelche	STe	Argentina	67	Late Holocene	MLP
Tequendama	Teq	Colombia	6	Early Holocene	MNC
Yukpa	Yuk	Venezuela	13	Late Holocene	MAHEA
Total			695		

Bold font represents the Early Holocene Pampean sample.

^a ICN, Instituto de Ciencias Naturales (Colombia); Peabody, Peabody Museum (USA); MDH, Musée de l'Homme (France); MLP, Museo de La Plata (Argentina); MNAAHP, Museo Nacional de Arqueología, Antropología e Historia del Perú (Peru); MMG, Museo de Minas Gerais (Brazil); MNUFRJ, Museu Nacional Universidade Federal de Rio de Janeiro (Brazil); NMNH, National Museum of Natural History (USA); INAH, Instituto Nacional de Antropología e Historia (Mexico); MAM, Museo de Antropología de México (Mexico); IP, Instituto de la Patagonia (Chile); MSR, Museo de San Rafael (Argentina); MNC, Museo Nacional de Colombia (Colombia); MAHEA, Museos de Antropología e Historia del Estado de Aragua (Venezuela).

Urrego and van der Hammen, 1977). Argentinean Pampas samples from Arroyo Seco 2 (dated between ~8,000 and 4,500 years ¹⁴C BP; Scabuzzo and Politis, 2007; Politis et al., 2009a,b,c), even when they came from an important archaeological site, have not been widely included in recent studies about the cranial diversity of South American populations. Moreover, recent dates obtained from the human remains of Chocorí and La Tigra (Ameghino, 1898, 1909; Lehmann-Nitsche, 1907) place both skeletons in the Early Holocene period (Politis et al., 2009b). Although these samples were studied during the later 19th and earlier 20th centuries (Vogt, 1881; Virchow, 1892; Ameghino, 1898, 1909; Lehmann-Nitsche, 1907; Hrdlička, 1912), they were excluded from American peopling investigations after the strong and definitive opinion of Hrdlička (1912) about the relatively modern date of those skeletal remains.

Here, we present the first craniometric analysis of several early skulls from the Argentinean Pampas. Specifically, we studied cranial variation of three sites dated on ~8,000 years cal. BP: Arroyo Seco 2, a site that has been excavated and studied by our group (Scabuzzo and Politis, 2007; Politis et al., 2009a,b,c), and Chocorí and La Tigra. They were primarily studied by Florentino Ameghino (1898, 1909) and Robert Lehmann-Nitsche

(1907) and recently dated by our group [see Politis et al. (2009b)]. We also studied the Fontezuelas skeleton, because this finding suggests that it is an Early Holocene antiquity (see below). The initial hypothesis of our investigation is that the skulls from the Argentinean Pampas are morphologically similar to the other early American skulls but differ from the later American samples. Therefore, we compared these skulls with several early American samples, such as Lagoa Santa from Brazil, Tequendama, Chequa, and Aguazuque from Colombia, Lauricocha from Peru, and early Mexicans as well as several late Amerindian samples (Pucciarelli et al., 2006, 2008). Finally, we discuss alternative hypotheses to explain the cranial variation between early and late-American samples.

MATERIALS AND METHODS

Samples

We analyzed 695 nondeformed male individuals from 33 American samples (Table 1; Pucciarelli et al., 2008). American samples corresponded to the four skulls from the Argentinean Pampas (see Fig. 1), seven early Holocene skeletal samples (~4,000–9,000 ¹⁴C years BP) from

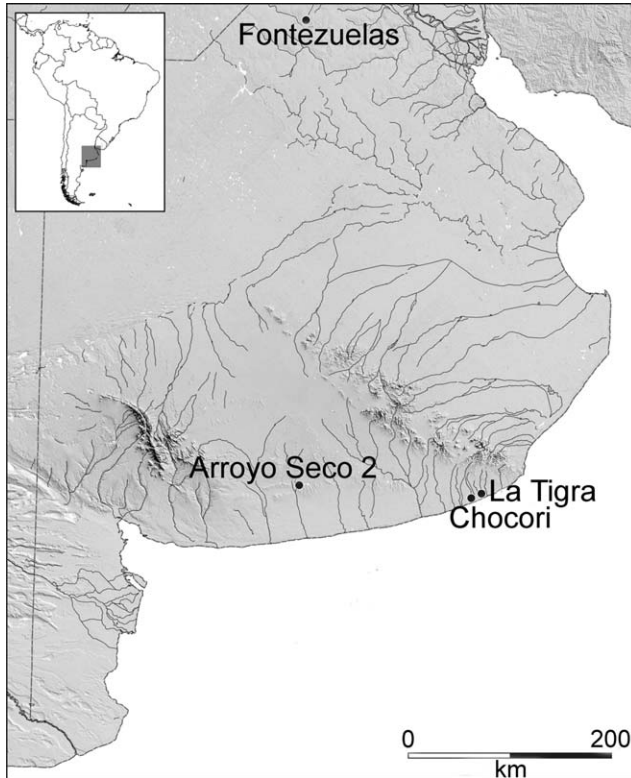


Fig. 1. Map showing the geographic locations of the Argentinean Pampas cranial samples analyzed.

Central and South America (Pucciarelli et al., 2006, 2008) and 26 samples of pre-Columbian late Holocene groups from different American geographical regions (Pucciarelli et al., 2006, 2008). These groups were distributed mainly from 20° North Latitude to 54° South Latitude, inhabiting regions along the Pacific corridor and the Atlantic Coast (Table 1). They also inhabited different ecological regions with a mean annual temperature ranging from 28° to 8°C and an annual rainfall from 3,000 to zero mm. The samples were composed of farmer groups (i.e., groups with an agricultural economy), horticulturalists, pastoralists, terrestrial hunter-gatherers, and maritime hunter-gatherers (Harlan, 1971; Pearsall, 1992; Perez et al., 2010).

Early Holocene Pampean human remains

The Arroyo Seco 2 archaeological site is located a few kilometers from the village of Tres Arroyos (see Fig. 1). The site was excavated by one of us (GP) during the 1980s and 1990s (Politis, 1984; Fidalgo et al., 1986; Barrantes, 1997; Gutierrez, 2004; Politis et al., 2009b; Steele and Politis, 2009). Arroyo Seco 2 has an early component containing a lithic assemblage composed of unifacial, marginally retouched tools associated with bone remains of guanaco (camelid), Pampean deer, and nine extinct megafauna: *Paleolama*, *Equus*, *Hippidion*, *Toxodon*, *Megatherium*, *Eutatus*, *Glossotherium*, *Macrauchenia*, and *Glyptodon*. Thirteen AMS ages on megafauna bones from the lower component run at different radiocarbon laboratories yielded an age range between $10,500 \pm 90$ ^{14}C years BP and $12,240 \pm 110$ ^{14}C years

BP (Steele and Politis, 2009). Besides this early component, the site contains one of the best existing records of South American human remains for the transition between the Early and Middle Holocene periods. To date, 45 human skeletons have been uncovered and 21 were directly dated from $\sim 7,800$ to $4,500$ ^{14}C years BP. Skeletons range from newborn to mature individuals and consist of both sexes (male = 14; female = 13; and undetermined = 18) (Scabuzzo and Politis, 2007; Politis et al., 2009a,b,c). The AS-19 individual studied here was a middle-aged adult male dated $6,860 \pm 60$ ^{14}C years BP ($\sim 7,700$ cal. years BP) and represented the unique skull with cranial vault nondeformed [see Perez et al. (2009)].

The Arroyo La Tigra site is located a few kilometers from the village of Mar del Sur (see Fig. 1) between two small creeks—Arroyo La Tigra and Arroyo Seco—on the Atlantic coast. The skeleton was recovered in 1888 by A. Canesa and deposited in the Museo de La Plata. This individual, an adult male, was first described by Ameghino (1898, 1909). Ameghino (1909) ascribed the remains to *Homo pampæus* and dated it to the Pliocene period, despite an original Quaternary assignment by S. Roth and R. Lehmann-Nitsche (Lehmann-Nitsche, 1907). Conversely, Hrdlička (1912) analyzed the cranial morphology of Arroyo La Tigra and pointed out that the traits were similar to those found in relatively modern skeletal remains from the Pampas and northern Patagonia, showing signs of artificial cranial deformation (annular type). However, recent studies using geometric morphometric techniques found no similarities between the individual from Arroyo La Tigra and individuals with indisputable annular cranial deformation [(Perez et al., 2009); also see Politis et al. (2009b)]. In addition, an AMS age of the human bone yielded an age of $7,270 \pm 60$ ^{14}C years BP [$\sim 8,100$ cal. years BP; (Politis et al., 2009b)].

The Arroyo Chocorí site is located 100 m from the Atlantic beach on the seashore near Mar del Sur and few kilometers from Arroyo La Tigra (see Fig. 1). The individual was found in 1888 by F. Larrumbe of the Museo de La Plata (Politis et al., 2009b). The skeleton was first studied by Lehmann-Nitsche (1907). This author assigned the individual to the Upper Pampean Formation, which he considered of Quaternary age. Ameghino (1909) included the Chocorí skeleton among the later representatives of the species *Homo pampæus* and considered it to belong to the late Pliocene age. Later, Hrdlička examined the bones and assigned them to an elderly person, “and much more probably male than female” (Hrdlička, 1912, p 239). He believed that skeleton was recent and did not deserve any consideration with regard to the study of the early peopling of the Americas. However, the AMS analysis on human bone yielded an age of $7,010 \pm 60$ ^{14}C years BP [ca. 7,800 cal. years BP; (Politis et al., 2009b)].

The Fontezuelas skeleton was discovered by Santiago Roth “half a league” from the Arrecifes creek, along the border of a secondary affluent, close to the Fontezuelas rail road station from which it got its name (see Fig. 1). Vogt (1881) was the first to publish this finding and placed it, based in Roth’s information, in the “Pampeano Superior” Formation. The human remains were found in association with extinct megamammal faunal remains. The most notable of these findings was that a *Glyptodon* carapace was lying on top of the skeleton. The contemporaneity of the carapace and the human remains was subject to debate. Although Roth, Virchow (1883), Ameghino

TABLE 2. Cranial measurements used in this study

Number	Symbol	Name	Description ^a	Caliper	Mode ^b
01	CL	Cranial length	Nasion-Opisthocranium ^c	Sliding (Poech type)	Projected
02	CB	Cranial breadth	Euryon-Euryon ^c	Spreading	Direct
03	CH	Cranial height	Basion-Vertex ^c	Spreading	Direct
04	PVL	Prosthion-Vomerbasio length	Inner Prosthion-Vomerbasio ^d	Sliding (Poech type)	Projected
05	BB	Bizygomatic breadth	Zygion-Zygion ^c	Spreading	Direct
06	UFH	Upper facial height	Nasion-Prosthion ^c	Sliding (Poech type)	Projected
07	FC	Frontal chord	Glabella-Bregma ^c	Sliding (Poech type)	Projected
08	FB	Frontal breadth	Pterion-Pterion ^c	Spreading	Direct
09	FH	Frontal height	Bregma-Vomerbasio ^d	Spreading	Direct
10	PC	Parietal chord	Bregma-Lambda ^c	Sliding (Poech type)	Projected
11	BBH	Basion-bregma height	Basion-Bregma ^c	Spreading	Direct
12	OL	Occipital length	Opisthion-Opisthocranium ^c	Sliding (Poech type)	Projected
13	BAB	Biasterionic breadth	Asterion-Asterion ^c	Spreading	Direct
14	OC	Occipital chord	Lambda-Opisthion ^c	Sliding (Poech type)	Projected
15	AML	Auditory meatus length	Distance from the external auditory meatus to the midpoint of the inner border of the petrous bone ^e	Sliding with vernier	Direct
16	AMB	Auditory meatus breadth	External auditory meatus width ^e	Sliding with needle	Direct
17	AMH	Auditory meatus height	External auditory meatus height ^e	Sliding with needle	Direct
18	ORL	Orbital length	Dacryon-superior orbital fissure ^e	Orbitometer	Direct
19	ORB	Orbital breadth	Dacryon-Ectoconchion ^c	Sliding (Poech type)	Projected
20	ORH	Orbital height	Maximum height from the upper to the lower orbital borders perpendicular to the horizontal axis of the orbit ^c	Sliding (Poech type)	Projected
21	NL	Nasal length	Nasospinale-staphylion ^c	Spreading	Direct
22	NB	Nasal breadth	Left alare-right alare ^c	Sliding with vernier	Direct
23	NH	Nasal height	Nasion-Nasospinale ^c	Sliding (Poech type)	Projected
24	ZL	Zygomatic length	Distance from the zygomaxillare anterior ^c to the posterior margin of the glenoid fossa ^e	Sliding with vernier	Direct
25	SZB	Sphenoid-zygotemporal breadth	Distance from the anterior border of the sphenoid bone in the greater wing to the lower point of the zygotemporal suture ^e	Sliding with needle	Projected
26	SZH	Stephanion-zygotemporal height	Distance from the stephanion ^f to the lower point of the zygotemporal suture ^e	Sliding (Poech type)	Projected
27	AL	Alveolar length	Prosthion-alveolon ^c	Sliding with vernier	Direct
28	AB	Alveolar breadth	Left ectomolare-right ectomolare ^c	Sliding with vernier	Direct
29	AH	Alveolar height	Palatal deep on the palatine suture, measured by place the lateral arms of the palatometer on the left and right ectomolare ^e	Coordinate-Palatometer	Direct

^a See Martin and Saller (1959), Howells (1973), Knussman (1988), Steele and Bramblett (1988), Buikstra and Ubelaker (1994), Pucciarelli et al. (2008), and Pucciarelli (2008) for landmark definitions and measurement descriptions.

^b For the projected measurements, the skull must be placed laterally on a square 50 × 50-cm white carboard, for reaching an acceptable parallelism with the caliper bar and/or its branches. Positioning must be done by carefully rotating the skull up to reach an auricular–infraorbital equalization (Frankfurt line). Previously, the correct anterior–posterior and vertical placement of the skull must be ensured by the equalization of the prosthion and inion points with respect to the horizontal plane and by the positioning of the palatal first molars perpendicularly to this plane. The Frankfurt orientation can be facilitated by a nylon thread placed not more than 1 cm above the skull and held parallel to one of the cardboard lines. The thread must be taken away after the correct placement has been reached and before measurement starts. Direct measurements may be made out of the Frankfurt orientation. It is recommended to take all projected measurements first and then all direct measurements or vice versa.

^c Howells (1973), Steele and Bramblett (1988), and Buikstra and Ubelaker (1994).

^d The point of intersection of the vomer and the basioccipital in the median sagittal plane.

^e Pucciarelli et al. (2008) and Pucciarelli (2008).

^f The point where the upper temporal line cuts the coronal suture (Steele and Bramblett, 1988).

(1889), and Lehman-Nitsche (1907) believed in the synchronicity of both remains and therefore proposed a Pleistocene age for the human skeleton, other authors like Hansen, Kolleman, and Hrdlička cast doubt about the association (Orquera, 1971, p 136–157). The human bones were bought by Dr. Larsen and sent to Zoologisk Museum of the Copenhagen University at the end of the 19th century. In the 20th century, a member of our group (HMP) had the opportunity to study the skeleton in the Zoologisk Museum of the University of Copenhagen and took detailed measurements. This cranium was probably from a male individual without cranial deformation. This skeleton has not been dated as yet.

Morphometric and statistical analyses

To study the morphological similarities between the skulls from Arroyo Seco 2 (AS2), Chocorí (Chc), La Tigra (LTi), and Fontezuelas (Fon) and the other American samples, we used 29 craniofacial variables (Table 2; Appendix 1), defined on the basis of the functional cranial theory. The theoretical framework of the functional cranial theory was inspired by van der Klaauw's (1948–1952) theory of the independent function of the cranial components in mammals as well as by the studies of Moss and Young (1960). Functional craniology assumes that a skull is composed of relatively independent cra-

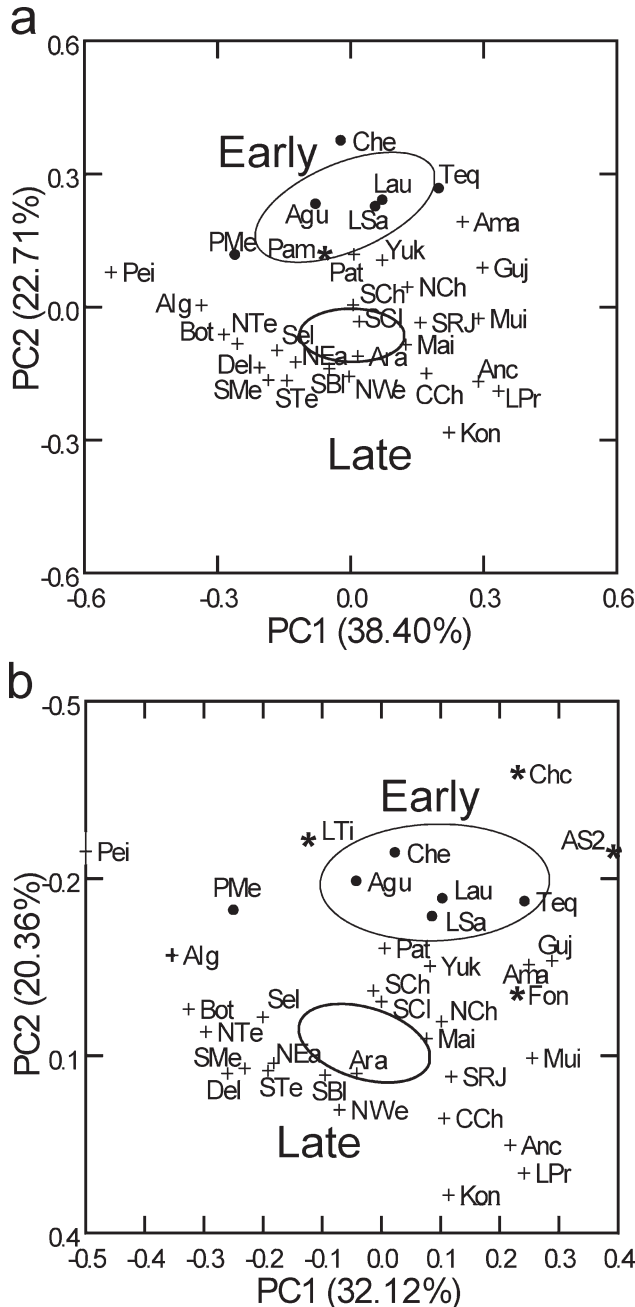


Fig. 2. The Principal Components Analysis of Mosimann shape variable measurements of the 33 American samples. (a) Ordination of mean samples. (b) Ordination of mean samples and Early Holocene Pampas region individuals. The asterisk (*) represents the Pampas Early Holocene samples, the dots (●) represent the Early Holocene samples, and the plus (+) represents the Late Holocene samples. Ellipses represent the 95% confidence interval around the grand mean or centroid of the Early Holocene and Late Holocene samples. Abbreviations are shown in Table 1; AS2 (Arroyo Seco 2), Chc (Chocori), LTI (La Tigra), and Fon (Fontezuelas).

nial units (or modules), and its growth and differentiation are not uniform processes. The craniofunctional method has already been successfully applied in several human and nonhuman primate studies (see Pucciarelli et al., 1990, 2006, 2008; among others). To avoid interobserver error, these measurements were only collected by

one investigator (HMP). The original variables were used to calculate ratios or Mosimann shape variables by dividing each original variable by the geometric mean (GM) of all variables (Jungers et al., 1995). The GM of craniofacial measurements was computed as the n th root of the product of the n variables (Jungers et al., 1995).

We performed the principal components analysis (PCA) based on a covariance matrix of the ratio variables. This analysis was performed over the mean values for each sample to obtain the distances between the four Pampas skulls and the other American samples. PC scores describe the main variation trends in cranial shape among samples, but the first PC scores can be interpreted as a low-dimensional representation of the Euclidean distance matrix among samples, proving excellent results to study between-group morphological differences (Thalib et al., 1999). In all cases, PCA generated the same results as a Principal Coordinates Analysis based on a Euclidean distance matrix.

We also used two traditional cranial indices, the transverse-longitudinal [TLI; The Cranial Index *sensu* Montagu (1960, p 605)], to measure dolichocrania, and the vertical-longitudinal [VLI; Cranial Length-Height Index *sensu* Montagu (1960, p 605)], to measure hypsicrania (Montagu, 1960). This is a simple and useful system with the aim of measuring the principal axes of variation in the cranial vault (i.e., from dolicho-platicephaly to brachy-hipsicephaly).

Finally, the PROTEST analysis was used to compare the pattern of ordination produced by the principal components and the two cranial indices with temporal differences among the samples (Peres-Neto and Jackson, 2001). The PROTEST analysis compares these scores by using the sum of the squared residuals between ordinations in their optimal superimposition, such as a measurement of association (pseudo-correlation, $m12$; Peres-Neto and Jackson, 2001). There are several superimposition strategies, but we used the Generalized Procrustes Analysis, which is the simplest approach (Peres-Neto and Jackson, 2001). Then, a permutation procedure (10,000 permutations) was used to assess the statistical significance of the Procrustean fit. The PROTEST analysis was performed using Vegan 1.8-8 package for R 2.6.1 (R Development Core Team, 2008).

RESULTS

The PCA of Mosimann shape variables showed that along the second PC score, the Early Holocene samples separated from the Late Holocene ones (Fig. 2a). Figure 2 showed the confidence intervals around the grand mean (black ellipses) of the Early Holocene and Late Holocene samples, showing the differences between the mean shapes of these samples. The first PC score showed changes associated with size differences among samples; the Pearson correlation between PC1 and GM was high and significant ($r = -0.821$; $P < 0.001$), whereas the correlation between PC2 and GM was non-significant ($r = -0.309$; $P = 0.080$). The most important variables associated with PC1 score were cranial breadth (CB), stephanion-zygotemporal height (SZH), frontal breadth (FB), occipital chord (OC), and bizygomatic breadth (BB), all positives. Cranial length (CL; positive), cranial breadth (CB; negative), parietal chord (PC; positive), and occipital length (OL; positive) were the most important variable associated with the PC2 score. The PC2 score showed the principal shape change between

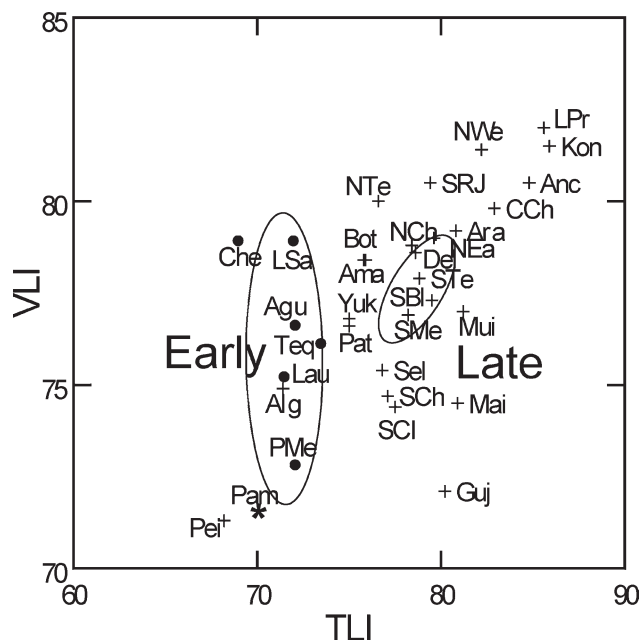


Fig. 3. Transverse-longitudinal (TLI) and vertical-longitudinal (VLI) indices of the 33 American samples. The asterisk (*) represents the Pampas Early Holocene samples, the dots (●) represent the Early Holocene samples and the plus (+) represents the Late Holocene samples. Ellipses represent the 95% confidence interval around the grand mean or centroid of the Early Holocene and Late Holocene samples. Abbreviations are shown in Table 1; AS2 (Arroyo Seco 2), Chc (Chocorí), LTi (La Tigra), and Fon (Fontezuelas).

early and recent American populations, from a long and narrow cranial vault to a shorter and wider cranial one. Specifically, the Early Holocene samples (Pam, PMe, Agu, Che, Lau, LSA, and Teq), some Late Holocene samples (Pei, Ama, Pat, and Yuk) were found along the superior quadrants. When we analyzed La Tigra (LTi), Arroyo Seco 2 (AS2), Chocorí (Chc), and Fontezuelas (Fon) samples independently, they were associated with other Early Holocene samples (Fig. 2b).

For the cranial indices, the scatterplot showed that the samples from Early Holocene separated from the Late Holocene ones along the transverse-longitudinal index (see Fig. 3). The Early Holocene samples and two of the Late Holocene samples (Pei and Alg) had the longest and narrowest vault. However, Early and Late Holocene samples were not differentiated along the vertical-longitudinal index (see Fig. 3).

The Procrustes analysis confirmed the diachronic pattern of shape differences (see Fig. 2) between Early and Late Holocene samples, showing a significant association between cranial shape (PC scores) and temporal dimension. This temporal pattern was stronger for the first two principal components of ratio variables (~60% of total variation; $m_{12} = 0.452$, $P < 0.001$) than for the first three (~75% of total variation; $m_{12} = 0.412$, $P < 0.001$) or first 10 principal components (~95% of total variation; $m_{12} = 0.370$, $P < 0.01$). Finally, indices (see Fig. 3) showed great concordance with temporal variation ($m_{12} = 0.563$, $P < 0.001$).

DISCUSSION

In summary, the Argentinean Pampas samples studied here were closely related to other Early Holocene Ameri-

can samples. In general terms, the Late American samples were differentiated from early samples such as the Arroyo Seco 2 skull and the other Pampas samples. Interestingly, we found that samples from the Argentinean Pampas, Lagoa Santa, and Tequendama samples had long and narrow cranial vault morphologies and included the Yukpas from Venezuela, the Paltacalos from Ecuador, the Pericues from Baja California, and the Algonkians from Canada. However, the PROTEST analysis showed that there was a significant agreement between cranial morphology and radiocarbon dating. These facts allowed us to speculate that early American samples could be morphologically different from late-American groups.

Two different hypotheses have been suggested to explain the observed differences in cranial morphology between early and late-American samples. In the recent years, the *two main biological components* hypothesis has been the most used to explain the cranial variation between early and late-American skulls (Neves et al., 2003; Pucciarelli et al., 2006, 2008). This hypothesis pointed out that the morphological diversity of American groups resulted from two successive migratory events that generated two morphological components within America. The first component (called Palaeoamericans) with a long and narrow cranial vault was derived from Pleistocene Southeast Asian groups that expanded into America around 14,000 years BP. The second component (called Amerindians) had a short and wide cranial vault. They migrated from Northeast Asia to America during the Early Holocene (~8,000 years BP; Neves et al., 2003; Pucciarelli et al., 2006, 2008). These investigations also pointed out that the first component corresponded with a generalized cranial morphology, whereas the second one belonged to a mongoloid cranial shape, which was largely affected by the low temperatures of the last glacial period. In addition, it has been pointed out that the early American skulls discovered in the continent, with a relatively long and narrow vault, did not show traces of adaptation to a cold environment, that is, they were *Homo sapiens* with a generalized craniofacial morphology as Australian and Melanesian groups, as was seen by Lahr (1996) among others. The postglacial Asiatic populations, the Amerindians, and the Circumpolar peoples from Beringia, differ from the early Americans mainly by its short and broad, brachycranial skull (Pucciarelli et al., 2008).

On the other hand, it has also been suggested that the cranial differences between early and late-American samples could be explained if we take into consideration that craniofacial variation among human populations could mainly result from the action of random (genetic drift) and nonrandom factors (directional selection and phenotypic plasticity) (Powell and Neves, 1999; Perez et al., 2009). The former factors could be related to founder effect events that occurred during the initial peopling of the Americas by small hunter-gatherer groups (Powell and Neves, 1999; Perez et al., 2007). The nonrandom factors could be related to climatic variation [i.e., morphological changes related to cold; (Bernal et al., 2006)] as well as to changes in diet [i.e., production of domesticated resources; Perez and Monteiro (2009)] and food-preparation technology (i.e., pottery) that took place between 5,000 and 2,000 ^{14}C years BP [see discussion in Perez et al. (2009)]. Directional selection and/or phenotypic plasticity can generate fast morphological changes and account for the craniofacial variation found among

American populations (Perez et al., 2007, 2009; Perez and Monteiro, 2009). Therefore, the influence of ecological variables—such the ones related to cold climate conditions and diet differences—could contribute to the morphological differences between early and late-American groups (Roseman, 2004; Harvati and Weaver, 2006; Perez and Monteiro, 2009; Perez et al., 2010). Particularly, these works showed that climate and diet variation, as seen in the Americas, could generate cranial variation among human populations, from long and narrow to short and wide skulls. These ecological factors, in particular diet, could also explain the great variation found in the cranial morphology of Late Holocene American samples—also from long and narrow to short and wide skulls (Perez et al., 2010).

Our results underscore the important differences in cranial morphology between early and late-American samples, as pointed out by several studies (Ameghino, 1909; Neves and Pucciarelli, 1989; among others). Particularly, we found additional evidence to support the pattern of differences between the early and late Holocene American groups. However, using cranial morphology alone is difficult to support one or the other hypotheses proposed to account for the morphological differences between early and late American samples. We emphasize the need for further studies to discuss alternative hypotheses regarding such differences. Therefore, we need to elucidate the probable sources of variation in craniofacial morphology during the Holocene, before being able to support alternative hypotheses.

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