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Genetic studies of the peopling of the Americas: What insights do diachronic mitochondrial genome datasets provide?

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ABSTRACT

The timing of the entry of the first humans into the Americas has been a source of debate for decades amongst archaeologists and geneticists. Here we briefly review the evidence for current hypotheses on the peopling process of the Americas and discuss how ancient mitochondrial DNA can provide a unique temporal perspective. We propose that, in absence of skeletal remains from a proto-Native American population for which DNA shows direct ancestry to modern indigenous lineages, high-resolution diachronic mitochondrial genetics will help refine our understanding of the human dispersal to and occupation of the Americas since the first entry in the continent. The relatively low cost of this methodology may empower indigenous communities and heritage organizations. Ultimately, it would promote the training and support of future research leaders who have a relevant cultural background to offer a fresh perspective on the peopling of the Americas.

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1. Introduction

The peopling of the Americas is a fascinating topic that continues to kindle arguments amongst scholars. The main reason for such debate is the absence of direct biological (e.g., human skeletal remains) or archaeological evidence that can link the direct ancestors of the first peoples to enter the Americas to present-day Native Americans.

Therefore, a number of peopling models have been proposed, and rejected, over the last half century to interpret cumulating data from archaeology, linguistics, paleoanthropology, and genetics. For example, the Clovis lithic technology is evidence for the oldest widespread culture in the American archaeological record (Goebel et al., 2008; Waters and Stafford, 2007). The ubiquity of Clovis sites across North America rapidly led to the long-standing theory that Clovis people were the first humans to settle the continent from Asia (Fiedel, 2017; Goebel et al., 2008; Waters and Stafford, 2007).

Alternatively, the Solutrean hypothesis was proposed to interpret archaeological and genetic data (Bradley and Stanford, 2004; Oppenheimer et al., 2014; Stanford and Bradley, 2012; Straus, 2000; Straus et al., 2005). In this scenario, ancestors of the First

Americans migrated from south-western Europe to north-eastern North America via a trans-Atlantic route, and developed the Clovis culture. However, a large body of data that includes the absence of European ancestry in the genome of a late Pleistocene individual buried with Clovis artifacts (Rasmussen et al., 2014) does not provide strong support for the Solutrean hypothesis (Raff and Bolnick, 2015). More importantly, a growing number of robustly dated pre-Clovis archaeological sites in North and South America show that Clovis people were not the First Americans (Dillehay et al., 2008; Gilbert et al., 2008; Halligan et al., 2016; Jenkins et al., 2012; Joyce, 2006; Overstreet, 2005; Waters et al., 2011).

The Paleoamerican model proposes yet another hypothesis with two distinct waves of migration from Asia (González-José et al., 2008; Hubbe et al., 2010b, 2010a). This model is deduced from reports of contrasting cranial morphological characters between present-day Native Americans and the archaeological record. Some recently extinct Native American populations (e.g., Fuegians from Patagonia and Pericúes from Baja California) and some ancient archaeological specimens from the Americas (Chatters et al., 2014; González-José et al., 2003; Hubbe et al., 2015) share cranial traits with Australo-Melanesians, whereas the cranial morphology of the large majority of present-day Native Americans is similar to that of modern East Asians (González-José et al., 2008; Hubbe et al., 2010b). One interpretation of these observations is that a first

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migration wave derived from an ancestral Asian population that gave rise to Australo-Melanesians and so-called Paleoamericans. Paleoamericans were then replaced by a second migration pulse that originated from a population ancestral to present-day Native Americans. However, this model is challenged by some morphological and genetic data [e.g., (Chatters et al., 2014; Fehren-Schmitz et al., 2015; García-Bour et al., 2004; Manríquez et al., 2011; Perez et al., 2009)], with the most compelling evidence coming from the recent work by Raghavan et al. (2015). In the latter study, the authors did not find a close affinity for cranial morphology between Australo-Melanesians and previously reported Paleoamericans. In addition, the genome-wide data from Fuegians and Pericúes did not support a shared ancestry of Paleoamericans with Australasians.

To date, the convergence of a large body of linguistic, morphological, archaeological, and genetic evidence points to a pre-Clovis arrival from Asia using the Bering land bridge, which connected East Asia and North America during the last Ice Age (Goebel et al., 2008; Greenberg et al., 1986; Hoffecker et al., 2016; Pitblado, 2011; Raghavan et al., 2015; Rasmussen et al., 2014; Reich et al., 2012; Schurr, 2004; Skoglund and Reich, 2016; Waters and Stafford, 2014). Moreover, the genetic data suggest that early populations remained isolated for many generations on their way to the Americas, forming the basal Native American genetic lineages derived from Asian ancestors (Achilli et al., 2013; Battaglia et al., 2013; Fagundes et al., 2008; Kitchen et al., 2008, 2008; Llamas et al., 2016a; Mulligan et al., 2008; Raghavan et al., 2015; Tackney et al., 2015; Tamm et al., 2007). This Beringian Standstill model, initially proposed on the basis of mitochondrial genetic data (Tamm et al., 2007), is strongly supported by paleoenvironmental evidence (Hoffecker et al., 2016, 2014). However, the absence of archaeological record in Beringia led to the hypothesis that the isolation could have occurred in Eastern Asia (Buvit and Terry, 2016; Madsen, 2015; Potter et al., 2017) or even in the Americas (Faught, 2017).

2. Setting the stage

Here, we review the evidence from archaeology, geology, and paleoenvironment that, in our opinion, creates a framework for consilience about the peopling of the Americas from Asia. This evidence is a workable starting point for testing hypotheses about the peopling of the Americas using genetic data.

2.1. Archaeological evidence supports a pre-Clovis entry

The Clovis complex—characterized by lanceolate, fluted projectile points—lasted from ~13,000 to ~12,615 calendar years before present (cal BP), although these dates vary slightly depending on the radiocarbon date calibration methods and the interpretation of the archaeological sites (Waters and Stafford, 2014). The hypothesis that Clovis people were the First Americans is seriously challenged by the existence of several robustly dated archaeological sites with evidence of human activity 1000 to 2000 years before the Clovis period. Monte Verde II, in Chile, is perhaps the most famous pre-Clovis site with direct dates from seaweed as old as 14,220 cal BP (Dillehay et al., 2008). Monte Verde was likely a permanent settlement given the very large number of man-made artifacts and household goods, as well as habitation structures, hearths, and remains of plants and animals used for human consumption (Dillehay et al., 2008). In North America, the 14,490-year-old Schaeffer (Joyce, 2006) and 14,775-year-old Hebior (Overstreet, 2005) sites in Wisconsin, the 14,550-year-old Page-Ladson site in Florida (Halligan et al., 2016), and the 13,815-year-old Manis site in Washington (Waters et al., 2011) all contain butchered animal remains, some of them associated with non-Clovis lithic artefacts.

Even if they were not permanent settlements, these hunting sites provide strong evidence for human presence in the Americas well before Clovis. Finally, the Paisley 5 Mile Point Caves in Oregon (Gilbert et al., 2008; Jenkins et al., 2012) contain numerous non-Clovis projectile points. Most importantly, human coprolites dated at ~14,300 cal BP that contained preserved human DNA represent irrefutable biological evidence of human presence at Paisley 5 Mile Point Caves before Clovis (Gilbert et al., 2008; Jenkins et al., 2012). Even if their validity is challenged (Fiedel, 2017, 2013), the pre-Clovis sites convincingly support an entry of the First Americans into the Americas proper by ~14,800 years ago at the latest. The initial time of entry remains elusive in the archaeological record, but genetic data can be used to infer the chronology of events.

2.2. Archaeological and paleoenvironmental evidence in Beringia

Stone artifacts and woolly rhinoceros foreshafts have been uncovered at the Yana Rhinoceros Horn Site, in extreme north Siberia (Lee et al., 2016; Pitulko et al., 2004). The 32,000-year-old Paleolithic site on the Yana River is evidence that humans were adapted to cold climate and could subsist on hunting in Beringia before the start of the Last Glacial Maximum [LGM; 26,500 to 19,000 cal BP (Clark et al., 2009)]. There is also evidence for human presence in Beringia after the end of the LGM, such as the Ushki Lake sites (~13,000 cal BP) on the Kamtchatka peninsula, eastern Siberia (Goebel et al., 2008), and the Upper Tanana Valley sites (~14,000 cal BP) in east-central Alaska (Holmes, 2001). However, there are no Beringian sites contemporaneous to the LGM period, which could be explained by: (i) the land bridge (most of central Beringia) is below sea level today, and eastern Asia (western Beringia) and Alaska/the Yukon Territory (eastern Beringia) are remote areas, imposing a heavy logistical burden on archaeological field research; or (ii) Beringia was inhospitable for humans at the height of the LGM. The latter point is at least partially refuted by paleoenvironment data supporting a Beringian refugium compatible with lasting human presence at the height of the LGM (Hoffecker et al., 2014). Indeed, the plains of the Bering land bridge—now under the Bering Sea—were covered by shrub tundra and boreal trees (Brubaker et al., 2005), most likely providing wood fuel and sustaining a rich fauna. In addition, southern Beringia seemed to have a relatively high level of plant productivity during the LGM due to the North Pacific oceanic influence that increased moisture (Hoffecker et al., 2016). In theory, the Beringian biome could have easily borne a low-density human population not exceeding a few tens of thousands of individuals for several thousand years (Hoffecker et al., 2016; Llamas et al., 2016a). This evidence strongly supports a Beringian Standstill, during which the gene pool ancestral to modern Native American lineages was formed after isolation from Asian counterparts (Tamm et al., 2007). However, it has been argued that the isolation could have occurred in East Asia (Buvit and Terry, 2016; Madsen, 2015; Potter et al., 2017) or the Americas (Faught, 2017) based on the absence of direct archaeological evidence from Beringia. A comprehensive genetic survey of past and present populations in Beringia, Asia, and the Americas could help pinpoint the exact location of the initial population differentiation that led to the Native American genetic lineages.

2.3. Land routes from Asia into the Americas

The climatic and geological records constrain the timing of the Beringian migration process of the First Americans. First, the Bering land bridge connected Chukotka and western Alaska during a relatively long period of the last Ice Age, between ~30,000 and ~11,000 years ago (Clark et al., 2014; Elias et al., 1996; Hoffecker

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