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The first human settlement of the New World: A closer look at craniofacial variation and evolution of early and late Holocene Native American groups

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ABSTRACT

During its expansion across the globe, *Homo sapiens* successfully survived to major adaptive challenges as a species, inviting scientific research to plunge into the particularities of continental settlement dynamics. A recurrent paleoanthropological concern is about the understanding of the great deal of craniofacial diversity that evolved into the Americas, which includes a vector of continuum variation between a generalized morphology observed among humans groups leading the Out-of-Africa dispersion, and a derived set of craniofacial traits classically labeled as “mongoloid” and that would have arise in Asia during the Holocene. Here, we use geometric morphometric techniques and multivariate statistics along with quantitative genetic approaches to look more closely into the human craniofacial evolutionary history during the Late Pleistocene–Early Holocene from Asia and the New World. We detected significant signals of deviation of the neutral evolutionary expectations, suggesting an important action of non-stochastic evolution (e.g. natural selection, phenotypic plasticity) in the Americas. We also found further support to the Recurrent Gene Flow model that refers to an ancestral, founder population experiencing a standstill in Beringia, and exhibiting high within-group craniofacial variation. This original, internally variable stock would have been the ancestral source of variation that fuelled the subsequent local micro evolution of other derived phenotypic patterns, giving origin to the craniofacial diversity observed among Holocene Native American samples.

1. Introduction

The origin and evolution of modern humans is one of the most striking areas of paleoanthropological research. Somewhere in this research field, settlement of the Americas can be viewed as a natural experiment to study many aspects of human evolution. One reason for this is that human expansions around the globe were coincident with global climatic changes, so that the paths that may have been followed by human populations that first colonized the Americas were influenced by the climatic and environmental effects of the last glaciations during the Late Pleistocene (Dixon, 2013). Furthermore, *Homo sapiens* was successful in occupying most possible environments, and mechanisms causing both lost or gain of within and between-group diversity (mutation, selection, genetic drift, migration and gene flow) likely intervened in all phases of the dispersal. Central questions around this debate are, how has the human skull evolved across anatomically modern humans' history and dispersion? and, how and when did *Homo sapiens* reach the Americas and dispersed into and across the New World?

The first settlement of the New World continues to be a highly controversial issue and is continually fuelled from various research fields such as geology, paleoecology, archaeology, skeletal biology, and genetics (e.g. Greenberg et al., 1986; Neves and Pucciarelli, 1991; Bonatto and Salzano, 1997a,b; Dixon, 2001; González-José et al., 2001a,b; 2008; Schurr, 2004; Zegura et al., 2004; Neves and Hubbe, 2005; Neves et al., 2005, 2007a; Tamm et al., 2007; Wang et al., 2007; Dillehay et al., 2008; Fagundes et al., 2008a,b; Goebel et al., 2008; Meltzer, 2009; Perego et al., 2009; Perez et al., 2009; de Azevedo et al., 2011, 2015; González-José and Bortolini, 2011; Reich et al., 2012; Bortolini et al., 2014; Marangoni et al., 2014; Raghavan et al., 2014a,b; Rasmussen et al., 2010, 2014; Raghavan et al., 2014b; Chatters et al., 2014; among others). The major consensus regarding how and when anatomically modern humans

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first entered the New World is that the Americas were first settled by populations coming from Asia via Beringia, at some temporal window at the end of the Pleistocene (~15–30 thousand years ago) and during the latter stage of the last glaciations, probably following a North-South direction along a Pacific coastal route (e.g. Dixon, 2001; Tamm et al., 2007; Wang et al., 2007; Fagundes et al., 2008a,b; González-José et al., 2008; Reich et al., 2012; but see also a brief review in Marangoni et al., 2014). The agreement begins to fade when attempting to detail the period in which it occurred, the area from which the colonizing populations came, the number of dispersal waves and the routes taken by these migrations (see a review in Marangoni et al., 2014), but also the microevolutionary processes involved. Researchers' views on various aspects of this process differ significantly, probably due to the fact that insights into the peopling of the Americas come from a variety of different types of data and disciplines (e.g. linguistic, paleoecology, archaeology, skeletal biology, genetics) but also because of different interpretations of the evidence. Moreover, recent publications presenting genomic data and population genetic analysis of contemporary Native Americans (Reich et al., 2012) and ancient genomes from early Siberian (Raghavan et al., 2014a) and Native American specimens (Rasmussen et al., 2010, 2014; Chatters et al., 2014; Raghavan et al., 2014b) reopened discussions of the pre-Columbian peopling of the Americas. The new evidence provides valuable information from comparative genetic studies, although a multidisciplinary reconciliation between genotypes and phenotypes, particularly human skull data (González-José et al., 2008; Perez et al., 2009; de Azevedo et al., 2011, 2015; Bortolini et al., 2014), is still needed as a essential step to understanding the evolutionary dynamics of populations occupying the Americas during pre-Columbian times.

Here we will focus on a classical discussion that has dominated part of the debate during the last decades and that includes two apparently mutually exclusive settlement hypotheses emerging from the analysis of skull morphology and molecular genetics (e.g. Single Wave versus Two Components/Stocks models, see a discussion in González-José et al., 2008). The main contrasting evidence coming from genes and morphologies is that the first indicates a single and Asiatic molecular coalescence for all Native Americans (e.g. Merriwether et al., 1995; Bonatto and Salzano, 1997a,b; Santos et al., 1999; Silva et al., 2002; Tamm et al., 2007; Fagundes et al., 2008a,b), whereas the latter points to a dual biological origin of American populations based on a significantly distinct morphology pattern observed between the earliest American populations (*Paleoamericans*) and that of recent Native Americans (e.g. Neves et al., 2003; Neves and Hubbe, 2005; Neves et al., 2007a; Hubbe et al., 2010).

Most molecular-genetics studies during the last twenty years point to a single origin in Northeast Asia (~15,000 BP) for almost all American populations, followed by local diversification (Merriwether et al., 1995; Bonatto and Salzano, 1997a,b; Santos et al., 1999; Silva et al., 2002; Tarazona-Santos and Santos, 2002; Tamm et al., 2007; Fagundes et al., 2008a,b). According to the molecular-genetics view, the initial differentiation from Asian populations was followed by a bottleneck in Beringia during the Last Glacial Maximum (around 23,000 to 19,000 years ago), and a strong population expansion out of Beringia between 18,000 and 15,000 years ago with a rapid settlement of the continent along a Pacific coastal route (Bonatto and Salzano, 1997a; Fagundes et al., 2008b). This pause by the ancestors of Native Americans when they reached Beringia would enable autochthonous mtDNA and Y-chromosome New World lineages to differ from their Asian sister-clades founder lineages. Also, the genetic data suggest more recent bi-directional gene flow between Siberia and the North American Arctic (Tarazona-Santos and Santos, 2002; Bortolini et al., 2002, 2003; Schurr, 2004; Tamm et al., 2007; Wang et al., 2007).

On the other hand, craniofacial morphology observed among some of the most ancient remains in the Americas (*Paleoamericans*) has been described as much closer to African and Australo-Melanesians populations than to the modern series of Native Americans (Neves et al., 2003; Neves and Hubbe, 2005; Neves et al., 2007a; Hubbe et al., 2010). Thus, differences in craniofacial morphology pattern between early and late Americans have been considered abrupt and have been explained by assuming the existence of two separate migration events into the continent: the first representatives are the *Paleoamericans*, having a distinct morphology that might be a retention of the morphological pattern seen in the first modern humans leaving Africa, between 70 and 55 thousand years ago (Mellars, 2006), and that would thus precede the morphological differentiation of East Asian populations that likely occurred during the Pleistocene/Holocene boundary and which would have given rise to all modern Native Americans through a second (more recent) wave into the Americas (Hubbe et al., 2010). This view assume the existence of a supra-population unit of morphological affinity (classically named as *Mongoloids*) joining recent North Asians and late Holocene Native Americans (Neves et al., 2003), with a Middle/Late Holocene survival of *Paleoamerican* morphology reported for Sabana de Bogota, Colombia (Neves et al., 2007b) and Baja California, Mexico (González-José et al., 2003). Thus, the morphology pattern of recent Native Americans [characterized by short and wide neurocrania, high and retracted faces, and high orbits and nasal apertures] is considered as completely different from that of *Paleamericans* [long and narrow crania, low and projecting faces, and low orbits and nasal apertures], and differences between this two morphologies are interpreted as being of roughly the same magnitude as the difference observed between recent Australian aborigines and recent East Asians (Neves and Hubbe, 2005; Neves et al., 2007a,b; Hubbe et al., 2010). However the Two-Component model disregards the significant amount of intermediate morphological variation that is present among Native American groups and places the full range of craniofacial variation under two discrete categories. In this context, there is an emerging view first published by González-José et al. (2008) that aims to integrate evidence from each research field considering the particular nature of change of different data (cultural, genetic-neutral, genetic plus environmental, etc) in order to accommodate the available evidence for each of the chronological phases of the settlement's sequence, and to postulate specific microevolutionary agents potentially responsible for the transition from one phase to the other.

This model (the Recurrent Gene Flow [RGF], González-José et al., 2008) takes into account a founding population occupying Beringia during the last glaciation characterized by high internal diversity in terms of craniofacial variation, mtDNA, Y chromosome lineages, and autosomal alleles. After a Beringian standstill and a posterior population expansion, which could have occurred concomitant with their entry into America, a more recent circumarctic gene flow would have enabled the dispersion (and persistence along circumarctic groups) of northeast Asian-derived characters and some particular genetic lineages from East Asia to America and vice versa (González-José et al., 2008). On the other hand, most modern American populations can be shown to have a mosaic of generalized-derived traits, with only a few displaying the derived extreme also present in northeast Asia (Inuits), and other groups presenting a rather generalized, ancestral morphology (noticeably, modern groups such as the Pericu from Baja California, Aztecs from Central Mexico, and *Paleoamericans* from Lagoa Santa). This model presents a synthetic view in which the main assertions of previous models may not be in serious contradiction with each other but collectively contribute to depict a common picture (González-José et al., 2008). For instance, the Two-Components model is viewed

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