

# The Origins and Context of Palaeoamerican Cranial Morphology: Implications for Discussions about Human Dispersal into the Americas

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## Abstract

The cranial morphology of the Early Holocene remains from Lagoa Santa, in central Brazil, have attracted the attention of researchers since the mid-nineteenth century and have been a central piece in discussions about the biological origins of early American populations. From the point of view of cranial morphology, these early populations have been described as being different from most of the modern Native American populations, generating a long standing debate about the origins of the early Holocene morphological patterns observed in the continent and its implications for our understanding of the processes of human dispersion into and occupation of the continent. Lagoa Santa (eastern central Brazil) is of high importance for this discussion, due to the high density of Late Pleistocene/Early Holocene sites and hundreds of human skeletons recovered from the local rockshelters and caves. These remains are unique in the continent, for they allow the study of the biological characteristics of early American groups from a population perspective, increasing the reliability of the conclusions drawn from the analysis of this material. This chapter summarises some of the morphometric analyses of this collection in the past decade and how these results address and contribute to the discussions about the settlement of the continent. Recent studies can be divided into two topics: the study of the origins of the morphology that characterizes early South American populations; and the study of how this morphological pattern is related to the morphology that characterizes recent Native Americans. To address the first topic, Early Holocene remains from Lagoa Santa were compared to Late Pleistocene remains from Europe and East Asia, and the results suggest that these populations share a common morphological pattern, for instance, they have closer morphological affinities with each other, despite the geographic distance between them, than with modern populations from their own continents. These analyses indicate that the Palaeoamerican morphology is a retention of the morphological pattern that characterized human populations around the planet by end of the Pleistocene and predates the diversification processes that gave rise to the actual human cranial morphological diversity on the planet. Regarding the second topic, different studies have tried to address the best dispersion models that would explain the diachronic morphological diversity in the continent. In the past decade, studies have defended models that assume 1) two discrete waves of human dispersion into the continent; 2) continuous gene-flow between Asia and the Americas during the Holocene; and 3) local morphological adaptations to new lifestyles and a different climate as possible causes for the observed diversity. However, to date no consensus has been achieved among authors addressing these questions and the debate about the best human dispersion model to explain the cranial morphological diversity across time in the continent is still unresolved. This lack of consensus might be the result of our limited understanding of the biological diversity that existed in the continent in the past, and to solve this problem future studies will have to include more comprehensive collections from the New World.

## Introduction

The initial occupation of South America dates to at least 14 cal kyr BP (Dillehay et al., 2008; Dillehay, 2009; Rothhammer and Dillehay, 2009), with the Pacific coast showing the earliest accepted archaeological evidence for human groups on the continent, associated with groups that probably depended heavily on coastal resources (Sandweiss et al., 1998; Dillehay, 2000; Dillehay et al., 2008). Early human evidence on the continent is more common in the Pacific rim and Andean regions (Dillehay, 2008), although there is no doubt that by 11 cal kyr BP most of the continent was already occupied (Salemme and Miotti, 2003), with groups dwelling in forest environments (Roosevelt et al., 1996; Guidon et al., 1998), bushy savannahs (Correal, 1990; Araujo et al., 2008; Araujo and Feathers, 2008;) and cold and semi-arid steppes and plains (Steele and Politis, 2009; Bayón et al., 2011).

These early settlements differ considerably from the early cultures described for North America, especially when compared to the megafauna-specialized Clovis culture (Dillehay, 2000). So far, South America lacks convincing evidence of a systematic exploitation of megafauna (Hubbe, A. et al., 2007; 2009, 2013; Borrero, 2009), although evidence of human and megafauna coexistence through the end of the Pleistocene/beginning of the Holocene has been reported in Brazil (Neves and Piló, 2003; Hubbe A et al., 2009, 2013) and Argentina (Politis et al., 2003; Borrero, 2009). It is probable that South America's occupation followed coastal routes (Rothhammer and Dillehay, 2009), as recently proposed for North America's Pacific coast (Dixon 2001; Erlandson et al., 2011). However, a clear connection between these dispersion movements is still to be established. There is little doubt that these Late Pleistocene/ Early Holocene groups were mobile, covering large territories to meet their subsistence needs. Certainly, the adaptation and colonization of new ecological niches must have posed a challenge to these initial groups, with social and ritual considerations having important roles in the creation of mobility strategies (Dillehay, 2008: 42).

It is likely that the lifestyle of early South Americans changed around 10 cal kyr BP when more permanent settlements start to appear in distinct regions of the continent (for example, Arriaza et al., 2008; Araujo et al., 2008; Dillehay et al., 2003; Dillehay, 2008; Piperno and Stothert, 2003; among others). This shift, which predates the domestication of plants and animals on the continent probably involved the establishment of logistic centres around which mobile groups were organized (Dillehay, 2008). These more permanent settlements can be seen as precursors to the diverse local cultural traditions that developed in the Middle Holocene.

From a biological perspective, little can be inferred about the first millennia of human presence on the continent, since human remains from this period are scant. Excluding a few individual skeletons in North, Meso and South America (Powell, 2005; Waguenspack, 2007; Feathers et al., 2010), osteological remains from the end of the Pleistocene are not found in the archaeological record. Therefore, attempts to reconstruct the biological characteristics and diversity of early Americans depend on estimates based on later material, which so far have been unable to offer a consensus regarding the origins of Native Americans' biological diversity. Early Holocene skeletal samples are more common in South America than in North America (Jantz and Owsley, 2001; Powell, 2005; Waguenspack, 2007) and have been described in Brazil (Hubbe et al., 2004, 2007; Neves and Hubbe, 2005; Neves et al., 2005, 2007a), Colombia (Neves et al., 2007b) and south Chile (Neves et al., 1999), although collections also exist in Peru (Benfer, 1990) and central Chile (Passig et al., 1986). The cranial morphology shared by early skeletons in the continent has been described as presenting a peculiar morphology. Recent studies have indicated that they share a morphological pattern not seen among most of the later Native Americans (Neves and Hubbe, 2005; Hubbe et al., 2010, 2011). Indeed, studies show a wide array of populations that would have closer morphological affinities to them than recent Native Americans: Australo-Melanesians (Powell and Neves, 1999; Jantz and Owsley, 2005; Neves et al., 2007a; Hubbe et al., 2010), Sub-Saharan Africans (Neves and Pucciarelli, 1989; Neves and Hubbe 2005), generalised Asian groups (Brace et al., 2004; Seguchi et al., 2011) or even European populations (Chatters, 2001).

This early morphological pattern, sometimes referred to as Palaeoamerican (Neves and Hubbe, 2005, but see Gonzalez-José et al., 2008 for a critic on its use), is characterized by long and narrow crania, low and projecting faces, and low orbits and nasal apertures (Neves and Hubbe, 2005; Hubbe et al., 2010, 2011). This pattern contrasts with the morphology present among recent Native American groups, that 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 (Gonzalez-José et al., 2003, 2008; Pucciarelli et al., 2006; de Azevedo et al., 2011). Although the Palaeoamerican and late Native American morphological patterns overlap to a great extent when individual variation is taken into account (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 recent human populations from distinct continents (Neves and Hubbe, 2005; Neves et al., 2013). When assessed within the comparative framework of worldwide craniometric human variation, early American groups often show stronger morphological affinities with 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 morphological differences between Early and Late American skeletons were initially noticed by nineteenth century scholars studying the skeletal remains from Lagoa Santa, in east-central Brazil. Following the typological paradigm accepted by those scholars, some of these authors deemed the differences between early and late groups large enough to constitute distinct human races, the early 'Lagoa Santa Man' (Rivet, 1908). In fact, the antiquity and the nature of the Lagoa Santa individuals called the attention of many scholars in Brazil, Europe and the United States (Lacerda and Peixoto, 1876; Kollman 1884; Ten Kate, 1885; Quatrefages, 1887; Hansen 1888; Virchow, 1892; Hrdlicka, 1912), especially since their morphological characteristics were so different from recent Native Americans (Lacerda and Peixoto, 1876; Ten Kate, 1885; Hansen, 1888; Rivet, 1908; Imbeloni, 1938). Today, Lagoa Santa is one of the two regions in the entire continent with enough individuals recovered from early contexts that permit their study from a population perspective, allowing for more reliable extrapolations about the biological characteristics of Early American groups. The second region is Bogotá Savannah, in central Colombia,

where a series of early skeletons have been recovered from local limestone rockshelters. This material has been covered in detail by Neves et al. (2007b) and represents a collection of ~20 skeletons dated to between 11.5 and 6.5 ky BP, coming from only a handful of sites. No other collection of early specimens presents numbers even close to these (Waguenspack, 2007; Neves et al., 2013).

Even when compared to the Bogotá Savannah, Lagoa Santa is remarkable in terms of its archaeological record. During almost two centuries of excavations in the area over 100 human skeletons dated to between 11.5 and 7.5 14C kyr BP were recovered. Consequently, the Lagoa Santa human remains represent by far the largest series of early skeletal remains from the Americas (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 (for example, Neves and Pucciarelli, 1989, 1991; Powell and Neves, 1999; Neves et al., 2004, 2005, 2007a, 2013; 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), as well as studies dealing with aspects of their lifestyle (Da-Gloria, 2012; Hubbe A et al., 2009; Mendonça de Souza, 1995; Neves and Corneiro, 1997; Neves and Piló, 2003; Prous and Fogaça, 1999).

The main concern regarding the Lagoa Santa remains has been to explain the origin of its peculiar morphological pattern when compared to most recent Native American populations. The existence of two distinct morphological patterns across time indicates that the process of human dispersion into the continent might have been more complex than traditionally assumed. Several studies of early American cranial morphology suggest 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 (Neves et al., 2004, 2007a, b; González-José et al., 2005; Neves and Hubbe, 2005; Hubbe et al., 2010). 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 (Powell, 2005; Perez et al., 2007, 2010) or were a result of the continuous influx of diversity from Beringia into the continent (González-José et al., 2008; de Azevedo et al., 2011), an interpretation consistent with most, though not all, genetic evidence (Bonatto and Salzano, 1997; Zegura et al., 2004; Tamm et al., 2007; Wang et al., 2007; Fagundes et al., 2008; Rothhammer and Dillehay, 2009; 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 along time originated, is key to understanding details about the human dispersion into the New World in the past. Two questions regarding the evolutionary context of the Palaeoamerican morphology have been extensively debated in the literature in recent years, and this chapter summarises the results of some of the recent work on this subject (for example, Hubbe et al., 2010, 2011; Neves et al., 2013). The first question relates to the origin of the Palaeoamerican morphology. More specifically, it addresses the question of whether the Palaeoamerican morphology is unique to the continent or if it can be traced back to ancestral populations outside the continent. Elucidating if the Palaeoamerican morphology is a local development or if it is related to the evolutionary history of modern humans outside the Americas is an essential first step in explaining its origin and how it related to the process of human dispersion into the continent. The second question relates to the origins of the recent Native American morphological pattern and its relationship to the early Palaeoamerican morphology. Many studies have focused on this question, since the definition of the degree of association between these morphological patterns can shed light on the pattern and number of dispersion waves into the New World.

In exploring these questions, Lagoa Santa has been of unique importance, due to the size and chronological frame of its skeletal collections. Therefore, very few studies dealing with early Americans' biological diversity have not included the Lagoa Santa material or parts of it. Due to its preponderance in the studies about the morphological characteristics of Early Americans and its contribution to the discussion about the tempo and mode of the human dispersion into the New World, this chapter will precede the discussion of the morphological analyses of early South American remains with a general description of Lagoa Santa's archaeological background and history of discoveries, complementing it with new data generated by the latest research of the past decades.

## Lagoa Santa archaeological record

The karstic region of Lagoa Santa (Figure 1) derives its importance from the studies of early humans in the continent from the long history of palaeontological and archaeological excavations of its caves and rockshelters, and the relatively well preserved archaeological packages dated to the beginning of the Holocene. The region became famous during the nineteenth century thanks to the systematic work of the Danish naturalist, Peter Lund, who explored hundreds of caves in the region between 1835 and 1844 and intensively excavated around 60 of them (Lund, 1844, 1845; Holten and Sterl,



Figure 1. Location of Lagoa Santa and other important archaeological regions with early human remains in South America



1999). Lund was primarily interested in the Quaternary faunal deposits in the region and based on his findings, described several new genera and species of extinct mammals that inhabited the region in the past. However, in the context of this chapter his most significant contribution was the discovery of human remains associated with extinct megafaunal specimens inside Sumidouro Cave (literally 'swallet cave'). The Sumidouro remains, recently dated to a minimum age of ca. 8,500 cal yr BP (Neves et al., 2007a), were among the first evidence of an older presence of human beings in the continent, quickly becoming a major topic of discussion among European and American scholars (for example, Hansen, 1888; Hrdlička, 1912; Lacerda and Peixoto, 1876; Rivet, 1908).

Lund's work certainly inspired many new researchers to explore the caves and rockshelters of the region during the following centuries. Of special interest to this chapter is the work of the French-Brazilian mission (Laming-Emperarie, 1979; Prous and Fogaça, 1999), who recovered the oldest evidence of human evidence in the region: a young female skeleton recovered from Lapa Vermelha IV, a 14 m deep fissure filled with sediment and faunal remains, but with scant evidence of formal human presence. The skeleton was not recovered inside a burial context, being probably the result of a body that was discarded into the fissure. The skeleton was originally dated to 11.4–16.4 cal kyr BP (Laming-Emperaire, 1979), based on its stratigraphic position between charcoal concentrations. New OSL dates agree with the date range of this skeleton, suggesting a range of between 12.7 and 16.0 cal kyr BP (Feathers et al., 2010). Although only one individual, the skeleton from Lapa Vermelha IV is currently one of the oldest in the Americas and attests for the presence of human beings in the region of Lagoa Santa since at least the final millennia of the Pleistocene.

Other research teams during the twentieth century excavated a great number of caves and rockshelters in the region with evidence of early human occupations, and generated relevant collection of early human skeletons. Hurt and Blasi (Hurt, 1960, 1964; Hurt and Blasi, 1969) excavated the Cerca Grande complex, from where 17 burials dated to 9,500 and 8,000 14C yr BP were recovered. Finally, Harold Walter led a team of amateur archaeologists who excavated many different sites, recovering early human remains from Lapa Mortuaria and a high number of skeletons from different sites in the region (see Neves and Hubbe, 2005 for a complete list of well-preserved skulls from Lagoa Santa, and Strauss, 2010 for a discussion of their chronology).

Since 1999, a long term archaeological project in the Lagoa Santa region has been led by Prof. Walter A. Neves (Universidade de São Paulo, Brazil). Over this decade of work, two rockshelters with deep archaeological packages were systematically excavated (Araujo et al., 2008), one of which – Lapa do Santo – has a high concentration of human burials. To date, 32 burials dated to between 9,200 and 7,000 14C yr BP were recovered from Lapa do Santo, showing a wide array of burial practices, including complex secondary ritual manipulation of human remains in a significant part of them (Strauss, 2010, 2011, 2012; Strauss et al., 2011a, 2011b).

The new dates generated for the region showed that Pleistocene individuals are quite rare and only the individual from Lapa Vermelha IV (Luzia) has been dated to before the Holocene. Despite the presence of Pleistocene dates at the bottom of the archaeological record in the rockshelters (for example, Araujo et al., 2008), the systematic use of these spaces as burial ground did not start until ~9,500 14C yr BP, suggesting a possible shift in the cultural background of groups living or moving across the region around this date.

During the last 13 years, the permanent lake shores of the region were prospected and evidence of human presence in the form of lithic artefacts has been recovered dated to c. 8,300 14C yr BP (Araujo and Feathers, 2008; Araujo et al., 2013), suggesting a possible increase in the logistic use of the regional resources by populations that established themselves in Lagoa Santa during the beginning of the Holocene. Inside rockshelters, the pattern of secondary burials described in Lapa do Santo contradicts the notion that early groups of Lagoa Santa had simple and homogeneous burial practices (Strauss, 2010, 2011, 2012; Strauss et al., 2011a, 2011b). In fact, the burials recovered from this site show a complex ritual processing of the dead, frequently dichotomizing cranial and postcranial remains by organizing bundles of the later (sometimes of more than one individual) around and/or inside opened skull cases (Strauss, 2010).

The project in Lagoa Santa also excavated palaeontological sites and systematically dated megafaunal remains of the region, through which it was able to show a significant chronological overlap between human groups and extinct megafaunal species. At least the saber-tooth cat (*Smilodon* sp.) and one type of ground sloth (*Catonyx cuvieri*) survived into the Holocene (Neves and Piló 2003), although no evidence of direct interaction between human and megafaunal species have been reported for the region (Hubbe, A. et al., 2009, 2012, 2013), suggesting that these hunter-gatherers were not focusing on large prey. The faunal assemblage recovered from the Lagoa Santa archaeological records is strongly dominated by deer (*Mazama* sp.) with a minor participation of medium and small mammals (armadillos, wild pigs and rodents), as well as birds, lizards and snails. The specialization towards smaller fauna is supported by the lack of a lithic points industry specialized to this end, with the local lithic assemblage being composed mainly of small and micro flakes made out of quartz, with only minor changes observed over the more than 3,000 years of occupation of the local rockshelters (Araujo et al., 2008). The

diet of these populations appears to have included a larger amount of cariogenic items (rich in carbohydrates) than typical hunter-gatherer populations, which resulted in unusually high prevalence of dental caries among the local groups (Neves and Cornero, 1997; Neves and Kipnis, 2004; Da-Gloria, 2012).

In summary, the early archaeological sites of Lagoa Santa show the presence of humans by the end of the Pleistocene, who progressively increased their use of the landscape, developing a specific cultural tradition that clearly reflects their adaptation towards the local landscape. The local cultural development, reflected in their technology, treatment of the dead and even dietary practices, contrast sharply with the typical image of early American groups elsewhere in the continent and favour the idea that by the beginning of the Holocene the Americas were occupied by diversified groups that developed specific and unique ways to handle the landscape around themselves (Dillehay, 2008).

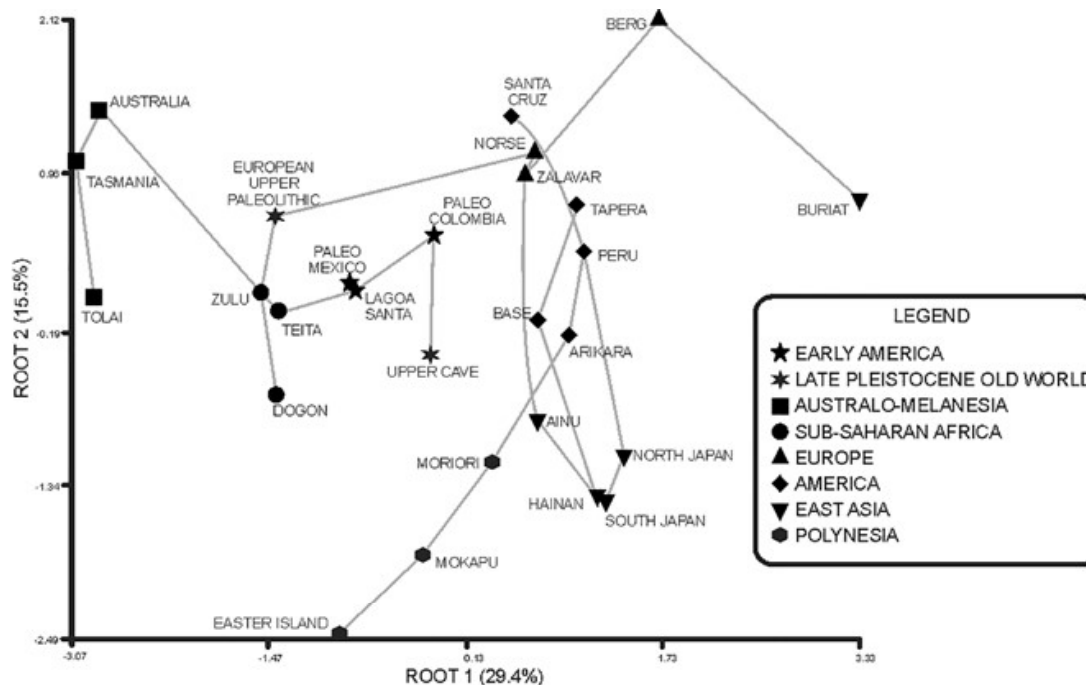


Figure 2. Cranial morphological affinities between early American and Late Pleistocene Old World series in reference to modern human worldwide morphological variation.

## Palaeoamerican morphology in its late Pleistocene context

As presented above, the early human groups that inhabited Lagoa Santa during the first millennia of the Holocene share a distinct cranial morphological pattern when compared to most of the late Native American populations. These differences might denote important biological differences as well as important levels of diversity in the continent during the Holocene, which might be a product of the complex processes of human dispersal into and occupation of the New World in the past. To explore the origins of this morphological diversity in the continent, two lines of research have been followed in the past decades. The first, resumed in this session, refers to the origins of Palaeoamerican morphology. The second, addressed in the subsequent session, addresses the origin of the Late Native American morphological variation and how it relates to Palaeoamerican morphology.

The main goal of the studies dedicated to understanding the origin of the Palaeoamerican morphology has been to contextualise this morphology in the continent as well as on the planet, to elucidate if this morphological pattern is unique to the Americas or if it can be seen in the context of the evolutionary processes that characterize modern human cranial morphology worldwide. Although this morphological pattern is better observed among Lagoa Santa populations, due to its large sample size, it is not unique to this region, being found widespread in South America by the end of the Holocene. In fact, every human skull dated to more than seven thousand years BP, compared so far with Lagoa Santa, shows high morphological affinities with this population and share the Palaeoamerican morphological pattern. In South America, it has been described in samples from east-central Brazil (Lagoa Santa; Neves and Hubbe, 2005; Neves et al., 2007a) and Colombia (Bogotá Savannah; Neves et al., 2007b), as well as in isolated specimens from south-east Brazil (Capelinha; Neves

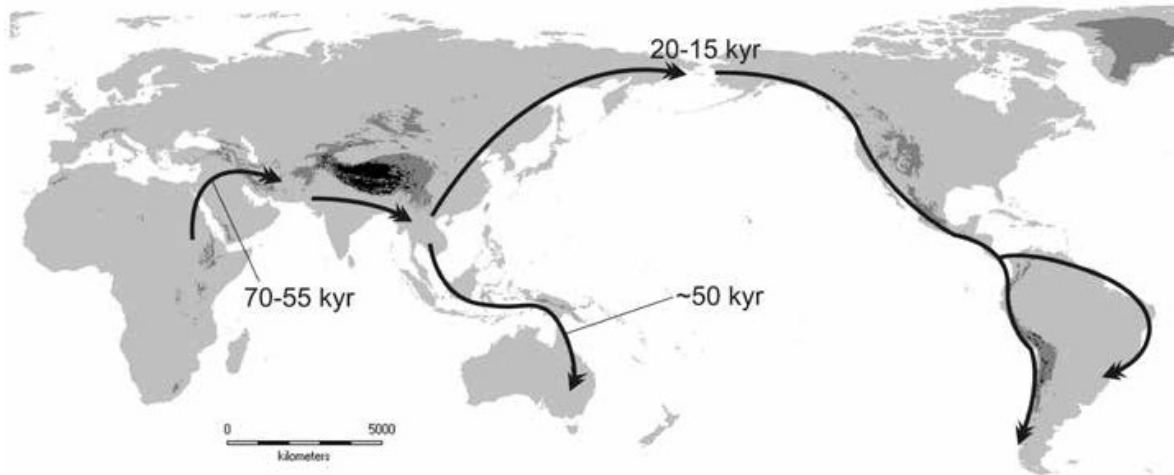


Figure 3. The morphology of early American groups might result from retention of the morphology of the first human groups, which left Africa between 70 and 55 kyr BP. In this sense, the settlement of the New World can be seen as a direct extension of the human dispersion out of Africa into Southeast Asia and Australia. Dates presented are an approximation based on the recent literature (Mellars, 2006; Dillehay, 2009; among others).

et al., 2005), north-east Brazil (Toca dos Coqueiros; Hubbe et al., 2007) and southern Chile (Palli Aike; Neves et al., 1999). However, distinct cranial morphology has also been observed in early skulls from Mesoamerica (Mexico; Gonzalez-José et al., 2003) and North America (Jantz and Owsley, 2001; Powell, 2005). Therefore, there is currently a consensus that the entire continent was occupied by human groups sharing a common morphological pattern by the end of the Holocene.

Cranial morphology is largely defined by stochastic evolutionary processes (for example, Harvati and Weaver, 2006a, b; Relethford, 1994; Roseman, 2004), with selective adaptation being restricted to extreme regions or localised anatomical regions in the skull (for example, González-José et al., 2005; Harvati and Weaver, 2006a,b; Hubbe et al., 2009). Consequently, cranial morphology has been used widely to reconstruct phylogenetic histories between human populations. Recently, a study compared the cranial morphology of Early Americans with Late Pleistocene individuals from East Asia and Europe (Hubbe et al., 2011), with the objective of testing whether Palaeoamerican morphology is a unique process to the New World or if it is related to the evolutionary processes that were shaping modern human morphology worldwide. The comparison is based on linear measurements of the skulls that together represent the morphology of the individuals included in the analyses. The Late Pleistocene and Early American groups were analysed within the frame of modern human cranial morphological variation, by comparing them to the reference series measured by Howells (Howells, 1973, 1989). Figure 2, adapted from Hubbe et al. (2011), shows the comparison between early Americans and Late Pleistocene Asians and Upper Palaeolithic Europeans, when compared to the worldwide morphological variation. The graph shows how similar series are to each other in two ways: the distribution of the samples along axes represents their morphological affinities according to the first two canonical variates, for instance, the closer the dots on the graph, the more alike their skulls. The lines connecting the series represent the Minimum Spanning Tree of the biological distance matrix and represent, according to this statistic, the shortest path connecting all series (see Hubbe et al., 2011 for details on the methods applied). In other words, series connected by lines are more similar to each other. The two approaches complement each other, giving a more reliable representation of the morphological affinities between series (see Hubbe et al., 2011, for justifications of the methods). When only the canonical variate information (position of the dots on the graph) is taken into account, all early samples appear closer to each other on the central region of the graph, in proximity to the Sub-Saharan African series, while the recent samples present a general geographic logic, with series from the same region appearing closer to each other. 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 the early series and modern samples from their respective geographic regions can be observed, with the exception of European Upper Palaeolithic and Norse. Therefore, this analysis strongly supports that early Americans are more similar from a cranial morphology point of view to other Late Pleistocene groups on the planet than to recent populations from the same continent.

In the last 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 (60-30 kyr BP), tend to be more similar to each other than to later populations from the same region

(for example, Stringer and Andrews, 1988; Bräuer, 1992a, b; Stringer, 1992, 2002; Grine et al., 2007, Harvati et al., 2007; Harvati, 2009).

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 analysis presented in Figure 2 favours the idea that this morphology might be a retention of the morphological pattern seen in the first modern humans leaving Africa (Neves et al., 2003), between 70 and 50 thousand 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 South-East Asia, with one branch expanding south into Australia and the other expanding north, towards Beringia, and subsequently into the Americas (Figure 3).

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 (Neves and Pucciarelli, 1998; Harvati, 2009) 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, favouring 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 Palaeolithic 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 Palaeoamerican morphology might reflect a retention of the ancestral modern human morphology observed in the late Pleistocene Old World has implications for 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 (Roseman, 2004; Harvati and Weaver, 2006a,b; Hubbe et al., 2009; von Cramon-Taubadel, 2009). Since crossing the Bering Strait is believed to be the best route for early groups getting into the New World (Dixon, 2001; Goebel et al., 2008; Dillehay, 2009), 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 a cold climate. The speed of this process, however, is hard to evaluate at the moment given that 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 kyr BP (Tamm et al., 2007; Gonzalez-José et al., 2008; Kitchen et al., 2008; Mulligan et al., 2008), although no major environmental or geographic barrier between Beringia and east 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 (Dixon, 2001; Fagundes et al., 2008; Dillehay, 2009). 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).

## Origins of morphological diversity during the Holocene

While the view on the origin of Palaeoamerican morphology described above has not been contested or contradicted by new analyses, the same cannot be said for the discussion about the origins of the morphology that characterizes most of the recent Native American groups. The increase of morphological diversity during the Holocene and the appearance of a new morphological pattern in the continent, closely resembling the morphology seen in modern east Asian groups, has been explained by either multiple dispersion waves into the continent (Neves and Hubbe, 2005; Neves et al., 2007a,b; Hubbe et al., 2010), a result of local microevolutionary processes (Powell, 2005; Perez et al., 2007, 2010) or the result of a continuous gene flow with north-east Asia during the Holocene (González-José et al. 2008; de Azevedo et al., 2011). Defenders of the first scenario argue that the differences between early and late morphological patterns are so large that they cannot be explained only by local microevolutionary forces. Under this scenario, the morphological pattern of Early Americans represents the morphology present on the planet by the end of the Pleistocene and was brought into the New World by



the initial settlers crossing the Bering Strait. A new morphological pattern, similar to the one seen among recent east Asian groups, was brought into the Americas by a second wave of dispersion (but not necessarily only one discrete migration), which largely replaced the early pattern, although groups sharing a similar morphology with the early groups have been reported during the mid-Holocene in Colombia (Neves et al., 2007b) and Late Holocene in Baja California (González-José et al., 2003), Patagonia (Lahr, 1995) and central Brazil (Atui, 2005).

The second scenario developed to explain the morphological diversity observed across time in the Americas assumes that the morphological changes can be explained by local changes in time. This scenario has received some support from dental morphological studies (Powell, 2005) and studies in Argentina comparing cranial shape to molecular data (Perez et al., 2010), but has been considered less parsimonious than multiple migrations from or continuous gene flow with Asia in studies that tested which scenario fitted best the morphological diversity in the continent as a whole (Hubbe et al., 2010; de Azevedo et al., 2011).

The third and most recent scenario proposed to explain morphological diversity in the continent assumes that the early populations that entered the continent showed already high levels of morphological diversity and that the continuous gene flow between American and north-east Asian groups shaped the morphological diversity of American groups across time (González-José et al., 2008; de Azevedo et al., 2011). This proposal overlaps with the dual dispersion model by assuming that the diversity observed in the continent depends on the influx of extra diversity from outside the continent. The difference between these scenarios, thus, is the nature by which this influx occurred, with the first scenario defending more discrete migrations and the second maintaining that gene-flow was constant and continuous between Asia and America throughout the duration of the Holocene.

This lack of consensus in the process of human occupation of the continent is also observed among studies of the genetic variation of Native American groups. Largely restricted to recent populations, molecular studies in the past 25 years have defended between one and three discrete migrations into the continent (Bonatto and Salzano, 1997; Zegura et al., 2004; Tamm et al., 2007; Wang et al., 2007; Fagundes et al., 2008; Perego et al., 2009; Reich et al., 2012), sometimes defending continuous gene flow with north-east Asia (Tamm et al., 2007; González-José et al., 2008) or even a period of isolation of Proto-Americans (Tamm et al., 2007; Kitchen et al., 2008) from Asia before the dispersion into the New World. This lack of consensus among molecular data has hindered attempts to conciliate the morphological with genetic evidence (for example, Greenberg et al., 1986; González-José et al., 2008) difficult and prone to criticism.

Consequently, although the increased morphological diversity in time and the shift in morphological pattern across time in the Americas suggests an influx of further diversity into the continent, at present it is impossible to offer a more definite opinion on whether this was a product of multiple discrete migrations into the continent or a result of gradual influx as a result of continuous contact and gene flow between north-east Asia and North America.

Finally, although authors tend to extrapolate their conclusion to the entire American continent, it has to be noted that the early American series available to date all come from South America. Morphological analyses can be seen to favour the notion that all early North, Central and South American groups shared a common morphology, since Lagoa Santa and Early Colombian groups show the same morphological pattern seen in other parts of the planet by the end of the Pleistocene. Consequently, the increase in morphological diversity and the late appearance of a new morphological pattern in the continent was probably a continent-wide event. However, it is possible and reasonable to assume that the processes by which this influx of morphological diversity occurred in the continent might have been different between North and South America. As argued extensively in the literature (for example, Dillehay, 2008), there is enough archaeological evidence to show that the early South American groups do not culturally resemble early North American groups. Therefore, the same might be true of the biological characteristics of early populations in each continent. For instance, it is possible that in North America this influx was a result of a continuous influx with Asia, whereas in South America this same event could have taken place through more discrete waves of dispersion. This scenario has some support from recent molecular studies that suggest that continuous gene flow with north-east Asia was probably restricted to the northern regions of North America (Tamm et al., 2007; Reich et al., 2012). Also, discrete dispersion waves in South America has received some support by molecular studies, who suggested two discrete dispersion waves inside the continent, based on rare mtDNA lineages (Perego et al., 2009) and a much higher degree of between populations diversity in non-Andean native South Americans (Tamm et al., 2007).

Yet, many other molecular studies would refute this idea and defend one single wave of dispersion into South America (Greenberg et al., 1986; Tamm et al., 2007; Reich et al., 2012) or even the Americas as a whole (for example, Zegura et al., 2004; Wang et al., 2007). At present, it is hard to corroborate or refute a particular scenario of how populations dispersed across the continent, which highlights the fact that our data about early American groups is biased by being restricted to

South America and that any model to explain the origins of the first South Americans does not necessarily apply to North America.

## Conclusions and future research directions

The importance of the Lagoa Santa region, with its dozens of late Pleistocene/early Holocene sites and hundreds of human burials, to the studies of the characteristics of early human groups in South America cannot be highlighted enough. The human presence in the region during the final millennia of the Pleistocene and early Holocene shows a series of groups adapted to the local environment, with lifestyle and burial practices remarkably different from that seen in other regions of South and North America. By itself, this shows that the early Holocene populations in the New World presented significant cultural diversity between themselves, being one more distinct piece of the mosaic of cultures that were present in the continent (for example, Dillehay, 2000, 2008; Dixon 2001; Arriaza et al., 2008; Goebel et al., 2008). This cultural diversity shows a quick process of differentiation in the initial periods of the human presence in the continent, showing that no matter who came into the Americas or how fast the colonization wave dispersed through the landscape, by 10,000 cal yr BP the continent shows signs of people adapting to their own landscape and developing clear local traditions that are defined by more than their technological background.

Yet, the same cannot be said from their biological characteristics, since as far as cranial morphology is concerned, the early Holocene populations of the continent show low levels of variation and a morphological pattern that is not the one most widespread among Late Holocene Native American populations. This strongly suggests a significant influx of extra morphological (and biological) diversity into the continent during the Holocene, either by a continuous gene flow with Asia or by multiple discrete dispersion waves into the continent during this time. Consequently, from the perspective of cranial morphology, the actual biological diversity of Native Americans does not derive exclusively from the early Palaeoamerican populations that settled the continent, and a linear causal connection between early and late populations on the continent should be established only when empiric data strongly supports it. In other words, our analyses of the Lagoa Santa remains in the past decades (Neves and Hubbe 2005; Neves et al., 2007b, 2013; Hubbe et al., 2010, 2011) as well as the ones presented here add to the growing body of evidence that the processes associated with the settlement and dispersion of human groups across the Americas were neither simple nor straightforward, and involved the complex interaction between different cultures and possibly biologically distinct populations during the entire period that humans occupied the continent.

Consequently, although the increased morphological diversity in time and the possible shift in morphological patterns across time in the Americas favours an influx of further diversity into the continent, at present it is impossible to offer a more definite opinion on whether this was the product of multiple discrete migrations into the continent or the result of gradual influx as a result of continuous contact and gene flow between north-east Asia and North America. This difficulty derives from the lack of good comparative data sets, with series that represent accurately the continent's past morphological diversity. Most studies of morphological diversity in South America do not incorporate the biological diversity seen during the Middle Holocene, including only representatives of early and late Holocene populations (for example, Hubbe et al., 2010; de Azevedo et al., 2011, but see Perez et al., 2010 for an exception), where in theory the Middle Holocene (between 7 and 4 kyr BP) must have been a period of intense morphological differentiation, either due to population replacement (dual-dispersion scenario), continuous influx of extra diversity from Asia via North America, morphological adaptation to new environmental factors (changes in life-style or climate) or any combination of these processes.

With this framework in mind, it is imperative that future work focuses 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. If the question about the origin of the morphological diversity seen in the Americas in the past is ever to be solved, more international collaborative initiatives must be established, focusing both on the analysis of larger datasets and on the creation of public and virtual databases that house information about the collection currently curated in the many archaeological and natural history museums of the continent.

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