AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 128:772–780 (2005)

Late Pleistocene/Holocene Craniofacial Morphology in Mesoamerican Paleoindians: Implications for the Peopling of the New World

Rolando González-José,[1,7]* Walter Neves,[2] Marta Mirazón Lahr,[3] Silvia González,[4]
Héctor Pucciarelli,[5,7] Miquel Hernández Martínez,[1] and Gonzalo Correal[6]

[1]*Secció d'Antropologia, Facultat de Biologia, Universitat de Barcelona, 08028 Barcelona, Spain*
[2]*Laboratorio de Estudos Evolutivos Humanos, Departamento de Biologia, Instituto de Biociências, Universidade de São Paulo, 05422.970 São Paulo, São Paulo, Brazil*
[3]*Leverhulme Centre for Human Evolutionary Studies, University of Cambridge, Cambridge CB2 3DZ, UK*
[4]*School of Biological and Earth Sciences, Liverpool John Moores University, Liverpool L3 3AF, UK*
[5]*Departamento Científico de Antropología, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad de La Plata, 1900 La Plata, Argentina*
[6]*Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá, Colombia*
[7]*Comisión Nacional de Investigaciones Cientificas y Téchnicas, CONICET, C1033AAJ Buenos Aires, Argentina*

KEY WORDS craniometrics; Early Holocene crania; settlement of Americas

ABSTRACT Several studies on craniofacial morphology showed that most Paleoindians, who were the first settlers of the New World, clearly differ from modern Amerindians and East Asians, their supposed descendants and sister group, respectively. Here we present new evidence supporting this view from the Late Pleistocene/Early Holocene horizon from Mexico, as well as from the most complete set of dated Paleoindian remains. We analyzed the phenotypic resemblance of early Mexicans with other South Paleoamerican and modern human series. Two independent approaches to the data were used. In the first case, individual specimens were tested for morphological similarity with a set of modern reference samples. In the second analysis, Mexican specimens were treated as a sample in order to compute minimum genetic distances. Results from both approaches tend to associate early Mexican skulls with Paleoindians from Brazil, an Archaic sample from Colombia, and several circum-Pacific populations. These results give support to a model in which morphologically generalized groups of non-Northeast Asian descent (the so-called Paleoamericans) entered the continent first, and then dispersed from North to South America through Central America. The large geographic dispersal of Paleoamericans, and their presence in Mexico in the Early Holocene, raise new issues about the continent's settlement scenario. Am J Phys Anthropol 128:772–780, 2005. © 2005 Wiley-Liss, Inc.

Paleoamericans[1] are believed to be the first settlers of the New World. During the last decade, a thorough study of human skeletal remains from North and South American Late Pleistocene/Early Holocene horizons led to the observation that traits characterizing both typical East Asians and recent Amerindians are absent from or extremely rare among most Paleoindians (Neves and Pucciarelli, 1989, 1991; Steele and Powell, 1992, 1993; Neves et al., 1999a,b; Powell and Neves, 1999; González-José et al., 2001; Jantz and Owsley, 2001, 2003). These results forced the adoption of the term "Paleoamerican,"[1] and led to a refinement of the hypotheses regarding the extracontinental relationships of the first Americans. The working hypothesis states that the origin of Paleoamericans must be traced back to a common ancestor for Paleoamericans and Australians, who departed from somewhere in southern Asia and arrived on the Australian continent and the Americas around 50,000 and 14,000 years before present (ybp), respectively. The majority of modern Amerindians are regarded by some to be part of a second, morphologically differentiated migration (Neves et al., 1999a, 2003). However, after analyzing the craniofacial morphology of several modern groups, Lahr (1995, 1996) concluded that some Amerindian groups (e.g., Fuegians and Patagonians) fail to cluster into the typical Northeast Asian descent morphological pattern, perhaps as a result of retention of

---

[1] The term "Paleoamerican" is used here to describe remains which present a generalized morphology when compared with their putative descendants (modern Amerindians) and sister group (East Asians). Conversely, the term "Paleoindian" is normally employed in the literature to refer specifically to Late Pleistocene/Early Holocene hunter-gatherers from the New World. Note that all Paleoamericans are also Paleoindians, but not all Paleoindians are necessarily Paleoamericans. Thus, "Paleoamerican" refers to the presence of a set of morphological traits in a given skull or sample of skulls, whereas "Paleoindian" is solely based in the chronological-cultural characteristics of a specimen or group of specimens.

Grant sponsor: FAPESP; Grant number: 99/00670-7; Grant sponsor: NERC-EFCHED, UK; Grant number: NER/T/S/2002/00467.

*Correspondence to: Rolando González-José, Centro Nacional Patagónico-CONICET, Bvd. Brown s/n, U9120ACV Puerto Madryn, Argentina. E-mail: rolando@cenpat.edu.ar

Received 5 January 2004; accepted 2 August 2004.

DOI 10.1002/ajpa.20165

plesiomorphic Paleoamerican traits (Lahr, 1995, 1996). Recently, González-José et al. (2003) presented the first evidence of a modern Amerindian group from the peninsula of Baja California in Mexico, showing clearer affinities with Paleoamerican remains than with modern Amerindians, thus providing further evidence for the survival of the Paleoamerican stock in some geographically isolated areas. Additionally, a recent study on the craniofacial attributes of Old World and New World populations found that some North Amerindian groups also fail to show close similarities to modern Asian groups (Brace et al., 2001). According to those authors, this fact may reflect that the origin of those Amerindian groups can be traced back to an extended Late Pleistocene stock inhabiting the northern part of the Old World and whose craniofacial morphology differs from that of modern East Asians (Brace et al., 2001). In summary, much controversy remains around the tempo and mode of morphological change between ancient and modern groups in the New World.

Van Vark et al. (2003) questioned the validity of morphological data when reconstructing ancestral/descendent relationships among populations separated by long intervals of time, reasoning that some morphological traits are primarily shaped by environmental processes. In a reply to Van Vark et al. (2003), Jantz and Owsley (2003) noted (correctly, in our view) that, in most cases, the accuracy of estimations of similarities largely depends on the number of variables used in the computation of distances. The criticism by Van Vark et al. (2003) was mainly focused on the comparisons of single Upper Paleolithic/Early Holocene specimens vs. modern samples. However, the observed morphological divergence between Paleoamericans and modern Amerindians is based on large samples from Brazil and Colombia (e.g., Neves and Pucciarelli, 1989, 1991; González-José et al., 2001; Neves et al., 2003). The latter are the only Paleoindian population samples, rather than single specimens, on the continent.

When studying single specimens, one must always be cautious, because the central tendency of the population from which the specimen was extracted is unknown. However, when an acceptable estimate of the central tendency and variance of the population is available, there is no biological reason to avoid the application of statistical comparative tools. The potential existence of environmental forces acting upon the development of craniofacial form is not sufficient to state that these forces played a role in the origin of overall morphological differences (Lahr and Wright, 1996, Relethford, 2002; Sparks and Jantz, 2002; González-José et al., 2004). To these authors and others, the main point is not whether adaptation to the environment occurs, but the magnitude of such influence on the estimates of multivariate minimum genetic distances. Several recent observations on some statistical properties of craniofacial variation, such as the great similarity between molecular and morphological apportionment of internal vs. external levels of variation, the stability of phenotypic covariance matrices, and the congruence between morphological and molecular classifications, are in agreement with the view that if environmental variation is randomly distributed from one character to another, then craniofacial traits can be considered selectively neutral on average (Relethford, 2002). Thus, the analysis of morphological change among past populations remains the main tool to study past historical and structural population processes.

Even when migrationist approaches are a good source for settlement hypotheses, microevolutionary models involving further evolutionary agents such as gene flow, local adaptation, and genetic drift are needed to achieve greater resolution of current debates. Taking into account these theoretical issues, testing the geographical distribution of the Paleoamerican multivariate cranial spectrum becomes a crucial step in investigating whether long-term phylogenetic processes rather than in situ local adaptation were responsible for the patterns observed.

Paleoindian and Archaic remains from Brazil and Colombia, respectively, constitute a well-preserved and dated sample, whose morphological particularities were extensively explored in several studies (Neves and Pucciarelli, 1989, 1991; Neves et al., 1999a,b; Powells and Neves, 1999; González-José et al., 2001). Other Paleoindian specimens of interest that cannot be accommodated in a large sample can then be compared with this Paleoindian and Archaic series in order to estimate genetic affinity or group membership. For instance, many conclusions were based on the information derived from single skeletons of Late Pleistocene/Early Holocene horizons from several regions of North America (Steele and Powell, 1992, 1993; Jantz and Owsley, 2001, 2003). Unfortunately, an estimate of the population basic statistical parameters (e.g., mean and variance) is impossible in the case of isolated individuals, since one cannot establish a priori how far off the group centroid the specimen studied would be. However, recent advances in multivariate analyses enable assessment of morphometric affinities of a single specimen to reference groups of other living populations (Albrecht, 1992; Van Vark and Schaafsma, 1992; González-José et al., 2002). Here we test for the presence of Paleoamerican morphology in southern North America by analyzing the affinities between five early skulls from Mexico, and Paleoamerican and worldwide modern reference samples.

MATERIALS AND METHODS

The sample

Five skulls from Central Mexico (male specimens from Tlapacoya, Cueva del Tecolote, Chimalhuacán, and Metro Balderas, and a female from Peñón III) were measured and compared to a sample of 31 Paleoamericans and 1,947 modern human crania in order to estimate patterns of morphological resemblance and dissimilarities. Photographs in lateral view of the skulls are shown in Figure 1, and further information about the early Mexican Paleoindian and Archaic data is presented in Table 1.

Tlapacoya, Cueva del Tecolote, and Metro Balderas are specimens represented only by the skull, while a complete and a partial skeleton are available for Chimalhuacán and Peñón III, respectively. Measurements available for each skull are listed in Table 2.

The five specimens were found in Central Mexico, and a detailed explanation of their C^{14} dating can be found in González et al. (2002, 2003). Modern samples from the Americas, Africa, Australia/Melanesia, East and South Asia, and Polynesia were used as reference samples. Raw data on these groups were taken from the data base of Howells (1973, 1989). Comparisons are based on the premise that phenotypic variation adequately reflects genetic variation, a premise supported by several quantitative genetic analyses (Cheverud, 1988; Relethford and Harpending, 1994; Konigsberg and Ousley, 1995; Relethford, 1996; Relethford et al., 1997). Furthermore, as discussed above, comparisons between genetic and craniometric apportionments of global diversity suggested that global

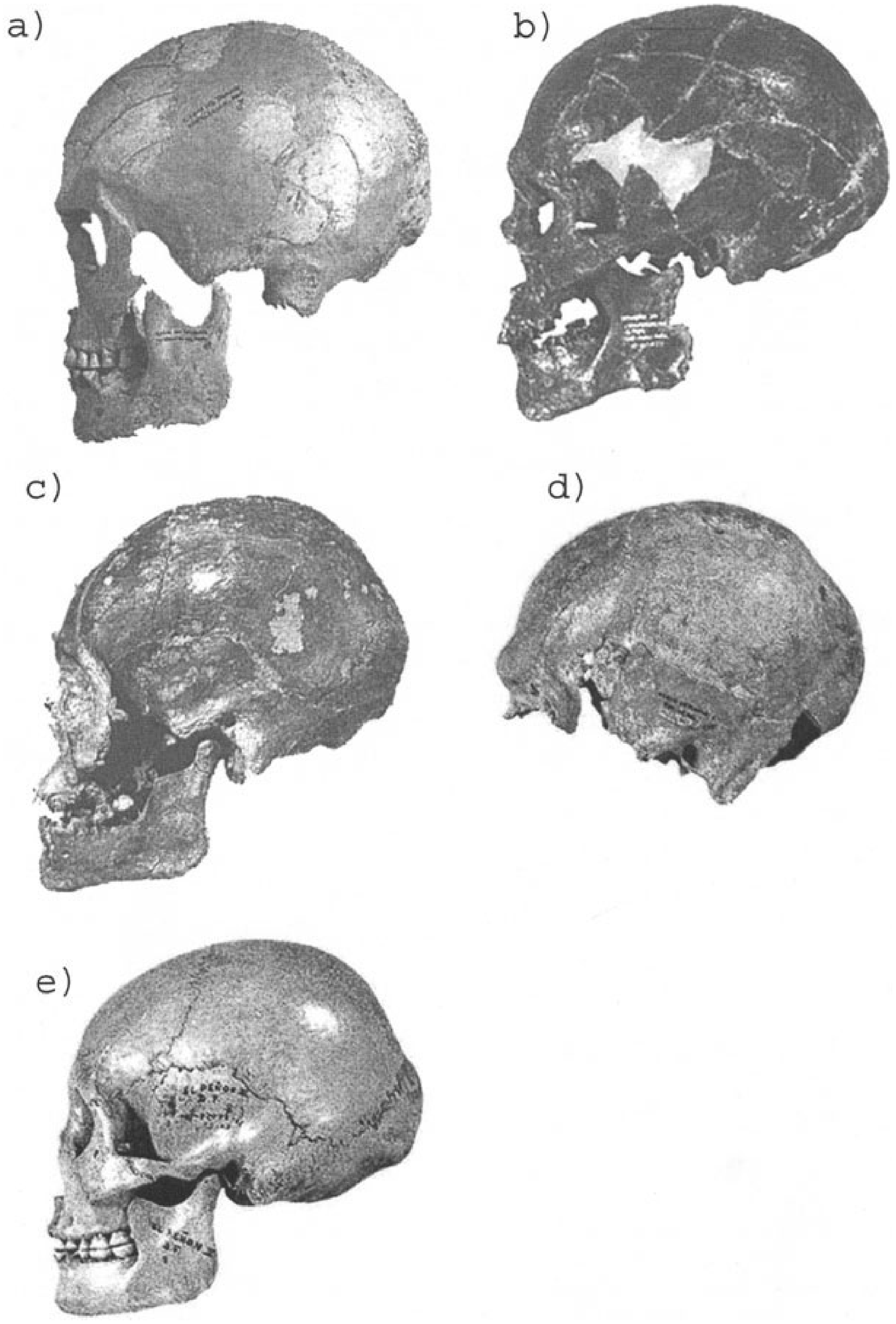

Fig. 1. Photographs in lateral view of five early Mexican skulls studied. **a:** Cueva del Tecolote. **b:** Chimalhuacán. **c:** Metro Balderas. **d:** Tlapacoya. **e:** Peñón III.

patterns of craniometric variation can be considered selectively neutral on average (Relethford, 2002).

Archaeological and chronological background of Mexican skulls

Peñón III. This site was discovered by chance in 1959 when digging for a well around the Peñón de los Baños Hill, which during the Late Pleistocene was an island surrounded by hot springs in the middle of Texcoco Lake. The partial skeleton was found under 2 m of travertine, embedded in a humic layer mixed with volcanic ash (Mooser and Gonzalez Rul, 1961). The layer was totally aceramic. The humerus was directly dated by AMS to 10,755 ± 75 radiocarbon years before present (RCYBP). The craniometric data used were taken by M.M.L.

Tlapacoya I. Tlapacoya Hill is an important prehistoric site in the southeast of the Basin of Mexico, in the middle of the former Chalco Lake. During the Late Pleistocene, the hill was either an island or part of a

TABLE 1. Early Mexican (TECO, CHIMA, METRO, TLAPA, and PIII), Paleoamerican (LAGO), and Archaic (BOGO) remains used in this study[1]

Region/location	Code	Sample	N	Age (years before present)
Mexico			4	
C. del Tecolote, Mexico	TECO/MEX	INAH-10613650	1	9,000–7,000[4]
Chimalhuacán, Mexico	CHIMA/MEX	INAH-10613653	1	10,500[4]
Metro Balderas, Mexico	METRO/MEX	INAH-10613653	1	10,500[4]
Tlapacoya	TLAPA/MEX	INAH-10226501	1	10,200 ± 65[5]
Peñón III	PIII/MEX	07/1959/DAF/INAH	1	10,755 ± 75[5]
South America			31	
Carrancas, Brazil	LAGO	MN 629	1	7,970 ± 40[4]
Carrancas, Brazil	LAGO	MN 630	1	7,970 ± 40[4]
Mortuária, Brazil	LAGO	MN 805	1	8,290 ± 50[4]
Mortuária, Brazil	LAGO	MN 807	1	8,290 ± 50[4]
Cerca Grande 6, Brazil	LAGO	MN 1325	1	9,028 ± 120[4]
Cerca Grande 6, Brazil	LAGO	MN 1353	1	9,028 ± 120[4]
Cerca Grande 6, Brazil	LAGO	MN 1355	1	8,240 ± 40[5]
Cerca Grande 6, Brazil	LAGO	MN 1357	1	9,028 ± 120[4]
Cerca Grande 7, Brazil	LAGO	MN 1388	1	9,130 ± 60[4]
Lapa Vermelha IV, Brazil[2]	LAGO	MN 1959	1	9,330 ± 69[3]/11,000[4]
Lagoa Santa, Brazil	LAGO	HW 001	1	8,000[6]
Lagoa Santa, Brazil	LAGO	HW 004	1	8,000[6]
Lagoa Santa, Brazil	LAGO	HW 005	1	8,000[6]
Lagoa Santa, Brazil	LAGO	HW 006	1	8,000[6]
Lagoa Santa, Brazil	LAGO	HW 009	1	8,000[6]
Lagoa Santa, Brazil	LAGO	HW 010	1	8,000[6]
Lagoa Santa, Brazil	LAGO	HW 013	1	8,000[6]
Lagoa Santa, Brazil	LAGO	HWs/n-CAALE	1	8,000[6]
Mortuária, Brazil	LAGO	CONFINS	1	8,290 ± 50[4]
Checua, Colombia	BOGO	CHEC 10	1	7,800 ± 60[4]
Tequendama, Colombia	BOGO	TEQI 02	1	7,500 ± 60[4]
Tequendama, Colombia	BOGO	TEQI-03	1	7,500 ± 60[4]
Tequendama, Colombia	BOGO	TEQI-12	1	7,235 ± 60[4]
Tequendama, Colombia	BOGO	TEQI-16	1	7,500 ± 60[4]
Gachala, Colombia	BOGO	GACHAsn	1	9,360 ± 45[4]
Checua, Colombia	BOGO	CHEC-07	1	7,800 ± 60[4]
Checua, Colombia	BOGO	CHEC-13	1	8,200 ± 60[4]
Tequendama, Colombia	BOGO	TEQI-18	1	7,500 ± 60[4]
Tequendama, Colombia	BOGO	TEQII-01	1	7,500 ± 60[4]
Tequendama, Colombia	BOGO	TEQII-02	1	7,500 ± 60[4]
Tequendama, Colombia	BOGO	TEQII-03	1	7,500 ± 60[4]

[1] Details on dating of Mexican specimens can be found in González et al. (2002, 2003) and Pompa y Padilla and Serrano Carreto (2001).
[2] Also known as "Luzia."
[3] Minimum AMS age.
[4] Stratigraphical age.
[5] Exact AMS age.
[6] Estimated age.

peninsula. The skull was discovered by chance in 1962 by motorway workers, and so it has no stratigraphic control (Lorenzo and Mirambell, 1986). The cranium was directly dated by AMS to 10,200 ± 65 RCYBP. The craniometric data used were taken by W.N. and H.P.

Metro Balderas. The skull was found in 1970 at a depth of 3.10 m depth during construction work for the Balderas Metro station in the center of Mexico City. The skull was reported to be embedded in one of the main tephra markers for the Basin of Mexico, the Tripartite Ash or Upper Toluca Pumice, which was recently reevaluated and dated to 10,500 years RCYBP (Arce et al., 2003). Volcanic ash samples taken from the inside of the skull were studied using microprobe analysis, and gave values of silica of 70–71%, associated with the Upper Toluca Pumice eruption (González et al., 2001). This has been the only way of dating the skull, as there is no collagen preservation for a radiocarbon date determination. The craniometric data used were taken by W.N. and H.P.

Chimalhuacan. This almost complete skeleton was found by chance in 1984 in Colonia Embarcadero (Chimalhuacan, Estado de Mexico), in association with some bone tools and obsidian flakes (Pompa y Padilla, 1988). However, there are no published records of stratigraphy associated with the find. There is no collagen preservation in this specimen, which shows the characteristic black color associated with strong mineralization of the bones. However, indirect dating was possible by analyzing the sediments found inside the skull, which were a mixture of lake sediments, diatoms, and volcanic ash from the Upper Toluca Pumice (González et al., 2002). Therefore, the date of Chimalhuacan Man is estimated at around 10,500 RCYBP. The craniometric data used were taken by W.N. and H.P.

Cueva del Tecolote. This is one of two cave burials found in 1959 by Cynthia Irwin Williams in Huapalcalco (Estado de Hidalgo). One of the burials had a canid mandible as an offering, while an offering of five complete dog skeletons was found near the other burial (Romano,

TABLE 2. Variables corresponding to five skulls studied here, with measurement codes as in Howells (1973)

	Tlapacoya	C. del Tecolote	Chimal-huacan	Metro Balderas	Peñón III[1]		Tlapacoya	C. del Tecolote	Chimal-huacan	Metro Balderas	Peñón III[1]
GOL	197	204	197	196	187	WNB	12		10	10	7
NOL	194	201	195	195	186	IML		36	40		37
BNL					95	XML		51	53		54
BBH					129	MLS		8	13		
XCB	133	132	140	145	132	WMH		23	23	26	26
XFB	114		113	122	112	SOS	9	8	7	8	5
STB	114		111	119	88	GLS	6	5	4	3	3
ZYB		140	145		134	FOL					39
AUB	122	126	133	130	125	FRC	129	119	111	111	116
WCB	76			73	69	FRS	25	22	23	19	23
ASB	109		119		110	FRF	55	44	53	46	46
BPL					98	PAC	114	120	120	124	119
NPH		58	77	66	63	PAS	21	22	23	29	25
NLH		43	56	49	46	PAF	52	61	63	65	66
OBH			36	38	35	OCC		108	98		91
OBB			42	45	38	OCS		38	32		29
JUB		123	121		120	OCF		52	39		41
NLB		26	25	26	24	VRR	128	128	113	130	
MAB		62		72	67	NAR	96	94	97	94	
MDH	37	27	31		25	SSR		97	99	99	
MDB	14	10	16	13	21	PRR			108	108	
ZMB		100	98		101	DKR			85	84	
SSS		24	25		21	ZOR		84	84	83	
FMB	109		101	106	101	FMR	84		85	80	
NAS	14		16	17	15	EKR			76	73	
EKB		102	100		98	ZMR		74	63	80	
DKS			12		8	AVR		81			
DKB	29		26	24	25						

[1] Radii measurements were not considered in Peñon III skull.

1974). There is no collagen preservation for the specimen, but Pompa y Padilla and Serrano Carreto (2001) attributed an age of 9,000–7,000 YBP to the Tecolote skull, based on stratigraphy and archaeological affinities. The craniometric data used were taken by W.N. and H.P.

Statistical procedures

Because the Late Pleistocene/Early Holocene sample from Mexico consists of only five individuals, classical statistical approaches to assess variation among samples could be inappropriate (Jantz and Owsley, 2001). Yet despite the fact that fossil sample sizes are usually low, the use of averages and multivariate centroids of such samples must be of interest in perceiving general tendencies by means of classical statistics. To solve this pitfall, we considered three independent approaches to the data. First, Mahalanobis distances were computed between the five early Mexican skulls individually and a set of reference samples, including the Paleoindian series LAGO and the early Archaic group BOGO (Table 1). We used only male series as references to Tecolote, Chimalhuacán, Tlapacoya, and Metro Balderas, while female series were used to compare the skull of Peñón III. In considering the set of populations studied by Howells (1973, 1989), we discarded a population highly admixed in recent times (Phillipines), as well as Maori groups because of their small sample sizes. Accordingly, the data set of Howells (1973, 1989) was reduced to the following series: Arikara (Amerindian, n = 69), Eskimo (Amerindian, n = 108), Peru (Amerindian, n = 110), Santa Cruz (Amerindian, n = 102), Australia (Australia/Melanesia, n = 101), Tasmania (Australia/Melanesia, n = 86), Tolai (Australia/Melanesia, n = 110), Ainu (East Asia, n = 86), Buriat (East Asia, n = 109), North Japan (East Asia, n = 87), South Japan (East Asia, n = 91), Easter Island (Polynesia, n = 86), Guam (Polynesia, n = 57), Mokapu (Polynesia, n = 100), Moriori (Polynesia, n = 108), Teita (Africa, n = 83), Dogon (Africa, n = 99), Zulu (Africa, n = 101), Bushman (Africa, n = 82), Hainan (South Asia, n = 83), Anyang (South Asia, n = 42), and Atayal (South Asia, n = 47).

Squared Mahalanobis distances between an individual and a sample were computed as

$$D^2{}_{1,j} = (x_1 - x_j)P_W^{-1}(x_1 - x_j),$$

where x_1 represents the vector of values for individual 1, x_j is the mean vector for population j, and P_w represents the pooled within-sample covariance matrix (Van Vark and Schaafsma, 1992; Powell and Neves, 1999). In the classical meaning of the Mahalanobis distances, the covariance matrix reflects within-group covariation patterns of the populations from which the specimens were extracted. In cases when the covariance structure of the population is unknown, the appropriate method is to use the pooled within-group covariance matrix derived from a large sample of modern populations, as described previously (Van Vark and Schaafsma, 1992; Powell and Neves, 1999; Jantz and Owsley, 2001; González-José et al., 2002). This conservative approach was adopted here, by estimating P_w from the data of Howells (1973, 1989). Calculations were based on the total number of observable variables by Howells (1973, 1989) for each specimen, in order to avoid inconsistencies caused by the use of few variables (Pietrusewsky, 2000). The squared Mahalanobis distances were used to obtain a typicality probability for each individual. Typicality probabilities were computed using a chi-square distribution of the squared Mahalanobis distance, with p (number of traits)

TABLE 3. Squared Mahalanobis distances and typicality probabilities (Tp) of each cranium relative to Paleoamerican (LAGO), Archaic (BOGO), and modern (codes as in Howells, 1973, 1989) reference samples[1]

CHIMA (36)	D^2	Tp	TECO (48)	D^2	Tp
Atayal	293.68	0.0000	BOGO	65.89	0.0017
Teita	299.39	0.0000	LAGO	78.22	0.0001
Zulu	299.69	0.0000	Australia	80.77	0.0000
Dogon	302.99	0.0000	Peru	84.00	0.0000
Bushman	306.39	0.0000	Easter Island	86.42	0.0000
METRO (36)	D^2	Tp	TLAPA (25)	D^2	Tp
Peru	49.48	0.0667	BOGO	74.60	0.0000
S. Cruz	58.70	0.0098	Australia	82.83	0.0000
Lago	61.59	0.0050	Mokapu	88.09	0.0000
Ainu	62.94	0.0036	Zulu	89.02	0.0000
Guam	63.09	0.0035	Peru	89.42	0.0000
PIII (42)	D^2	Tp			
BOGO	121.00	0.0000			
Peru	134.78	0.0000			
Teita	135.62	0.0000			
S. Cruz	135.87	0.0000			
Tolai	137.52	0.0000			

[1] Nearest five reference samples are shown for each specimen. In parentheses, number of variables used.

degrees of freedom (Albrecht, 1992). This statistic describes how "typical" that fossil is compared to reference samples, without assuming that the individual was in fact a member of the group (Powell and Neves, 1999). Since it is already known that no early Mexican skull was sampled from one of the reference populations, regardless of the value of distance obtained, typicality probabilities are a more useful statistic than posterior probabilities (Albrecht, 1992; Jantz and Owsley, 2001). Additionally, a principal components analysis (PCA) was performed using the four most complete Paleoindian specimens from Mexico (Tecolote, Chimalhuacán, Metro Balderas, and Peñón III), the Paleoindian and Archaic series, and modern samples of both sexes. Before computing the principal components (PCs), all observations were standardized to z-scores within each sex to remove sex-related size variation (Williams-Blangero and Blangero, 1989). PCA was performed on a consensus set of 26 of the variables of Howells (1973, 1989) (GOL, NOL, XCB, XFB, AUB, NPH, NLH, OBH, OBB, NLB, MDH, FMB, NAS, DKB, WMH, SOS, GLS, FRC, FRS, FRF, PAC, PAS, PAF, OCC, OCS, and OCF). We used these 26 variables, instead of the 57 original variables used by Howells (1973, 1989), in order to minimize the effect of missing data within the early Mexican fossils. Thus, analyses were carried out on a data set with an average of 5% of missing values in the Paleoindian/Archaic sample and an average of 9% of missing values in the early Mexican specimens, which were replaced by multiple regression estimation (Sokal and Rohlf, 1995). A multiple regression equation for each replaced variable was computed from the complete modern data base, rather than using only the remaining early Mexicans or South American Paleoindians.

Finally, the sex-standardized data set used in the PCA analysis was modified by collapsing the four early Mexican specimens into a single sample (coded as MEX) to obtain minimum genetic distances to other Paleoindian, Archaic, and modern samples. Distances were obtained after an R-matrix analysis (Harpending and Jenkins, 1973; Relethford and Blangero, 1990). An R-matrix is the normalized covariance matrix of allele frequencies across populations. R-matrix analysis has several advantages over other methods of estimating genetic similarities and distances (Relethford and Harpending, 1994). This method was first proposed by Harpending and Jenkins (1973), and was further extended to quantitative traits by Relethford and Blangero (1990). R-matrix analyses make explicit assumptions regarding the mode of transmission of the underlying genotypic variation expressed in the phenotype, and evolutionary and demographic parameters affecting population structure (Williams-Blangero and Blangero, 1989). This approach assumes an additive polygenic model for the traits in which the expectation of environmental deviations is zero. Assuming complete heritability, the distance matrix obtained represents a matrix containing the minimum genetic distances derived from the phenetic variation (Williams-Blangero and Blangero, 1989; Relethford and Blangero, 1990). Here we provide minimum genetic distances after adjusting for small sample size bias, following Relethford et al. (1997).

RESULTS AND DISCUSSION

Results concerning Mahalanobis distances and typicality probabilities computed among early Mexican specimens and reference samples are presented in Table 3.

Typicality probabilities (tp) across the board are low. Since the intention of tp is to determine the probability of a skull falling within the multivariate normal distribution of one of the reference groups, low tp across-the-board indicate, in accordance with Albrecht (1992), that the individual falls outside the range of the reference group. The computation of tp seems to be a controversial issue, characterized by a lack of consensus about the method to be used, as well as the relative effect of using different numbers of variables (for a debate on this issue see Van Vark et al., 2003, vs. Jantz and Owsley, 2003). Despite the low values of tp, the pattern of distances to reference samples is very constant, and early Mexican skulls show no clear resemblance to Amerindians or East Asians. In spite of METRO, which shows greatest similarity to Peruvians, note that only 6 out of 25 comparisons displayed in Table 3 tend to tie an early Mexican specimen to an Amerindian sample. Conversely, 19 of the 25 comparisons reflect the

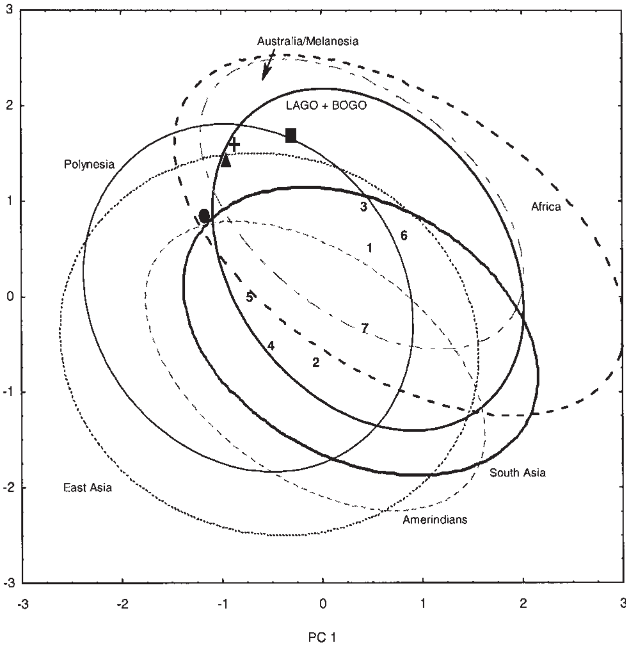

Fig. 2. Ninety percent confidence ellipses for first two principal components. Individual early Mexican skulls and centroids are plotted: TECO, square; CHIMA, circle; METRO, triangle; PIII, cross; 1, Paleoamerican + Archaic centroid; 2, Amerindian centroid; 3, Australo-Melanesian centroid; 4, East Asian centroid; 5, Polynesian centroid; 6, African centroid; 7, South Asian centroid.

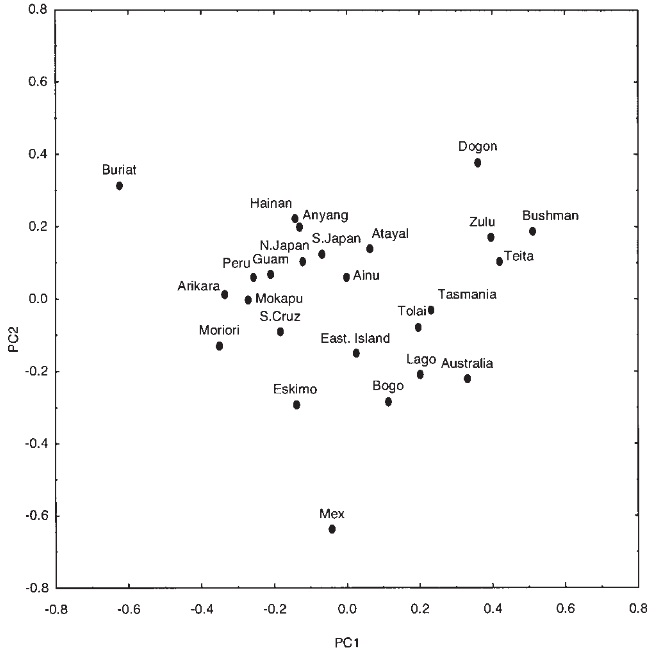

Fig. 3. Principal coordinates plot of samples using R-matrix data from analysis by Relethford and Blangero (1990). PC1 and PC2 collectivelly account for 44.7% of variation.

greatest similarity to Africans (6/25), Paleoindians (5/25), Australians (3/25), Polynesians (3/25), South Asians (1/25), or the Ainu (1/25). When first-place positions are explored, all five are circum-Pacific, either recent or early. Among second-place positions, 4 out of 5 are circum-Pacific, and the remaining one is African. Third places also present the same pattern of distances. Therefore, methods based on tp failed to assign clearly the specimens to a reference group, but Mahalanobis distances reflect either relatively similar values towards Paleo-South Americans and circum-Pacific populations, or, as in the case of CHIMA, exclusion of both recent Amerindians and East Asian groups among the five closest populations. It remains an open question whether tp are unaffected by the number of variables used (Jantz and Owsley, 2003).

Because of the difficulty in interpreting Mahalanobis distances among single specimens and reference samples, we chose to use more classical tools to explore the affinities of early Mexicans, by carrying out a principal components analysis (PCA) to further evaluate resemblances of the four most complete specimens. The plot of the first two principal components scores for 26 variables across the four most complete early Mexicans, LAGO, BOGO, and modern reference samples is displayed in Figure 2.

Here, the pattern of association seems to be much clearer. It reflects the differentiation between the two groups under scrutiny, South American Paleoindians plus the Archaic group on the one hand, and modern Amerindians and East Asians on the other. Even when the degree of overlapping between the ellipses constructed is high, all the early Mexican individuals fall within the range of variation of LAGO + BOGO, Africans, Australians, or Polynesians, being near the centroids of Australians and Polynesians. Note that no early Mexicans fall within the 90% confidence ellipse of modern Amerindians, and only Chimalhuacán can be attributed almost equally to Africans, East Asians, or Polynesians. Components 1–6 collectively account for 64% of the variation, and the first two components account for 36% of the variation. The first component is primarily influenced by width dimensions (XCB, XFB, and AUB) and overall cranial length (GOL). The first PC seems to express mainly the transversal profile and length of the vault. The second PC is primarily influenced by the length and curvature of the parietals (PAC and PAF). The third PC (not shown) is influenced by occipital length and curvature (OCC and OCF) and neurocranial height (VRR).

To summarize, analyses of individual skulls against reference samples suggest that the early Mexican fossils studied do not share a common craniofacial morphology with Amerindians or East Asians, as reported elsewhere for South Paleoindians, some North Paleoindian specimens (Neves and Pucciarelli, 1989, 1991; Steele and Powell, 1992, 1993; Neves et al., 1999a,b; Powells and Neves, 1999; González-José et al., 2001, 2002; Jantz and Owsley, 2001, 2003), and some modern groups like Fueguian-Patagonians (Lahr, 1995, 1996) and the Pericúes from Baja California (González-José et al., 2003). Further analyses must involve more Amerindian populations in order to better understand the levels of variability on the continent.

The principal coordinates plot obtained after the R-matrix analysis is shown in Figure 3.

An inspection of principal coordinate 1 reflects that, in congruence with the results presented above, Paleoindians from Brazil and the Archaic group from Colombia fall closer to Australian groups (positive values) than to Amerindians (negative values). The early Mexican sample occupies an intermediate position along PC1, between the African-Australian-South Pacific cluster and the East Asian-Amerindian one. The lack of a clear clustering of early Mexicans with Amerindians or East Asians along PC1 supports the concept of a "generalized" morphology proposed for Early Holocene South Americans (Neves and

Pucciarelli, 1989, 1991; Steele and Powell, 1992, 1993; Lahr, 1995; Neves et al., 1999a,b; Powell and Neves, 1999; González-José et al., 2001; Jantz and Owsley, 2001; Neves et al., 2003), since all those groups probably formed part of a first-dispersal route out of Africa (Lahr, 1995, 1996; Neves et al., 2003). These results also suggest that the morphological proximity to Australians could be better explained by the absence of extreme adaptive responses among the first Americans (e.g., facial flatness shown in extremis by Buriats and Eskimos), rather than by migratory routes from the Old World different from the trans-Beringian route. Principal coordinate 2 separates the early Mexicans from Africans and East Asians. Their outlying position could be an effect of the small sample size.

Three different analyses of data were carried out, depending on the consideration of early Mexican materials as single specimens or else pooled in a sample. Furthermore, missing data replacement was used in some analyses and avoided in others, and sex was managed in two ways. All the independent approaches to craniofacial variation performed here are congruent in suggesting that Late Pleistocene/Early Holocene American skulls and modern Amerindians or East Asians show different craniofacial morphologies, thus supporting the adoption of the term Paleoamerican to define the particular morphology of most Paleoindians. Moreover, Paleoamericans tend to show more affinities with Africans, Australians, and Polynesians, specifically when a principal component analysis using sex-standardized data is performed. In general terms, the craniofacial morphology of Paleoamericans is characterized by longer, higher cranial vaults and lower, more narrow faces than modern populations. This Paleoamerican morphological pattern seems ubiquitous in the Late Pleistocene- Early Holocene of South America. Obviously, some level of internal variability is foreseeable for Paleoamericans, and in this context, migrationist interpretations need to be complemented with the interplay of local microevolutionary factors in order to accurately explore variability within Paleoamericans and between Paleoamericans and Amerindians. Paleoindian sites with intensive burial activities are being currently excavated by one of us (W.N.) in South America (Neves et al., 2003), and the increasing number of individuals will promote the exploration of levels of internal variability, not to mention lifestyle and quality of life, and their subsequent comparison with modern samples. Unfortunately, further microevolutionary approaches to data are largely constrained by the scarcity of available remains at present, especially in North and Central America.

This study does not support continuity between Early and Late Holocene groups in the Americas: Archaic remains from Colombia are not an intermediate point between Paleoamericans and modern groups. Moreover, the data presented here support the idea that the first settlers of the New World preceded the origin of the more specialized morphology observed in modern populations from Northeast Asia. Obviously, local adaptation is important in this discussion, because it must be viewed as a potential explanation for the divergence between two populations sharing a common ancestor, or alternatively, as a factor responsible for the convergence of different groups in similar environments (Powell and Neves, 1999). For instance, in considering "non-Asian descent" traits in Paleoamericans, it is possible that these traits were developed in situ by specific groups due to geographic isolation, local adaptation, or drift. If local adaptation is the main factor responsible for the differences, then one must expect to detect a clinal attenuation of traits rather than regional patterns. Conversely, if morphological differences can be explained ultimately by divergence in deep historical times (before humans entered the New World), rather than by the effect of local selective forces, then a common pattern of variation is more likely to be expected across different regions and environments in the Americas. Certainly, to assume that selective forces operate in the same direction throughout different functional and developmental complexes of the skull is quite unrealistic (Relethford, 2002). Note that if selective forces are considered neutral on average (Williams-Blangero and Blangero, 1989; Relethford and Blangero, 1990; Relethford, 2002), then multivariate estimations of divergence based on a great number of traits must reflect in some way the minimum genetic difference among groups.

Thus, in a scenario of "contact" between the two hypothesized stocks, some degree of admixture is expected, especially in geographically isolated areas, where Paleoamericans probably would have received an attenuated impact in demographic terms, and could contribute more to the admixed gene pool. In this context, further research in marginal areas like Tierra del Fuego/Patagonia (Lahr, 1995, 1996; Neves et al., 1999b,c; González-José et al., 2001, 2002) or Baja California, Mexico (González-José et al., 2003), where geographical isolation must play an important role in shaping population dynamics, will shed light on some interesting issues about the settlement of the Americas.

ACKNOWLEDGMENTS

We are especially indebted to the Instituto Nacional de Antropología e Historia, Mexico, and particularly to J.C. Jiménez López, for permission given to M.M.L., W.N., and H.P. to study the early Mexican material. We are also indebted to William W. Howells for making his data available via the Internet. M.M.L. and S.G. acknowledge the support of NERC-EFCHED in the UK (grant NER/T/S/2002/00467). Three anonymous reviewers and C. Larsen provided valuable advice, which improved the quality and readability of the paper.

LITERATURE CITED

Albrecht GH. 1992. Assessing the affinities of fossils using canonical variates and generalized distances. Hum Evol 7:49–69.

Arce JL, Macias JL, Vazquez L. 2003. The 10.5 KA Plinian eruption of Nevado de Toluca Volcano Mexico: stratigraphy and hazard implications. Bull Geol Soc Am 115:230–248.

Brace LC, Russell NA, Seguchi N, Oe H, Sering L, Qifeng P, Yongyi L, Dashtseveg Tumen D. 2001. Old World sources of the first New World human inhabitants: a comparative craniofacial view. Proc Natl Acad Sci USA 98:10017–10022.

Cheverud JM. 1988. A comparison of genetic and phenotypic correlations. Evolution 42:958–968.

González S, Huddart D, Morett-Alatorre L, Arroyo-Cabrales J, Polaco OJ. 2001. Mammoths, volcanism and early humans in the Basin of Mexico during the Late Pleistocene/Early Holocene. In: Cavarreta G, et al., editors. The world of elephants, proceedings of the 1st International Congress, Rome. 704–706.

González S, Jiménez-López JC, Hedges R, Pompa y Padilla JA, Huddart D. 2002. New carbon-14 dates for early humans in México. Mammoth Trumpet 17:16.

González S, Jiménez-López JC, Hedges R, Huddart D, Ohman JC, Turner A, Pompa y Padilla JA. 2003. Earliest humans in the Americas: new evidence from México. J Hum Evol 44:379–387.

González-José R, Dahinten SL, Luis MA, Hernández M, Pucciarelli HM. 2001. Craniometric variation and the settlement of the Americas: testing hypotheses by means of R matrix and matrix correlation analyses. Am J Phys Anthropol 116:154–166.

González-José R, Pucciarelli HM, Neves WA, Hernández M. 2002. Paleoamerican and Archaic remains from Patagonia as viewed from modern variation. Coll Anthropol 26:75.

González-José R, González-Martín A, Hernández M, Pucciarelli HM, Sardi M, Rosales A, Van der Molen S. 2003. Craniometric evidence for Palaeoamerican survival in Baja California. Nature 425:62–65.

González-José R, Van der Molen S, González-Pérez E, Hernández M. 2004. Patterns of phenotypic covariation and correlation in modern humans as viewed from morphological integration. Am J Phys Anthropol 123:69–77.

Harpending HC, Jenkins T. 1973. Genetic distances among Southern African populations. In: Crawford MH, Workman PL, editors. Methods and theories of anthropological genetics. Albuquerque: University of New Mexico Press. p 177–199.

Howells WW. 1973. Cranial Variation in man. Papers of the Peabody Museum. Cambridge, MA: Peabody Museum.

Howells WW. 1989. Skull shapes and the map. Papers of the Peabody Museum. Cambridge, MA: Peabody Museum.

Jantz RL, Owsley DW. 2001. Variation among early North American crania. Am J Phys Anthropol 114:146–155.

Jantz RL, Owsley DW. 2003. Reply to Van Vark et al.: is European Upper Paleolithic cranial morphology a useful analogy for early Americans? Am J Phys Anthropol 121:185–188.

Konigsberg LW, Ousley SD. 1995. Multivariate quantitative genetics of anthropometric traits from the Boas data. Hum Biol 67:481–498.

Lahr MM. 1995. Patterns of modern human diversification: implications for Amerindian origins. Yrkb Phys Anthropol 38: 163–198.

Lahr MM. 1996. The evolution of modern human diversity: a study of cranial variation. Cambridge: Cambridge University Press.

Lahr MM, Wright RVS. 1996. The question of robusticity and the relationship between cranial size and shape in *Homo sapiens*. J Hum Evol 31:157–191.

Lorenzo JL, Mirambell L. 1986. Tlapacoya: 35, 000 años de historia en el Lago de Chalco. Colección científica, serie prehistoria. Mexico City: Instituto Nacional de Antropología e Historia.

Mooser F, González Rul F. 1961. Erupciones volcánicas y el hombre primitivo en la Cuenca de México. In: Homenaje a Pablo Martinez del Río en el XXV aniversario de la edición de los Orígenes Americanos, Instituto Nacional de Antropología e Historia de México. p 137–141.

Neves WA, Pucciarelli HM. 1989. Extra continental biological relationships of early South American human remains: a multivariate analysis. Cienc Cult 41:566–575.

Neves WA, Pucciarelli HM. 1991. The origin of the first Americans: an analysis based on the cranial morphology of early South American human remains. J Hum Evol 21:261–273.

Neves WA, Powell JF, Ozolins EG. 1999a. Extra-continental morphological affinities of Lapa Vermelha IV, hominid I: a multivariate analysis with progressive numbers of variables. Homo 50:263–282.

Neves WA, Powell JF, Ozolins EG. 1999b. Extra-continental morphological affinities of Palli-Aike, southern Chile. Interciencia 24:258–263.

Neves WA, Blum M, Kozameh L. 1999c. Were the Fueguians relicts of Paleoindian nonspecialized morphology in the Americas? Curr Res Pleist 16:90–92.

Neves WA, Prous A, González-José R, Kipnis R, Powell J. 2003. Human skeletal remains from Santana do Riacho, Brazil: Implications for the settlement of the New World. J Hum Evol 45:759–782.

Pietrusewsky M. 2000. Metric analysis of skeletal remains: methods and applications. In: Katzenberg MA, Saunders SR, editors. Biological anthropology of the human skeleton. New York: Wiley-Liss. p 375–415.

Pompa y Padilla JA. 1988. Nueva evidencia en México: datos preliminares del Hombre de Chimalhuacán. In: Origenes del Hombre Americano. Mexico City: SEP.

Pompa y Padilla JA, Serrano Carreto E. 2001. Los más antiguos Americanos. Arqueol Mexi 9:36–41.

Powell JF, Neves WA. 1999. Craniofacial morphology of the first Americans: pattern and process in the peopling of the New World. Yrbk Phys Anthropol 42:153–188.

Relethford JH. 1996. Genetic drift can obscure population history: problem and solution. Hum Biol 68:29–44.

Relethford JH. 2002. Apportionment of global human gentic diversity based on craniometrics and skin color. Am J Phys Anthropol 118:393–398.

Relethford JH, Blangero J. 1990. Detection of differential gene flow from patterns of quantitative variation. Hum Biol 62: 5–25.

Relethford JH, Harpending HC. 1994. Craniometric variation, genetic theory, and modern human origins. Am J Phys Anthropol 95:249–270.

Relethford JH, Crawford MH, Blangero J. 1997. Genetic drift and gene-flow in post famine Ireland. Hum Biol 69:443–465.

Romano A. 1974. Restos óseos humanos precerámicos de México. In: Romero MJ, editor. Panorama historico y cultural. México DF: Instituto Nacional de Anthropolgia e Historia. p 29–81.

Sokal RR, Rohlf FJ. 1995. Biometry: the principles and practice of statistics in biological research. New York: Freeman.

Sparks CS, Jantz RL. 2002. A reassessment of human cranial plasticity: Boas revisited. Proc Natl Acad Sci USA 99:14636–146399.

Steele DG, Powell JF. 1992. The peopling of the Americas: the paleobiological evidence. Hum Biol 63:301–336.

Steele DG, Powell JF. 1993. Paleobiology of the first Americans. Evol Anthropol 2:138–146.

Van Vark GN, Schaafsma W. 1992. Advances in the quantitative analysis of skeletal morphology. In: Saunders SR, Katzenberg MA, editors. Skeletal biology of past peoples: research methods. New York: Wiley Liss. p 225–257.

Van Vark GN, Kuizenga D, L'Engle Williams F. 2003. Kennewick and Luzia: lessons from the European Upper Paleolithic. Am J Phys Anthropol 121:181–184.

Williams-Blangero S, Blangero J. 1989. Anthropometric variation and the genetic structure of the Jirels of Nepal. Hum Biol 61:1–12.