

Chapter 8

Cranial Morphology of Early South Americans: Implications for Understanding Human Dispersion into the New World

Mark Hubbe, Walter Neves, and Katerina Harvati

8.1 Introduction

During the last two decades, studies assessing the morphological affinities of early American crania have shown that crania dating to over 7,000 years BP generally show a distinct morphology from those observed in most later populations. This observation is better supported in South America, where larger samples of early specimens are available in population samples from central Brazil (Lagoa Santa; Neves and Hubbe 2005; Neves et al. 2007b) and Colombia (Bogotá Savannah; Neves et al. 2007a), as well as in isolated specimens from southeast Brazil (Capelinha; Neves et al. 2005), northeast Brazil (Toca dos Coqueiros; Hubbe et al. 2007), and southern Chile (Palli Aike; Neves et al. 1999). Distinct cranial morphology has also been observed in early skulls from Meso-America (Mexico; González-José et al. 2005) and North America (Jantz and Owsley 2001; Powell 2005). Furthermore, it has recently been demonstrated that the observed high levels of morphological diversity within the Americas cannot simply be attributed to bias resulting from the small available samples of early crania, as was previously suggested (Van Vark et al. 2003).

Recent Native American cranial morphology varies around a central tendency characterized by short and wide neurocrania, high and retracted faces, and high orbits and nasal apertures, although there is considerable variation around this central tendency (de Azevedo et al. 2011; González-José et al. 2003, 2008; Pucciarelli et al. 2008). In contrast, the early South and Meso-American crania tend to vary around a different morphology: long and narrow crania, low and projecting faces, and low orbits and nasal apertures (Hubbe et al. 2010, 2011; Neves and Hubbe 2005). As with the case of late Native Americans, early populations also show considerable variation around this central tendency, and their morphology overlaps to some extent with the morphology of late Native Americans.

M. Hubbe (✉)

Department of Anthropology, The Ohio State University, 4034 Smith Laboratories,
174 W 18th Street, Columbus, OH 43210, USA

Instituto de Investigaciones Arqueológicas y Museo, Universidad Católica del Norte,
Calle Gustavo LePaige 380, San Pedro de Atacama 141-0000, Chile
e-mail: hubbe.1@osu.edu

W. Neves

Laboratório de Estudos Evolutivos Humanos, Departamento de Genética e Biologia Evolutiva, Universidade de
São Paulo, Rua do Matão, 277, São Paulo 05508-090, Brazil

K. Harvati

Paleoanthropology, Department of Early Prehistory and Quaternary Ecology, Senckenberg Center for Human
Evolution and Paleoecology, Eberhard Karls Universität Tübingen, Rümelinstr, 23, Tübingen 72070, Germany

Although some authors defend that this overlap suggests there is not a clear differentiation between early and late groups in the continent (de Azevedo et al. 2011; González-José et al. 2008), when contrasted to modern worldwide variation, these differences are not subtle, being of roughly the same magnitude as the difference observed between East Asian and Australo-Melanesian populations, considered among the most morphologically distinct modern populations worldwide in terms of cranial morphology (Neves and Hubbe 2005; Neves et al. 2007a, b). When assessed within the comparative framework of worldwide craniometric human variation, early American groups show morphological affinities with some Australo-Melanesian and African samples, while most Amerindian groups share the morphological pattern observed today among recent East Asian populations (Neves and Hubbe 2005; Hubbe et al. 2010).

The existence of two distinct morphological patterns through time in the prehistory of the Americas has implications for our understanding of the settlement of the New World. Several studies of early American morphology have concluded that the differences observed between early and later American groups are too large to be accommodated into a single expansion event into the continent. Instead these works have argued for two dispersal events into the Americas by populations sharing a common ancestor in East Asia (González-José et al. 2005; Hubbe et al. 2010; Neves and Hubbe 2005; Neves et al. 2003, 2007a, b; see also Dixon 2001 for archaeological evidence in support of this idea). Others, however, consider that the morphological differences between early and late Native American populations result from differences accumulated through time in concert with local microevolutionary forces, such as genetic drift and natural selection, acting on cranial shape (Perez and Monteiro 2009; Powell 2005) or were a result of the continuous influx of diversity from Beringia into the continent (de Azevedo et al. 2011; González-José et al. 2008), an interpretation consistent with most, though not all, genetic evidence (Bonatto and Salzano 1997; Fagundes et al. 2008; Rothhammer and Dillehay 2009; Tamm et al. 2007; Wang et al. 2007; Zegura et al. 2004; but see Perego et al. 2009; Reich et al. 2012).

Consequently, the study of the origins of the morphological pattern of early Americans, as well as the process through which the morphological diversity seen in the continent through time originated, is key to understanding details about human dispersion into the New World in the past. Here, we summarize the results of our recent work on this subject (Hubbe et al. 2010, 2011), which show that: (1) early Americans share a similar morphological pattern of Late Pleistocene populations from the Old World (Europe and East Asia); and (2) that the differences observed between early and late American populations is greater than what would be expected by local micro-evolutionary processes, suggesting that the continent was settled through more than one dispersion wave from East Asia. Some of the results presented here (Hubbe et al. 2010) have been shown to be conditional on the comparative samples used to describe the morphological pattern of early Americans (Azevedo et al. 2011). Azevedo and colleagues defend a scenario previously proposed by González-José et al. (2008) of continuous influx of diversity into the Americas, based on analyses of Eskimo groups' morphological affinities. Although their analyses include more samples than ours, their results may be biased by arctic groups that show a later origin (Reich et al. 2012) and possibly morphological adaptations to cold environments (Hubbe et al. 2009). For these reasons, we do not believe their results can be used to rule out our own, nor can we dismiss theirs. Consequently, here we present our results and discuss them in a more cautious manner, assuming the continuous influx as a possible scenario as well to explain the origin of the observed biological diversity in the Americas.

8.2 Materials and Methods

The comparative samples included in this study comprise early American, European Upper Paleolithic, Late Pleistocene Asian, and recent modern human series (Table 8.1). The Early American series includes Late Pleistocene/Early Holocene samples from Lagoa Santa (Central Brazil; Neves and

Table 8.1 Series included in the analysis and related information

Series/specimen	Geographic region/chronology	Sample size	Missing values replaced (%)	Chronology	References	
Early humans	Mladec 1	European Upper Paleolithic	1	16.7	~31 kyr	Harvati (2009)
	Predmost 3	European Upper Paleolithic	1	0	Early upper Paleolithic	
	Predmost 4	European Upper Paleolithic	1	25.0	Early upper Paleolithic	
	Abri Pataud	European Upper Paleolithic	1	29.2	Early upper Paleolithic	
	Chancelade	European Upper Paleolithic	1	0	Late upper Paleolithic	
	CroMagnon 1	European Upper Paleolithic	1	4.2	27–28 kyr	
	CroMagnon 2	European Upper Paleolithic	1	29.2	27–28 kyr	
	DV13	European Upper Paleolithic	1	50.0	25–29 kyr	
	DV14	European Upper Paleolithic	1	0	25–29 kyr	
	DV15	European Upper Paleolithic	1	41.7	25–29 kyr	
	DV16	European Upper Paleolithic	1	45.8	25–29 kyr	
	DV3	European Upper Paleolithic	1	0	25–29 kyr	
	Grimaldi	European Upper Paleolithic	1	41.7	24–25 kyr	
	OhaloII	European Upper Paleolithic	1	20.8	19 kyr	
	Upper Cave	Late Pleistocene Asia	2	6.3	~30.0–11 kyr	Howells (1996)
	Paleo Colombia	Paleoamerican	13	9.0	11–6.5 kyr	Neves et al. (2007a)
	Lagoa Santa	Paleoamerican	19	17.3	11.0–7.5 kyr	Neves and Hubbe 2005
	Paleo Mexico	Paleoamerican	4	32.0	~10 kyr	González-José et al. (2005)
	Modern humans	Base	America	16	13.0	~1.0 kyr
Tapera		America	48	11.8	~1.0 kyr	
Arikara		America	69	–	Sub-recent	Howells (1973, 1989)
Peru		America	110	–	Sub-recent	
Santa Cruz		America	102	–	Sub-recent	
Dogon		Sub-Saharan Africa	99	–	Sub-recent	
Teita		Sub-Saharan Africa	83	–	Sub-recent	
Zulu		Sub-Saharan Africa	101	–	Sub-recent	
Australia		Australo-Melanesia	101	–	Sub-recent	
Tasmania		Australo-Melanesia	87	–	Sub-recent	
Tolai		Australo-Melanesia	110	–	Sub-recent	
Ainu		East Asia	86	–	Sub-recent	
Buriat		East Asia	109	–	Sub-recent	
Hainan		East Asia	83	–	Sub-recent	
North Japan		East Asia	87	–	Sub-recent	
South Japan		East Asia	91	–	Sub-recent	
Berg		Europe	109	–	Sub-recent	
Norse		Europe	110	–	Sub-recent	
Zalavar		Europe	98	–	Sub-recent	
Easter Island	Polynesia	86	–	Sub-recent		
Mokapu	Polynesia	100	–	Sub-recent		
Moriori	Polynesia	108	–	Sub-recent		

Hubbe 2005), paleo-Colombia (Savannah of Bogotá; Neves et al. 2007b), and paleo-Mexico (Central Mexico; González-José et al. 2005). The European Upper Paleolithic sample is composed of isolated Late Pleistocene individuals (Harvati 2009). The Late Pleistocene Asian series is composed of the two better preserved specimens from the Upper Cave, Zhoukoudian (UC-101 and UC-103; Cunningham

Table 8.2 Craniometric variables included in the analysis

Variables ^a
Basion-nasion length (BNL)
Basion-bregma height (BBH)
Bistephanic breadth (STB)
Biasterionic breadth (ASB)
Nasion-prosthion height (NPH)
Nasal height (NLH)
Bijugal breadth (JUB)
Nasal breadth (NLB)
Bimaxillary breadth (ZMB)
Bifrontal breadth (FMB)
Interorbital breadth (DKB)
Malar length, inferior (IML)
Malar length, maximum (XML)
Foramen magnum length (FOL)
Frontal chord (FRC)
Parietal chord (PAC)
Occipital chord (OCC)
Nasion radius (NAR)
Subspinale radius (SSR)
Prosthion radius (PRR)
Dacryon radius (DKR)
Zygoorbitale radius (ZOR)
Frontomalare radius (FMR)
Zygomaxillare radius (ZMR)

^aNomenclature and definition after Howells (1973, 1989)

and Jantz 2003; Kamminga and Wright 1988; Harvati 2009; Howells 1996). Finally, 20 modern human samples from Howells' database (Howells 1973, 1989, 1996) and two Late Holocene population samples from coastal southeast Brazil (Base and Taperá; Hubbe et al. 2010; Neves and Hubbe 2005) were included as modern reference series.

With the exception of the European Upper Paleolithic specimens, all series included here were measured following Howells' protocol (1973, 1989). The Upper Cave specimens and the early American and Brazilian coastal series were measured by Neves, while the remaining modern human series were retrieved from Howells' database (Howells 1996). The European Upper Paleolithic measurements included in this study were extracted from 3D landmarks collected by K. Harvati with a Microscribe MX digitizer. For comparison with the European Upper Paleolithic specimens, 24 of Howells' linear dimensions (Table 8.2) were selected. For the tests of the best dispersion scenarios into the Americas, 19 neutral variables (not affected by climate factors) that did not show high percentages of missing values in the early series were selected from Howells database.

We present here the results reported in two of our recent publications (Hubbe et al. 2010, 2011). First, we analyze the morphological affinities between early Americans and Upper Paleolithic Europeans and Late Pleistocene Asians in relation to modern human cranial morphological variation. This was achieved through Canonical Variates Analysis (CVA) and Mahalanobis Squared Distances (D^2 ; Mahalanobis 1936). Details on the methods and the rationale behind the tests can be found in Hubbe et al. (2011). In summary, CVA shows the morphological affinities based on the major axis of variation of the original data when the differences between the series are maximized (Van Vark and Schaafsma 1992), while D^2 gives a measurement of dissimilarity among the series when all information available in the original variables is taken into account (Mahalanobis 1936). To visually present the affinities among the series, D^2 values were used as the basis for a Minimum-Spanning Tree (MST; Gower and Ross 1969) that was superimposed on the morphospace expressed

by the first two canonical variates extracted. As a consequence, the results are presented in a graph that reveals two levels of morphological relationships among the series: one where only the two major axes of variation are observed (CVA) and the other where all of the variation seen in the original data is considered (MST based on D^2).

The second set of analyses presented here was detailed in Hubbe et al. (2010). The goal of this set of analyses was to test (1) whether a dual dispersion model into the continent explains better the morphological differences seen across time than a single migration model; and (2) if the differences seen can be explained by neutral evolutionary processes (genetic drift) or if differences are too high for neutral processes to have generated them alone. For the first approach we created geographic distances matrices that represent three dispersion models (linear distances, single dispersion, and dual dispersion into the continent), following the methods detailed in Hubbe et al. (2010). The linear distance model is the control, where distances between each series were calculated directly, irrespective of geographic barriers, such as the Pacific Ocean. The single dispersion model assumes that all American series share only one common ancestor, i.e., the Americas' settlement was a result of only one dispersion wave at the end of the Pleistocene. Finally, the dual dispersion model assumes that early and late Americans share their last common ancestor outside the continent and thus the Americas were settled through two dispersion waves: the first one gave rise to the early morphological pattern and the second one brought the late morphological pattern and largely replaced the earlier population in the continent (Fig. 8.1). Each model was compared to the morphological distances observed between the series through Mantel matrix correlation tests (Mantel 1967) and Dow-Cheverud tests

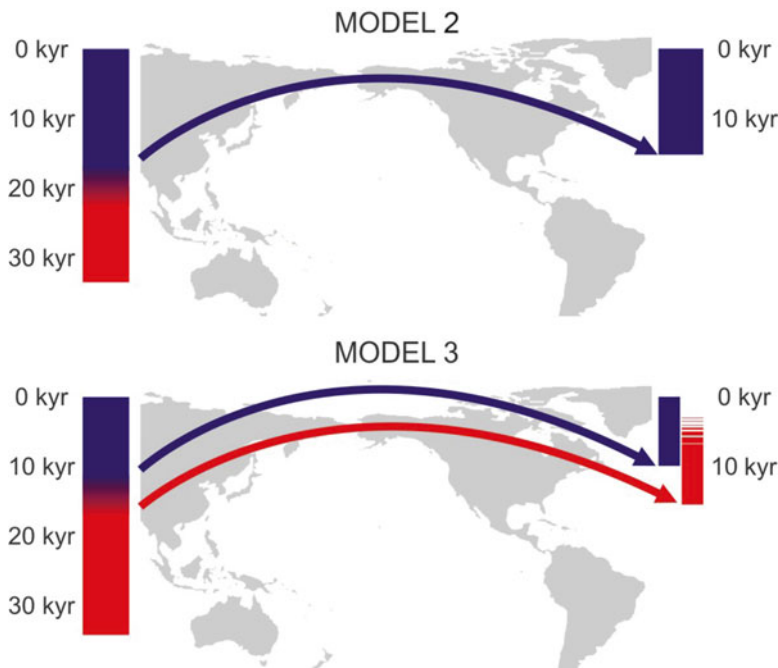


Fig. 8.1 Representation of the geographic dispersion models tested for the occupation of the Americas. Model 1 is not represented because it is a control model (assuming direct linear distances among all groups). The bars represent the morphological change observed in East Asia (*left*) and the Americas (*right*) during Late Pleistocene/Early Holocene. The *red* color represents the morphology present in Asia by the end of the Pleistocene and the *blue* color represents the morphology present nowadays in Asia and the Americas. Model 2 assumes that the morphological differentiation in East Asia occurred before America's settlement and that the New World was occupied only once; Model 3 assumes two distinct dispersions into the continent. See text for detailed description of each model. The dates presented are just approximations, but they assume America's settlement to have occurred around 15,000 BP

(Dow and Cheverud 1985), following the definitions presented elsewhere (Hubbe et al. 2010; Konigsberg 1997; Pinhasi and von Cramon-Taubadel 2009; Smouse and Long 1992; Waddle 1994). The comparison between models permits testing the goodness of fit of each one to the morphological data, and consequently allows us to test which contrasting model best explains the morphological diversity (Smouse and Long 1992).

For the second test, we calculated the rate of morphological differentiation between early and late Americans assuming three different scenarios: (1) early Americans are the direct ancestral populations of late Americans; (2) early and late Americans share a common ancestor by the time of the initial occupation of the continent (15,000 BP); and (3) their last common ancestor dates to 20,000 BP. Lynch (1988) reports the expected range of the rate of morphological differentiation under neutral expectation for mammals to fall between 0.01 and 0.0001, i.e., values above or below this range cannot be a result solely of neutral evolutionary processes. The methods of calculation and premises of the test are detailed in Hubbe et al. (2010) and will not be further explored here.

No specimens with more than 50 % of their variables missing were included in these analyses. Although 50 % is a high tolerance for missing values, this threshold is necessary to guarantee a minimum sample size for some of the early series. For all analyses, males and females were grouped together and size effect was adjusted by dividing each measurement by the geometric mean of the individual (Darroch and Mosimann 1985; Jungers et al. 1995). CVA was performed in Statistica 7 (Statsoft, Inc.) and Minimum Spanning Tree, Neighbor Joining Tree, and Mantel correlation tests were performed in NTSYSpc 2.10 t (Rohlf 1986/2000).

8.3 Results

Figure 8.2 shows the comparison between early Americans, Late Pleistocene Asians, and Upper Paleolithic Europeans, when compared to the worldwide morphological variation. The distribution of the samples along the axes of the graphs represents their morphological affinities according to the first two canonical variates, while the lines connecting the series represent the Minimum Spanning Tree of the D^2 matrix and represent, according to this statistic, the shortest path connecting all series. When only the canonical variate information is taken into account, it can be observed that, while recent samples present a general geographic logic, with series from the same region appearing closer to each other, all early samples appear closer to each other in the central region of the graph, in proximity to the sub-Saharan African series. As expected, late and recent Native American groups appear to be associated with East Asian populations in the first Canonical variate, as do some of the European samples (Norse and Zalavar). Furthermore, the MST connects all early samples to each other and to sub-Saharan Africa. No connection between early series and modern samples from their respective geographic regions can be observed, with the exception of European Upper Paleolithic and Norse.

Table 8.2 presents the Mantel test correlation results between the morphological distances and each of the geographic dispersion models. All correlations between geographic and morphological distances were highly significant. However, the correlation coefficients varied widely, indicating very different levels of support for each of the three models. As expected, the control model (linear distances) showed the lowest correlation coefficient. By far the highest correlation coefficient obtained was for the dual-dispersion model.

In order to test if this model presents a better statistical fit to the morphological distances than the other two models, Dow-Cheverud tests were applied. Table 8.3 presents the results of these tests, comparing the dual dispersion model against the other two models. As can be observed, the bipartite origin is clearly a stronger scenario than the control and one-migration models.

Figure 8.3 presents the mean rates of morphological differentiation calculated for all possible pairwise comparisons between early and late American series. The presented results must be

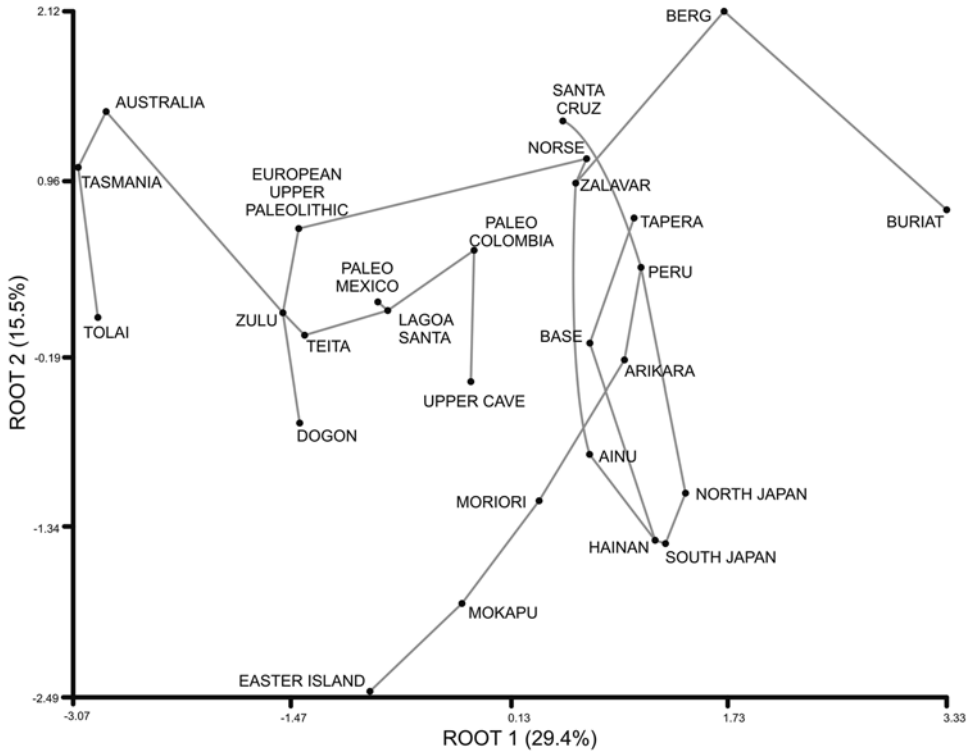


Fig. 8.2 Morphological affinities of the series according to the first two Canonical Variates (black dots) and to the Minimum Spanning Tree (gray lines) of the Mahalanobis' Squared Distances between series

Table 8.3 Mantel correlations between Mahalanobis Squared Distances (D^2) and each of the geographic distance models tested

Dispersion model	D^2 calculated from 24 variables	D^2 calculated from 19 variables (without variables associated with climatic adaptation)
Model 1 Linear geographic distances (control)	$r=0.24545$	$r=0.22735$
	$r^2=0.06025$	$r^2=0.05169$
	$p=0.0018$	$p=0.0048$
Model 2 One migration through Beringia	$r=0.24827$	$r=0.25660$
	$r^2=0.06164$	$r^2=0.06584$
	$p=0.0117$	$p=0.0115$
Model 3 Two migrations through Beringia	$r=0.41192$	$r=0.47900$
	$r^2=0.16968$	$r^2=0.2294$
	$p=0.0004$	$p=0.0001$

r two-way Mantel correlation r , p associated probability of r after 10,000 permutations

interpreted in relation to the reported expected rate of morphological change for mammals under neutral evolutionary expectations, which ranges from 0.0001 to 0.01 (Lynch 1990). Accordingly, we show very high rates of morphological differentiation in general; in all scenarios a large part of the pairwise comparisons fall above the upper limit of the neutral expectation (0.01). The highest values in all cases are given by the comparison between Archaic Colombia and Peru, as a result of their high between-group variation. In the first scenario the mean rates range from 0.002 to 0.0378, with an average of 0.08. Clearly, these values refute the idea that late Native American morphology can be generated

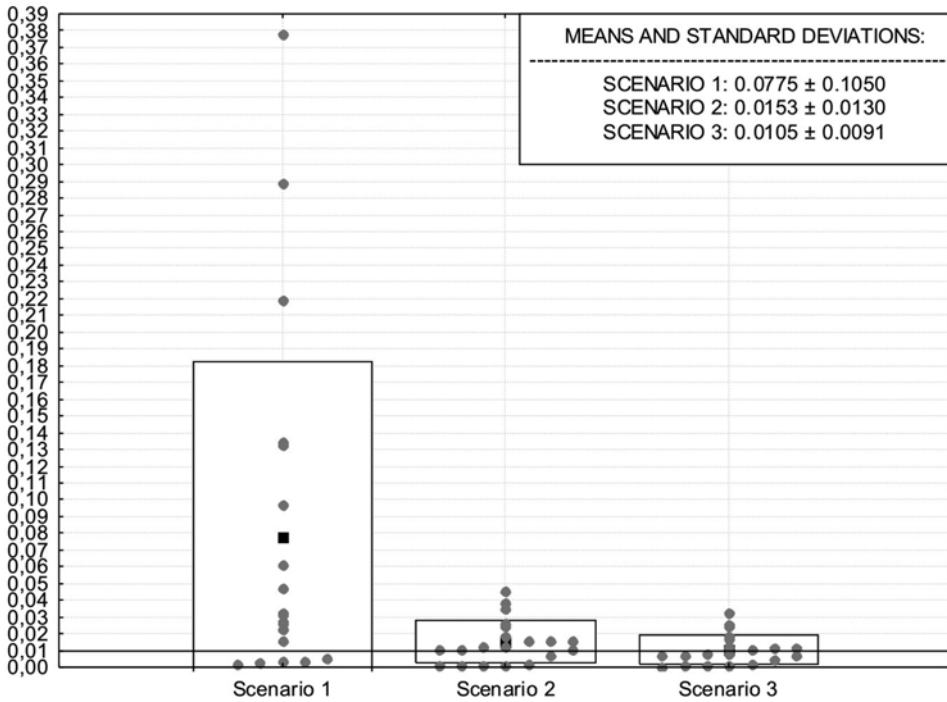


Fig. 8.3 Boxplot of the pairwise mean rates of morphological differentiation (*gray dots*) calculated between early and late American series. The *black squares* represent the average of the pairwise mean rates for each scenario and the *rectangle* represents the confidence limit defined by one standard deviation above and below the mean rates. The *black horizontal line* shows the upper limit of the neutral expectation range (0.01)

through neutral evolutionary processes from the early American one. However, as the divergence time is increased (scenarios 2 and 3), the mean rates calculated approach the neutral limit of 0.01. Differences between the last two scenarios are too small to allow for any differentiation among them, but both scenarios favor the idea that the last common ancestors between early and late Americans antedates the arrival of the first human groups in the New World.

8.4 Discussion

Over the past few decades, there has been a growing consensus that all modern human groups shared a late common ancestor in Sub-Saharan Africa and, as a consequence, all Late Pleistocene/ Early Holocene groups derive from a single dispersion out of that continent. This idea is based on the fact that early modern humans, dating to the time period of the late modern human expansion (60,000–30,000 BP), tend to be more similar to each other than to later populations from the same region (e.g., Bräuer 1992; Grine et al. 2007; Harvati 2009; Harvati et al. 2007; Stringer 1992, 2002; Stringer and Andrews 1988).

In this context, the origin of early American morphology is a relevant question, especially given that it also differs from the morphology that is seen in contemporary East Asia, the region from which these groups most likely dispersed into the New World. The results presented here favor the idea of Neves and colleagues (2003; Fig. 8.4), who suggested that this morphology might be a retention of the

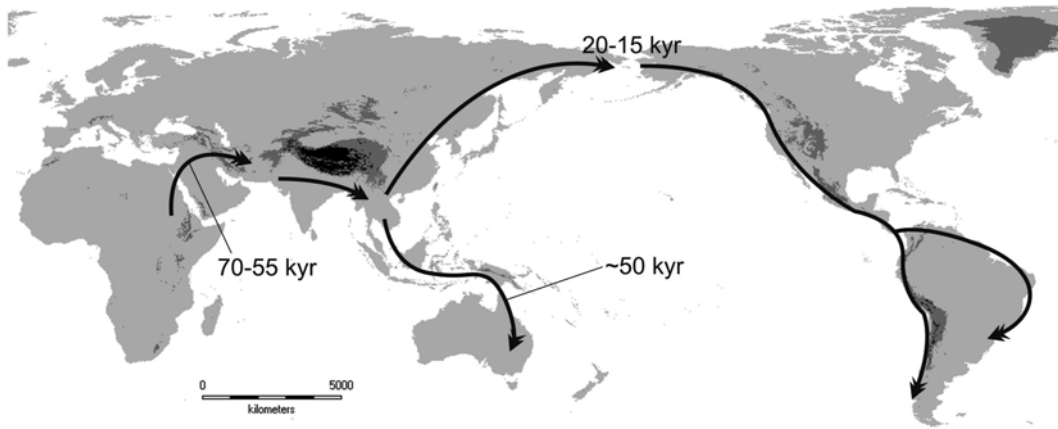


Fig. 8.4 Following Neves et al. (2003), the morphology of early American groups might result from retention of the morphology of the first human groups, which left Africa between 70,000 and 55,000 BP. In this sense, the settlement of the New World can be seen as a direct extension of the human dispersion out of Africa into southeast Asia and Australia. Dates presented are an approximation based on the recent literature (Dillehay 2009; Mellars 2006; among others)

morphological pattern seen in the first modern humans leaving Africa, between 70,000 and 50,000 years ago (Harpending et al. 1998; Macaulay et al. 2005; Mellars 2006; Takasaka et al. 2006), and would thus precede the morphological differentiation in East Asian populations that likely occurred during the early Holocene. In this case, the first modern human expansion out of Africa into Asia, which likely followed a coastal route along South Asia (Lahr 1995; Mellars 2006), separated after reaching southeast Asia, with one branch expanding south into Australia and the other expanding north, towards Beringia, and subsequently into the Americas.

Retention of ancestral traits has also been observed in Late Pleistocene specimens from Africa (Grine et al. 2007), Europe (Harvati et al. 2007), East Asia (Harvati 2009; Neves and Pucciarelli 1998), and Australia (Schillacci 2008). A common undifferentiated morphological pattern across Eurasia in the Late Pleistocene is consistent with the predictions of the Single Origin Model of modern humans, favoring a common recent ancestor for Late Pleistocene groups around the Old World (Stringer and Andrews 1988).

Therefore, these studies broadly support the idea that the morphological diversity seen among modern human groups today is a process of late differentiation that probably took place during the Holocene. In this scenario, the closer morphological affinities observed between early Americans, European Upper Paleolithic, and Upper Cave samples presented here suggest that the largely undifferentiated Late Pleistocene modern human morphology also dispersed into the New World.

The fact that early American morphology might reflect a retention of the ancestral modern human morphology observed in the Late Pleistocene Old World has implications for our understanding of the settlement of the New World, especially if adaptation to cold climate is one of the forces responsible for the morphological differentiation in modern humans, even if only of specific anatomical regions (Harvati and Weaver 2006; Hubbe et al. 2009; Roseman 2004; von Cramon-Taubadel 2009). Since crossing the Bering Strait is believed to be the best route for early groups getting into the New World (Dillehay 2009; Dixon 2001; Goebel et al. 2008), this crossing through a harsh, cold environment must have been a relatively quick process, otherwise these populations would show evidence of cranial morphological adaptation to cold climate. The speed of this process, however, is hard to evaluate at the moment given that at present the duration of the processes of morphological adaptation and response to environmental factors is poorly understood.

This suggestion goes against molecular evidence, which has recently proposed a period of biological isolation of proto-American groups, possibly in Beringia, between 35 and 25,000 BP (Kitchen et al. 2008; González-José et al. 2008; Mulligan et al. 2008; Tamm et al. 2007; also see Chap. 4), although no major environmental or geographic barrier between Beringia and eastern Siberia existed to explain this isolation. Also, the idea of rapid migration following a coastal route has been proposed in recent years to explain the settlement of the New World (Dillehay 2009; Dixon 2001; Fagundes et al. 2008). It is reasonable to assume that the same pattern of dispersal was also adopted by earlier human groups prior to their arrival in the Americas (Mellars 2006). Therefore, it is possible that rapid coastal migration had already been adopted in Asia by Late Pleistocene human groups for a relatively rapid crossing of the Bering Strait. In this context, coastal environments could represent quick range-expansion pathways, providing a relatively homogeneous ecological system for groups to spread without the necessity of significant technological innovations (but see Westley and Dix 2006, for a critique of the diachronic stability of coastal environments).

Regarding the processes of human dispersion into the continent, the second part of our results demonstrates that both chronological and geographical models assuming independent origins for these two populations via Beringia fit these morphological differences considerably better than the alternative models (Table 8.4). Under the assumption that morphological differentiation among modern humans during the Final Pleistocene and the Holocene was mainly a result of neutral microevolutionary processes (Harvati and Weaver 2006; Hubbe et al. 2009; Manica et al. 2007; Relethford 2004), the observed rates of morphological differentiation favor the idea that early and late American samples included in this study shared a last common ancestor outside the New World. At the same time, the geographic bipartite model resulted in a generally better fit to the morphological distances among groups.

Our results do not support the hypothesis that the morphological differences between early and late American groups are a result of in situ neutral evolution. Rather they fit better a two-wave dispersal model for the settlement of the New World. These results are again at odds with the majority of molecular evidence on Native American origins (Tamm et al. 2007; Wang et al. 2007; Zegura et al. 2004), although they agree with a recent study of rare mitochondrial haplogroups (Perego et al. 2009), which also favors two origins for early Americans associated with distinct crossings from northeast Asia within a short period of time (17,000–15,000 BP).

Recently, the two-dispersal model has been questioned by Azevedo et al. (2011), who showed that, by increasing the number of Native American populations in the analyses, the dual-dispersal scenario is not favored. Instead, they propose that the Americas were settled through a continuous influx of populations that brought the observed biological diversity into the continent. Although our analyses are limited in the number of American samples, Azevedo and colleagues (2011) postulate that the continuous influx of diversity from northeast Asia occurred largely in the northern extreme of North America, based on the morphological affinities of Eskimo populations with other American samples. However, it is difficult, for the reasons explored in their work as well as the biological relationship of Eskimos with other Native Americans (Reich et al. 2012), to refute our results or theirs. Yet, both models (two-dispersal and recurrent gene flow) assume that the morphological diversity observed in the Americas across time was not a result of local differentiation processes and depended

Table 8.4 Results of the Dow-Cheverud test between the bipartite model (Model 3) against the other ones

		Dow-Cheverud results based on 24 variables	Dow-Cheverud results based on 19 variables
Model 3—Two migrations through Beringia versus			
Model 1	Linear geographic distances (Control)	$r=0.14537$ $p=0.0840$	$r=0.21975$ $p=0.0143$
Model 2	One migration through Beringia	$r=0.16969$ $p=0.0656$	$r=0.23062$ $p=0.0155$

r two-way Mantel correlation r , p associated probability of r after 10,000 permutations

on the input of diversity from Asia during the Holocene, and thus they favor the major conclusion of this chapter, i.e., that the Americas were occupied by multiple dispersion waves. Whether the influx of diversity was through discrete dispersion waves (as postulated by the dual-dispersion scenario) or through a continuous influx of diversity through Beringia (as defended by the recurrent gene flow model) remains to be properly tested.

The disparity between our results and those of most genetic studies points to a large gap in our understanding of the peopling of the New World. Our findings show that this disparity cannot be easily accommodated through climatic selection pressures and that local micro-evolutionary differentiation appears as a less probable explanation for the morphological differences between early and late Native American groups. We propose that the disparity might derive either from diverging sampling strategies between craniometric (that includes both extinct and extant series) and molecular studies (mainly restricted to extant groups); or from the fact that genetic quantitative traits such as cranial morphology might reflect different micro-evolutionary processes from those affecting autosomic or uniparental DNA markers. The first alternative has been proposed before (Neves et al. 2007b); however, recent efforts in recovering ancestral DNA from early Americans have failed so far in identifying distinct mitochondrial haplogroups in these samples (Gilbert et al. 2008; Kemp et al. 2007; Raff et al. 2011). The second alternative, on the other hand, has received some support based on the fact that parts of the skull morphology respond differentially to environmental pressures (Harvati and Weaver 2006; Hubbe et al. 2009; von Cramon-Taubadel 2009). Unfortunately, these possibilities cannot be satisfactorily evaluated until results derived from molecular and morphological data collected from the same populations (extinct and/or extant) are contrasted directly.

8.5 Conclusions

In conclusion, the comparative analysis of the morphological affinities of early South American groups suggests that:

1. The different morphological pattern presented among these populations is similar to the morphology that characterized modern humans before the Holocene. These analyses support previous studies (Grine et al. 2007; Harvati 2009; Harvati et al. 2007; Neves et al. 2003; Stringer 1992, 2002), suggesting that the morphological differentiation that characterizes modern human groups occurred long after the initial expansion of early modern humans (*Homo sapiens*) out of Africa. More importantly, our analyses favor the argument that this morphological differentiation occurred only after the first human expansion into the New World at the end of the Pleistocene.
2. The morphological diversity documented through time in the New World is best accounted for by a model postulating the entrance of further diversity into the continent after its initial occupation. At the present moment, it is not possible to clearly determine if this diversity was originated through two discrete waves of human expansion into the continent, as defended here, or if it is a result of a constant influx of diversity from northeast Asia through the Holocene, as defended by Azevedo and colleagues (2011). It is unlikely, though, that the observed morphological diversity in America is the result of diachronic trends of differentiation inside the continent.

With that framework in mind, our future work will focus on Middle Holocene populations in order to test the biological origin(s) of early South Americans, and how the initial occupation(s) of the continent gave rise to the actual continental biological and cultural diversity.

Acknowledgments We are grateful to André Strauss for allowing the usage of his VB code and to Phillip Gunz for helping with the transformation of the 3D landmarks into linear measurements. Christina Torres-Rouff kindly assisted with the English. This work was supported by FONDECYT (Project 11070091), the Max Planck Gesellschaft, the “EVAN” Marie Curie Research Training Network MRTN-CT-019564, FAPESP (Process 04/01321-6), and CNPq (Process 301126-04.6).

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