Cranial Morphological Diversity of Early, Middle, and Late Holocene Brazilian Groups: Implications for Human Dispersion in Brazil

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ABSTRACT   The history of human occupation in Brazil dates to at least 14 kyr BP, and the country has the largest record of early human remains from the continent. Despite the importance and richness of Brazilian human skeletal collections, the biological relationships between groups and their implications for knowledge about human dispersion in the country have not been properly explored. Here, we present a comprehensive assessment of the morphological affinities of human groups from East-Central, Coastal, Northeast, and South Brazil from distinct periods and test for the best dispersion scenarios to explain the observed diversity across time. Our results, based on multivariate assessments of shape and goodness of fit tests of dispersion and adaptation models, favor the idea that Brazil experienced at least two large dispersion waves. The first dispersive event brought the morphological pattern that characterize Late Pleistocene groups continent-wide and that persisted among East-Central Brazil groups until recently. Within the area covered by our samples, the second wave was probably restricted to the coast and is associated with a distinct morphological pattern. Inland and coastal populations apparently did not interact significantly during the Holocene, as there is no clear signal of admixture between groups sharing the two morphological patterns. However, these results cannot be extended to the interior part of the country (Amazonia and Central Brazil), given the lack of skeletal samples in these regions. Am J Phys Anthropol 000:000–000, 2014.   © 2014 Wiley Periodicals, Inc.

The human presence in Brazil dates back to at least 14 kyr BP, with the oldest sites in the country contemporary with the earliest widely accepted archaeological sites in the Americas (Bueno et al., 2013). Although the archaeological remains for the first millennia of human presence in the country are scant, by the end of the Pleistocene/beginning of the Holocene all the major biomes in the country showed the presence of human groups adapted to them, with clear trends in interregional cultural diversity (Bueno et al., 2013). Brazil holds the largest collection of skeletal remains in the continent from this period, recovered from caves and rockshelters in the Lagoa Santa region, East-Central Brazil (Neves and Hubbe, 2005; Neves et al., 2013).

The Lagoa Santa human skeletal collection has been pivotal in the discussion of the biological characteristics of early Americans since the 19th century. With few exceptions, studies of the Lagoa Santa remains highlight the fact that these remains present a different cranial morphological pattern from the one seen among most recent Native American groups (sometimes referred to as Paleoamerican; Neves and Hubbe, 2005, but see Gonzalez-José et al., 2008 for a critique on its use), suggesting high diachronic morphological diversity during the Holocene in the continent (Neves and Hubbe, 2005; Hubbe et al., 2010). This diversity was initially noticed by 19th century scholars, who, following the typological paradigm accepted then, described this population variability as a different race that lived in the country in the past, the "Lagoa Santa Man" (Rivet, 1908), which contrasted with the shellmound dwellers from the Brazilian coast ("Sambaqui Man"; Lacerda, 1882; Lima, 1999–2000).

The antiquity and morphological characteristics of the Lagoa Santa individuals caught the attention of many scholars in Brazil, Europe, and the United States (e.g., Lacerda and Peixoto, 1876; Kollman, 1884; Ten Kate, 1885; Quatrefages, 1887; Hansen 1888; Virchow, 1892; Hrdlička, 1912; Imbeloni, 1938). In short, the Lagoa Santa specimens would represent one extremity of a morphological diversity in the continent that did not fit the general view of the American Homotype (Hrdlička,

1907), which proposed high biological homogeneity for all Native American groups.

Presently, the Lagoa Santa human remains represent the largest series of early skeletal remains from the Americas, with over 80 measurable skulls dated to between 10 and 7 kyr BP (Neves and Hubbe, 2005). This material has been repeatedly used in studies about the biological diversity and the mode of dispersion of human groups into the continent (Neves and Pucciarelli, 1989, 1991; Powell and Neves, 1999; Neves et al., 2003, 2005, 2007a; Powell, 2005; Van Vark et al., 2003; González-José et al., 2008; Hubbe et al., 2010, 2011; de Azevedo et al., 2011; Seguchi et al., 2011). One of the main concerns regarding the Lagoa Santa remains has been to explain the origin of the morphological differences across time in the continent. Some studies have argued that the variability seen in the continent is a product of local microevolutionary differentiation processes (Powell, 2005), which is largely supported by results from molecular studies on living Native American groups (Merriwether et al., 1995; Zegura et al., 2004; Tamm et al., 2007; Wang et al., 2007; but see Perego et al., 2009 and Reich et al., 2012 for different views) and prehistoric remains (Kemp et al., 2007; Gilbert et al., 2008; Perez et al., 2009). However, other authors have argued that the morphological differences observed between Lagoa Santa remains (and other early series) and Late Native Americans are too great to be the result of local evolutionary forces, and thus advocate for an influx of diversity into the continent during the Holocene, either through two discrete waves (Neves and Hubbe, 2005; Hubbe et al., 2010) or as a result of continuous or recurrent gene flow from Asia (Gonzalez-José et al., 2008; de Azevedo et al., 2011). To date, the origin of the observed variability across time is still an open debate, although there is a consensus that the early human groups in the continent shared a different morphological pattern from the recent Native American groups (Neves and Hubbe, 2005; Bernardo et al., 2011).

Despite the importance of the Brazilian collections in continental studies, there are no studies focused on the human dispersion into the country in the past based on the morphology of human skeletal remains. Part of the reason such a study has never been attempted before is that a gap exists in the archaeological record in many regions of the country, especially in North and Northeast Brazil. However, the available osteological collections can be used to test some basic models of human dispersion and differentiation into the country. Therefore, this study aims to describe the biological diversity (as seen from cranial morphology) in Brazil in the past and evaluates a series of hypotheses about the processes that originated this diversity.

HUMAN DISPERSION IN BRAZIL

The archaeological record for many Brazilian regions is full of gaps, complicating the discussion about the tempo and mode of human occupation of the continent. These gaps are even more pronounced for the Late Pleistocene, when only a handful of sites are known in Brazil (Bueno et al., 2013).

As far as can be said from the archaeological record in the country, the initial human occupation of Brazil dates to the end of the Pleistocene (Prous and Fogaça, 1999). Sites older than 12 kyr BP have been reported (Guidón and Delibrias, 1986; Guidón and Arnaud, 1991; Beltrão,

1974; Vialou et al., 1995), but their chronology has been disputed, partly because they appear as complete outliers from what is observed in the rest of the continent. However, during the last two millennia of the Pleistocene (Bueno et al., 2013), Brazil was already completely occupied. In Amazonia, early human presence has been dated to 11.5 kyr BP (Roosevelt, 1995, 1996; Roosevelt et al., 2002). In northeastern Brazil, the rockshelters from São Raimundo Nonato show human evidence dating to between 13 and 9 kyr BP (Parenti, 1993; Guidón and Arnaud, 1991; Guidón et al., 2000). In Central Brazil (Goiás, Mato Grosso, Minas Gerais and Bahia) many rockshelters show the presence of human groups by the end of the Pleistocene (Vialou et al., 1995; Miller, 1983; Prous and Malta, 1991–1992; Prous et al., 1992; Prous and Fogaça, 1999; Feathers et al., 2010). From the central and southern region, similar sites have been described (Miller, 1987; Beltrão, 1974). From the coast, no Pleistocene sites are known, but variation on the sea level between the end of the Pleistocene and Mid-Holocene might have submerged or destroyed many archaeological sites in coastal areas (Martin et al., 1984; Ângulo and Lessa, 1997).

These initial occupations follow a pattern that seems to be continent-wide (Dillehay, 2008) and are characterized by low density of groups, formed by a small number of individuals who relied on high mobility and exploitation of regions with abundant resources, without any particular specialization. Evidence also suggests that these groups did not rely on megafauna mammals as their main food source (Neves and Piló, 2003; Borrero, 2009; Hubbe et al., 2013).

This pattern of small groups and low density began to change by 10 kyr BP, when population density increased, which is also reflected in the number of archaeological sites described from this moment onwards (Bueno et al., 2013). Human groups started to exploit the local environments in a more systematic way and specialization appeared all over the country, with the clear emergence of inter-regional cultural diversity. Around 7 kyr BP, the Amazon region exhibited the earliest evidence of pottery in the Americas (Roosevelt, 1995:123), with plant management appearing shortly after this period, possibly associated with more complex societies (Mora et al., 1991; Miller, 1992; Magalhães, 1994; Roosevelt, 1995; Neves, 2007). Although most coastal sites may have been submerged or destroyed by the variation of the sea level, there are a few shellmounds dated to circa 8 kyr BP (Lima et al., 2004; Calippo, 2004). In Lagoa Santa, important changes in mortuary practices have been demonstrated initially around 8.5 kyr BP (Strauss, 2010). In the lowlands of Brazil, many different archaeological traditions (the Umbu tradition, in Southern Brazil characterized by the presence of bifacial points; the Humaitá tradition presenting heavy instruments like chopping tools and thick scrapers; and the Itaparica tradition in central and northeast Brazil, characterized by the production of limaces) demonstrate local adaptations of hunter-gatherer groups (Kern, 1981; Ribeiro, 1990; Schmitz, 1984, 1987; Schmitz et al., 1980; Okumura and Araujo, 2014). Consequently, during the initial millennia of the Holocene, human populations became definitely established in Brazil, and created strategies suited to the particular environments each group found itself (Bueno et al., 2013).

The Mid-Holocene in Central Brazil (7–5 kyr BP) was marked by a diminished archaeological record, probably associated with climate changes that pushed populations

to larger rivers and water bodies (Araujo et al., 2005, 2005−2006). Evidence of human dispersion and/or contact between different groups is rare, but it may also reflect the low availability of archaeological evidence in this period. Exceptions are the coastal sites ("Sambaquis"), which are found from 6 to 1 kyr BP across most of the southeastern and southern Brazilian coast (Lima, 1999–2000). Although the majority of these sites are characterized as shellmounds, there are other local adaptations, namely sites associated with the Itaipu tradition (Dias, 1992), as well as shallow sites ("acampamentos conchíferos") where the shells were concentrated in pits (Prous and Piazza, 1977).

During the Late Holocene Brazil shows evidence for the spread of ceramics, associated with different regional traditions (e.g., Aratu/Sapucaí, Itararé; Prous, 1992). The last major evidence for human movement in the country refers to the expansion of the Tupi-Guarani Tradition from Amazonia towards Southern and Eastern Brazil (Brochado, 1984, 1989; Urban, 1992; Noelli 1996, 1998, 2008; for a contrary view see Neves EG, 2008; Viveiros de Castro, 1996). Although the exact origin and the initial time of this dispersion are still a matter of debate, the Tupi-Guarani tradition at some point was disseminated across the entire Brazilian territory, as attested to by its pottery tradition found in archaeological sites all over the country (Noelli, 1996, 2008).

Evidence from molecular biology suggests that living Tupi populations located in the Amazon region retain a wider range of genetic variation than those located in southern Brazil (Black et al., 1988), supporting the idea of an Amazon origin for this group. Marrero et al. (2007), evaluating the frequency of haplotypes between populations of Tupi-Guarani tradition, observed a progressive decrease of the occurrence of haplogroup B from northern to southern Brazil, a scenario compatible with a migratory event following this geographical orientation, under a process of genetic drift. This same logic was observed when the linguistic diversity of different dialects belonging to the Tupi-Guarani was analyzed. The greater diversity found in the Amazon region relative to other regions of Brazil presents Amazonia as the best candidate for the central origin of this tradition. However, this apparent convergence between genetic, archaeological and linguistic markers is not confirmed when assessed concurrently. Callegari-Jacques et al. (2007, 2011) demonstrated by comparison of genetic distances and linguistic affiliations that there was no strong correlation between genes and language among populations of Tupi-Guarani and Jê families, suggesting that geographic distances between populations acted as better predictors of population structure. These results were only partially supported by the more comprehensive analysis by Ramallo et al. (2013), who observed a clear isolation by distance signal among Tupi speaking groups, but a more intricate scenario for Jê speaking groups. Craniometric data were also used to investigate whether the spread of Tupi-Guarani tradition along the Brazilian territory in the past was carried out by physical dispersion of people from the Amazonian region (Neves et al., 2011). Comparing skulls from different linguistic families and archaeological traditions, the authors suggested that the spread of the Tupi-Guarani Tradition from the Amazon was demic in nature and not solely the result of cultural diffusion.

In summary, the archaeological evidence allows one to delimitate four broad periods of human dispersion and adaptation in Brazil: an initial period, associated with the end of the Pleistocene, characterized by the arrival of small human groups to the territory; a second period, during the initial millennia of the Holocene, when populations established and adapted to different environments settled in the previous phase; a third period during the mid-Holocene, when, at least in Central Brazil, there is a demonstrative gap in the archeological record, characterized by climate changes, and may be associated with the dispersion of human groups towards areas with greater access to water resources; and a final period during the Late Holocene, as the expansion of different regional ceramic traditions (e.g., Aratu/Sapucaí, Itararé) occurred, particularly the Tupi-Guarani groups across Brazil, which may have resulted in the replacement, absorption, or incorporation of the autochthonous groups.

Although this scenario is certainly an oversimplification of the demographic and cultural dynamics of the populations that occupied and adapted to the Brazilian environments, it allows us to contrast the morphological affinities between the series available for each period, and thus serves to inform a series of hypotheses to be tested from the perspective of the biological diversity.

There are no collections available from the initial millennia of the human presence in the continent, so our hypotheses focus exclusively on the Holocene. Previous studies have indicated the substantial impact that human dispersion and settlement strategies have on biological diversity. Given the documented morphological shift observed in South America during the Holocene (e.g., Neves and Hubbe, 2005; Neves et al., 2007a, b; Hubbe et al., 2010), the hypotheses test the ways by which this diachronic morphological difference appeared in Brazil.

1. The morphological changes across the Holocene in the country are a product of local and gradual evolutionary processes during the Holocene, as proposed by some authors (e.g., Powell, 2005; Perez et al., 2009) for the Americas as a whole.
2. The morphological affinities observed among Brazilian groups across time is a product of two different dispersion waves into the country (e.g., Hubbe et al., 2010), with the early morphological pattern being completely replaced by a second morphological pattern during Mid-Holocene.
3. During the Late Holocene, the demic dispersion of the Tupi-Guarani tradition replaced the previous groups occupying East-Central Brazil, completely obliterating signs of the Paleoamerican morphology in the country.

MATERIALS AND METHODS

The analyses presented here are limited to available human osteological collections from Brazil. Table 1 includes details of the samples, and Figure 1 shows their geographical location. Series are concentrated on the eastern fringe of the Brazilian territory, and no groups from deep inland regions are available for analysis. Brazilian inland skeletal remains are usually scarce because of acidic tropical soil, which prevents the preservation of organic remains (Okumura et al., 2007). This dearth in the osteological representation of Brazil has to be kept in mind, as inevitable preservation limitations at this point preclude discussions of past human dispersion on

TABLE 1. Information on the cranial series included in the study

Period	Series	Sites/Groups Included	Sample Size	Aprox. Chronology (kyr BP)	% missing values	Primary subsistence practice	Reference
Early Holocene	Lagoa Santa	Sumidouro	14	9.5–7.5	3.96	Hunter–Gatherer	Neves and Hubbe, 2005
Mid Holocene	São Paulo shellmounds	Buracão, Piaçaguera	17	4.9–4.1	3.92	Fisher–Hunter–Gatherer	Okumura, 2008
	São Paulo riverine shellmounds	Capelinha, Moraes, Estreito, Itaoca I, Pavão III & XVI	12	~5.9	4.17	Fisher–Hunter–Gatherer	Okumura, 2008
	Paraná shellmounds	Guaraguaçu A & B	24	4.9–4.1	7.41	Fisher–Hunter–Gatherer	Okumura, 2008
	Santa Catarina shellmounds	Cabeçuda	42	4.9–4.1	5.42	Fisher–Hunter–Gatherer	Okumura, 2008
	Umbu	Cerrito Dalpiaz, Abrigo do Aterrado	3	5.9–1.7	20.37	Hunter–Gatherer	Neves et al., 2004
Late Holocene	Marajó	Marajó Island (North of Pará)	4	<1.0	8.33	Agriculture	Neves et al., 2011
	Santa Catarina ceramic sites	Cabeçudas, Enseada, Forte Marechal Luz	37	1.4–0.6	4.50	Agriculture	Okumura, 2008
	Northern Brazil Tupi	Guajajara/Tenetehara from North of Maranhão and West of Pará	21	<0.5	1.25	Agriculture	Atuí, 2005
	Central Brazil Botocudo	Botocudos from Espírito Santo, Minas Gerais and South of Bahia	34	<0.5	0.65	Hunter–Gatherer	Atuí, 2005
	Kamakã	Aimorés from North of Espírito Santo and South of Bahia	5	<0.5	5.56	Hunter–Gatherer	Atuí, 2005
	Kaingang	Coroado from South and Southeast of Brazil	4	<0.5	6.94	Hunter–Gatherer	Atuí, 2005
	Southern Brazil Botocudo	Botocudos from São Paulo, Santa Catarina and Rio Grande do Sul	6	<0.5	6.48	Hunter–Gatherer	Atuí, 2005
	Guarani	Praia do Retiro (Santa Catarina), and São Pedro do Sul (Rio Grande do Sul)	4	<0.5	5.56	Agriculture	Atuí, 2005
TOTAL			236				

a national scope. Other caveats must also be noticed: first, the sample included in this article lacks individuals from the Late Pleistocene, thereby restricting our analyses to the Holocene (with the exception of one individual from Lagoa Santa, "Luzia," who was included with the Early Holocene samples); and second, some of the series are composed of a small number of individuals, and they might not represent accurately the morphological pattern of their original population. Although available in some regions, isolated specimens were not included in the analyses, due to the difficulty they pose when estimating population parameters.

To test our hypotheses, we applied multivariate analyses to explore the morphological affinities between series. Initially, we explored the morphological affinities among groups by calculating Mahalanobis Squared Distances (D^2; Mahalanobis, 1936) between all pairs of series. D^2 provides a measurement of dissimilarity that considers differences observed between groups' centroids but corrects the contribution of each variable to the final distance by their covariance so that the distance is not inflated by the correlation between them.

To visually present the affinities among the series, the D^2 matrices were represented via a Ward's Clusters (Ward, 1963) and a nonmetric multidimensional scaling

Fig. 1. Geographic location of the series included in the study.

MODEL 1 - SINGLE DISPERSION WAVE INTO BRAZIL

MODEL 2 - TWO DISCRETE DISPERSION WAVES INTO BRAZIL, WITH THE REPLACEMENT OF THE EARLY MORPHOLOGY

MODEL 3 - TWO DISCRETE DISPERSION WAVES INTO BRAZIL, WITH THE LATE SURVIVAL OF THE EARLY MORPHOLOGY
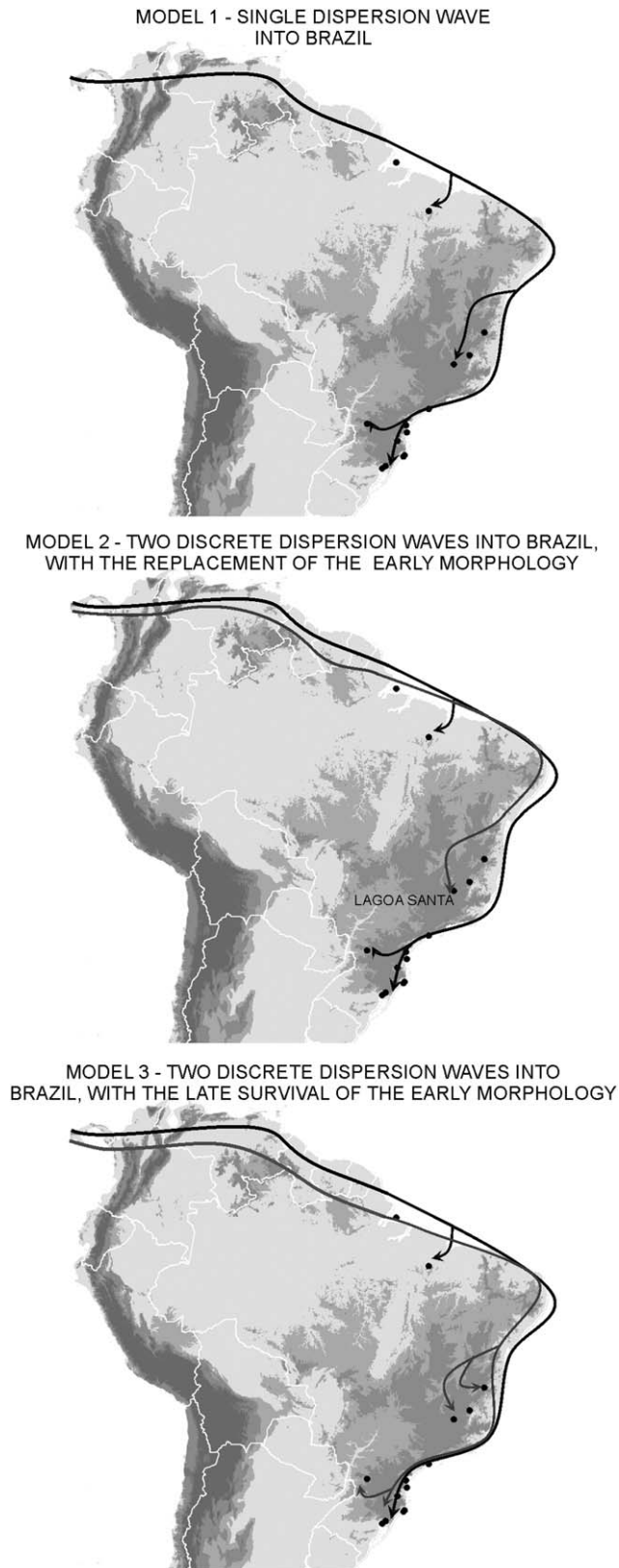
Fig. 2. Illustration of the three dispersion models tested against the morphological distances between series.

(MDS; Cox and Cox, 2001). Ward's method tends to maximize the formation of clusters with similar number of branches, by minimizing within cluster variance and maximizing between cluster variance (Ward, 1963). Ward's Clusters may generate artificial groupings, by including outliers within larger clusters. However, they are particularly useful in within-species studies, where differences between populations are relatively small. They have been used in other human studies and yield results consistent with the expected pattern of worldwide human variation (Okumura, 2008; Neves et al., 2013). The D^2 matrix was also represented in a two-dimensional scatterplot showing the MDS solution, which complements the cluster and allows the identification of any unreasonable groups generated by the Ward's cluster.

To formally test the hypotheses, different dispersion and adaptation models were contrasted with the morphological differences expressed by the D^2 matrix. This analysis follows recent studies that translate dispersion or evolutionary models into distance matrices which can then be compared to the morphological distances observed between the series (Smouse and Long, 1992; Waddle, 1994; Konigsberg, 1997; Pinhasi and von Cramon-Taubadel, 2009; Hubbe et al., 2010, 2011). The comparison between series permits testing the goodness of fit of each model to the morphological data, and consequently tests which model best explains the morphological diversity observed in the series (Smouse and Long, 1992).

For this analysis, we assumed that morphological differentiation in modern humans is largely a product of stochastic microevolutionary processes, following isolation by distance or range expansion (resulting from multiple founding effects) patterns of differentiation (Relethford, 1994, 2002, 2004; Manica et al., 2007), with influence of natural selection majorly restricted to extremely cold climates (Roseman, 2004; Harvati and Weaver, 2006; Hubbe et al., 2009). Under these assumptions, it is expected that the morphological distance between two series should be correlated to the geographic and chronologic distance separating them if both series departed from a single mother population. However, when two populations disperse into the same region distinct from the one where they originally diverged, and keep themselves biologically isolated (e.g., as in successive colonization events), the geographic distance between them will not be correlated with their biological differentiation, as the real separation between populations exceeds the actual observed geographic distance between them. Thus, under these evolutionary assumptions, every time the ancestral population of two series is not located in the geographic space between them (either in the same locality of one of them or between them) their biological distance will be poorly correlated to their geographic location. In this situation, a more reasonable model to calculate the distance between these series would be, instead of using linear distances between them, to calculate the distance from the first series to the location of the common ancestral population and from this to the second series.

We created three dispersion models that derive from the linear geographic distances among series. In all models, geographic distances were calculated as great circle distances based on the Haversine (e.g., Pinhasi and von Cramon-Taubadel, 2009). To simplify the comparison between the models, we assumed that all migrations followed a dispersion route close to the coast. This decision

was made here due to the lack of series from the inland regions of the country, and because changing the coastal routes to inland routes would not change much the relationship between the series included here. Also, we compared the morphological distances between series to a control model, which is simply the linear geographic distance between all pair of series. If the assumption above is correct (i.e., that dispersion geographic models correlate to the evolutionary path that separates populations), then these models must present a better fit to the morphological distances than the one obtained with the control. Figure 2 illustrates the different geographic dispersion models.

All geographic models presented here are relatively simple and do not model in detail alternative routes within the coastal part of the country (e.g., including rivers as potential routes of dispersion) due to the lack of archaeological data that could inform on these possible routes. However, given the large chronological differences and geographic distances between the series, regional changes in the distances would not impact the results in any significant way, and therefore more detailed geographic models would not change the conclusions drawn from the present models.

Model 1 (Fig. 2a) assumes that all series included in our analyses derive from only one major dispersion event into Brazil and that the morphological differentiation between the series is a result of local microevolutionary processes associated with their increasing geographic distance and consequent decrease in gene flow. In other words, this model predicts that the same human group dispersed throughout the entire territory and that no important geographic and cultural barriers prevented its dispersion and gene flow between populations. In this model, the geographic distances between all pairs of groups were calculated as the closest geographic distance between them, while forcing the migration to follow a pathway close to the Brazilian coast. Consequently, geographic distances between groups will be slightly increased when compared to the control model, especially for the series that are farther apart.

Models 2 and 3 represent a different transformation of the geographic distances presented in Model 1 and test alternative dispersion scenarios to explain the morphological diversity among the series. Model 2 (Fig. 2b) is the expected outcome of Hypotheses 2 and 3, and it assumes that South America was occupied by two dispersion waves, each bringing a distinct cranial morphological pattern into the continent. In this case, we assumed that the last common ancestor between the Brazilian series was located outside the continent and that the earliest dispersion gave rise to the Lagoa Santa populations (Neves and Hubbe, 2005; Neves et al. 2007a), while the second dispersion completely replaced the early morphological pattern, so that all Middle and Late Holocene series are descendants of this late dispersion. The geographic distances matrix in this case was constructed by placing a hypothetical last common ancestor to all series on the northernmost tip of Brazil. In this model, distances between early groups and the remaining series were calculated as the distance between Lagoa Santa and the last common ancestor coordinate, plus the distance from this coordinate to the location of each of the remaining series. Distances between the remaining series were kept the same as in Model 1. In practical terms, this model increases considerably the geographic distances between the early Lagoa Santa group and the rest of the series, mimicking a model of dual entrance into Brazil with isolation between Lagoa Santa and the remaining groups. The location of the hypothesized last common ancestor does not affect much the correlation results, as long as it is placed outside the territory that includes the series studied; this explains why we placed it just outside the country for this study.

Model 3 (Fig. 2c) is a derivation of Model 2 and is based on previous studies, which suggest that late native groups from the East-Central Brazilian plateau (Lacerda and Peixoto, 1876; Ten Kate, 1885; Atui, 2005; Bernardo et al., 2011), and Holocene Umbu groups from Southern Brazil (Neves et al., 2004) may have retained the morphological pattern of the earlier groups, and as such tests directly Hypothesis 3 (Tupi-Guarani expansion replaced the earlier morphological pattern from East-Central Brazil). Accordingly, in this model the series of Lagoa Santa, Umbu, Botocudo from Central Brazil, Kaingang and Kamakã are more closely related to each other than to the series occupying the coastal fringe of the country and the series related to the Tupi-Guarani groups. For this model, distance calculations followed the same logic as in Model 2, but now distances among groups sharing the early morphological pattern were equal to the ones in Model 1, and the distances between each of these and the remaining series were calculated as the distance from the first to the last common ancestor coordinates and back to the latter. Consequently, this model tests the existence of two dispersion routes into the continent, represented by distinct morphological patterns, which persisted separated until Late Holocene.

A fourth model that represents the impact of life-style changes on morphology was also tested against the morphological distances. It has been proposed (Perez et al., 2009) that the morphological changes observed in the continent across the Holocene could be a result of adaptation to new life-styles, in particular the adoption of agriculture. To test if life-style can explain the morphological differences among the series, a simple binary matrix of differences was constructed, where series sharing a common life-style (preagriculture or agriculture) received a value of 0, and series with different life-style received the value of 1. This model complements the test of our first hypotheses, which assumes that the morphological diversity in Brazil is the product of local adaptation processes. This is admittedly a very simplistic model, which will only test if agriculture explains the morphological differences, but given the information available for the series at present, a more refined model cannot be created.

The fit of each model to the D^2 matrix between series was measured via Mantel matrix correlation tests (Mantel, 1967). To evaluate if the results are affected by morphological changes occurring during the Holocene (i.e., temporal trends of morphological changes), Mantel partial-correlations were calculated between D^2 and the models, using the chronologic differences between series as a covariate (Pinhasi and von Cramon-Taubadel, 2009). To test if two significant models differed in their goodness of fit, Dow–Cheverud tests (Dow and Cheverud, 1985) were applied (e.g., Hubbe et al., 2010, 2011).

All analyses were based on 18 linear craniometric variables (Table 2) from Howells' protocol (Howells, 1973,

1989). Variables were selected to minimize missing values (Table 1) in the series. Although some of these variables have been shown to respond adaptively to extreme cold climates (Roseman, 2004; Hubbe et al., 2009), all variables were maintained since none of the populations included in the study were subjected to extreme climatic conditions. Preliminary analyses with a reduced set of 14 variables, not affected by climate, did not present significant differences from the results shown here (data not shown).

Missing values in the series were replaced using multiple regressions. Initially missing values were replaced by the average of the variable in the dataset (i.e., the global mean), and then multiple linear regressions were done for each variable, using all the remaining variables as the predictors. The predicted values for the missing values were then used to replace them (see Hubbe et al., 2011 for further details). Within-group averages were

not used, because some of the groups have very low sample sizes and, therefore, might not be good estimators of the original population parameters. However, the percentage of missing values in each series was low, usually around 5% (Table 1), and therefore it is not expected that the replacement method will affect the results in any significant way.

For all analyses, size effect was adjusted by transforming the variables within each individual into *z*-scores and sexual dimorphism was reduced by further transforming each variable into *z*-scores within sex and then pooling sexes together. All statistical analyses presented here were done in R (R Core Team, 2013), with functions written by MH, complemented by functions from package MASS (Venables and Ripley, 2002).

RESULTS

Morphological affinities

Figures 3 and 4 show the MDS and Ward's cluster analyses based on the Mahalanobis distances, respectively. In both analyses, the series appear separated in two major clusters, although the MDS indicates a few series (Lagoa Santa, Southern Brazil Botocudo, and Northern Brazil Tupi) as outliers. The first cluster has all the coastal sites (shellmounds), the Northern Brazil specimens (Marajó), Umbu, and part of the recent Native Americans series (Northern Brazil Tupi, Guarani, and Southern Brazil Botocudo). Within this cluster, the shellmound series appear closely associated, as do the series from Guarani and Marajó (especially in the MDS), despite the geographic distance between them. The other cluster joins the early series from Lagoa Santa and the recent series of Central Brazil Botocudo, Kamakã and Kaingang.

Dispersion and adaptation models

Table 3 shows the results of the Mantel tests between D^2 and each of the dispersion and adaptations models. From all the models tested those that present significant correlations with the morphological distances were

TABLE 2. *Linear craniometric measurements included in this study*

| Craniometric measurements |
| --- |
| Glabello-occipital length (GOL) |
| Nasio-occipital length (NOL) |
| Maximum cranial breadth (XCB) |
| Maximum frontal breadth (XFB) |
| Bistephanion breadth (STB) |
| Biasterionic breadth (ASB) |
| Mastoid breadth (MDB) |
| Bifrontomallare breadth (FMB) |
| Interorbital breadth (DKB) |
| Supraorbital substense (SOS) |
| Glabella subtense (GLS) |
| Frontal cord (FRC) |
| Frontal subtense (FRS) |
| Frontal fraction (FRF) |
| Parietal cord (PAC) |
| Parietal subtense (PAS) |
| Parietal fraction (PAF) |
| Bregma radius (BRR) |

All measurements follow Howells (1973, 1989) description
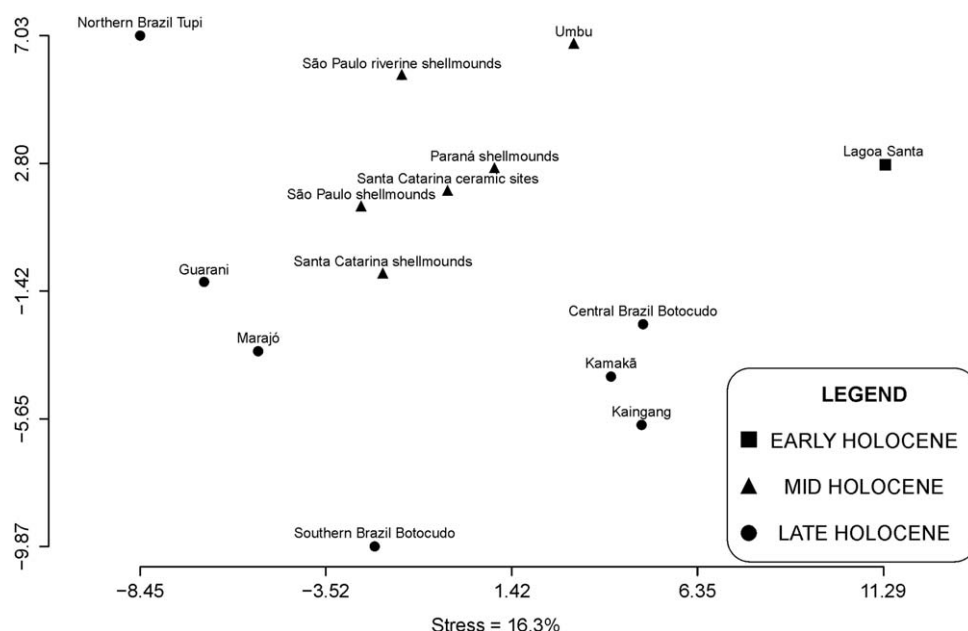
Fig. 3. Non-metric MDS solution of the Mahalanobis distance matrix.
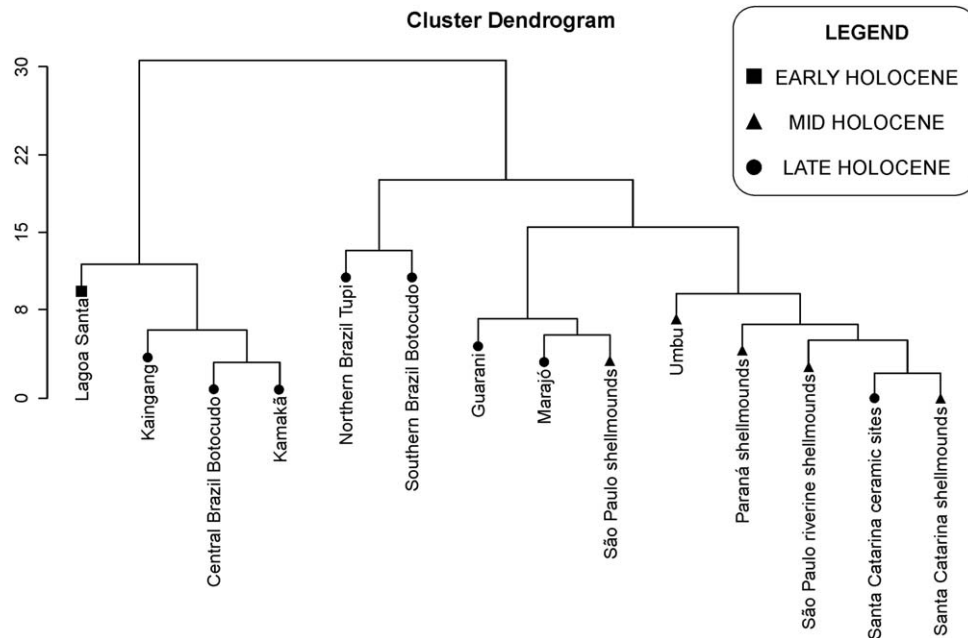
Cluster Dendrogram

Fig. 4. Ward's clusters of the Mahalanobis distance matrix.

TABLE 3. Mantel correlations and partial correlations between the Mahalanobis distance's matrix and each dispersion and adaptation model

Model	Correlation	Partial correlation accounting for time
Control—linear geographic distances	$r = 0.1349$ $P = 0.2329$	$r = 0.1709$ $P = 0.1780$
Model 1—single dispersion wave into Brazil	$r = 0.1580$ $P = 0.2065$	$r = 0.1971$ $P = 0.1593$
Model 2—two discrete dispersion waves into Brazil, with the replacement of the early morphology	**$r = 0.3528$ $P = 0.0392$**	$r = 0.2759$ $P = 0.0631$
Model 3—two discrete dispersion waves into Brazil, with the late survival of the Early morphology	**$r = 0.2416$ $P = 0.0066$**	**$r = 0.2453$ $P = 0.0072$**
Model 4—morphological differences are a result of the transition to agriculture	$r = 0.0106$ $P = 0.4730$	$r = 0.0309$ $P = 0.4094$

In bold - models considered statistically significant (p<0.05).

Models 2 and 3, which assume dual dispersion into the continent, with (Model 3) and without (Model 2) survival of the early morphology in East-Central Brazil groups until Late Holocene. A Dow-Cheverud test show that neither model can be considered a better fit to the morphological dataset ($r = 0.0783$; $P = 0.3025$). However, the partial correlations that corrects for the effect of time differences between series suggest that the significance observed between D^2 and Model 2 is due to the chronological differences between the series, since the correlation becomes non-significant ($P = 0.06$) after correcting for time. Conversely, Model 3 was significantly associated with morphological distances even when time differences were factored into the analysis. Model 4, which tests if differences were due to the adoption of agriculture, was not significantly correlated with D^2. Finally, it must be highlighted that although Model 3 was statistically significant, it explains only a small portion of the variation in the data ($r^2 = 0.0584$), and the vast majority of the variation in the morphological distance matrix is therefore not accounted for by the model.

DISCUSSION

Our results corroborate early studies suggesting a high morphological diversity among Brazilian groups during the Holocene. When the dispersion and adaptation models were tested, our results suggest that the best scenario to explain the origin of the morphological differences observed in Brazil across time is one that considers two dispersion waves into the country (supporting Hypothesis 2), with Central Brazil groups retaining the morphological pattern that characterized the early groups in the national territory (rejecting Hypothesis 3). In this scenario, all coastal series would be the result of a second dispersion wave through the coast that largely replaced and/or displaced populations living in this area before. Hypothesis 1, which explains the morphological diversity through local microevolutionary processes or adaptation to new life styles, is rejected by our results.

Therefore, despite the limitation in geographic coverage of the series available to study, the best scenario to

explain the observed morphological diversity in the country is one that considers Brazilian groups to be divided into two morphological patterns (Fig. 2c). The first one (Paleoamerican) is found among early series from Lagoa Santa, as well as among recent groups occupying east-central Brazil (Central Brazil Botocudo and Kamakã) and the interior parts of Southern Brazil (Kaingang). The series representing the archaic coastal populations, as well as recent Native groups from Northern and Southern Brazil (Tupi, Guarani and Southern Brazil Botocudo), share the second morphological pattern. The three specimens associated with the Umbu Tradition also align themselves with the second group, despite previous studies suggesting that they share a morphological pattern closer to Early South Americans (Neves et al., 2004; Neves and Okumura, 2005).

The moment of origin or development of the two morphological patterns in Brazil is, however, harder to establish. The Paleoamerican morphological pattern seen among Early Holocene samples has been observed in Early Colombian series (Neves et al., 2007b), in Meso America (González-José et al., 2005), as well as in isolated individuals from North-eastern Brazil (Hubbe et al., 2007), and Chile (Neves et al., 1999). Moreover, the same morphology has been observed in Late Pleistocene specimens from Europe and East Asia, and Hubbe et al. (2011) suggested that the morphology shared by Lagoa Santa individuals could be considered a retention of the morphological pattern shared by populations at the end of the Pleistocene worldwide. As populations across the entire continent, as well as the Old World, shared a similar morphological pattern, it is reasonable to assume that their ancestors, the groups that were occupying the continent at the end of the Pleistocene, also share the same morphological characteristics.

Considering that early sites in the continent tend to be associated to the coast (Sandweiss et al., 1998; Dillehay, 2000), it is very likely that early groups in the country followed the Atlantic coast. Unfortunately, any early archaeological site that might have existed on the coastal regions were submerged or destroyed by the sea level variation. However, in some rare cases, the early morphology has been identified in sites that are currently not very far from the coast, like the riverine shellmound of Capelinha, in southeast Brazil (Neves et al., 2005). Nonetheless, the largest samples from the coast are from sites dated from Mid to Late Holocene (shellmound groups) and all of them present the morphological pattern that characterizes later groups (Figs. 3 and 4; see also Okumura, 2008).

The second morphological pattern is first seen among the shellmound groups, and must be the result of a coastal migration that apparently did not mix with groups sharing the early morphological pattern. The existence of distinct morphological patterns in the populations occupying the country's territory opens an interesting possibility for discussion on the nature of the interactions between coast and inland. Although some authors have proposed an independent cultural development between coast and interior (Silva, 1967; Laming-Emperaire, 1975), many favor the presence of contact between these groups (Barreto, 1988; Schimtz et al., 1993; Schmitz, 1996). The presence inland of coastal cultural material (polished stone zoomorphs and geomorphs), faunal remains (mollusk shells and shark teeth; Tiburtius et al., 1950–1951; Prous and Piazza, 1977; Barreto, 1988; Figuti et al., 2004), as well as the later pottery associated to Itararé and Tupi-Guarani Traditions, also contribute to the idea of some sort of contact between coastal and inland groups in portions of Brazil (Beck, 1971; Rohr, 1971; Prous, 1979; Reis, 1980; Neves, 1988; Batista da Silva et al., 1990; Araujo, 2001).

Inland, our results suggest the survival of the early morphological pattern until Late Holocene. The Botocudo of Central Brazil had already been described as sharing the same morphology of the Lagoa Santa groups (Lacerda and Peixoto, 1886; Ten Kate, 1885; Atui, 2005), but the remaining series were not studied before. This opens the possibility that the expansion associated with the Tupi-Guarani Tradition during the Holocene did not completely replace the previous groups living in the interior (Neves et al., 2011; Bernardo et al., 2011). A recent study of mitochondrial DNA extracted from the same Central Botocudo skulls included in this study reported the presence of unusual mitochondrial lineages present among Polynesian groups today (Gonçalves et al., 2013). If the Polynesian origin for the lineages is confirmed, this would support the idea that the Botocudo have in fact a different biological background. Conversely, Gonçalves et al. (2013) also suggest the possibility that the presence of these lineages among the Botocudo may be a result of some degree of admixture with African slaves brought to the country during the colonial period. Consequently, the molecular data available to date, although showing the presence of unique lineages among the Central Botocudo Indians, does not contribute to the discussion of their biological relationship with other Brazilian groups, or to the understanding of the morphological affinities between Botocudo and Lagoa Santa, Kamakã and Kaingang groups.

Finally, it cannot be stressed enough that all the discussion presented here is tentative and based on an osteological record that is largely incomplete. The conclusions presented here must be tested with further samples and also contrasted with other types of evidence such as molecular and archaeological data. Therefore, this article helps to contextualize the possible scenarios of human dispersion into Brazil, but it also shows rather clearly how scant the available skeletal record is. The excavation and study of new osteological collections from periods and regions poorly represented in our analyses will certainly redefine and refine the proposition presented herein about the tempo and mode of human dispersion into Brazil.

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