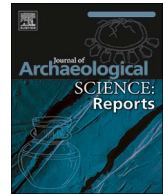




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Ancient maternal lineages in hunter-gatherer groups of Argentinean Patagonia. Settlement, population continuity and divergence

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ABSTRACT

First Patagonian occupation moments have been estimated, through the study of different archaeological sites, between 18,500–14,500 cal BP. There is consensus that Patagonian populations had a hunter-gatherer organization until European contact, featuring low demography, different levels of mobility and in some regions relative geographic isolation. Both archaeological and bioanthropological hypothesis suggest a common population origin for the region, and point that their biological differences would stem from genetic drift, geographic isolation and adaptation to the environment. In this study we analyze HVR-1 mitochondrial sequences from 70 ancient and 306 extant samples from native groups with the aim to test these hypotheses. We observe a southward diversity decrease and a significant genetic differentiation between northern, southern and insular Patagonian groups. In addition, phylogenetic tests indicate a common origin for all populations, despite divergence events that may have occurred in each analyzed region. In particular some haplotypes found in Northern Patagonia suggest the existence of genetic flow from central Argentina and Chile.

1. Introduction

Different disciplines take the occupation and evolution of the human groups that inhabited the Southern Cone of the American continent as their study subjects. (Rothhammer and Dillehay, 2009; Bodner et al., 2012; Prates et al., 2013; Menéndez et al., 2015; Perez et al., 2016; Galland and Friess, 2016; among others). However, archaeology is currently the one that has made most of the contribution to understand the peopling and evolution of the first human groups to occupy the south of the continent, generating debates about their temporality and cultural adaptations (Salemme and Miotti, 2008; Prates et al., 2013; Borrero, 2015; Borrero, 2016; among others). Patagonia has a central role in these discussions, because it possesses several early archaeological sites that demonstrate the diversity of adaptations of hunter gatherer groups to a changing environment during at least the last 15,000 cal BP.

In the last decades, morphological and genetic research have begun to provide information about different aspects of this process, allowing to postulate and contrast different hypothesis about migratory routes, demography, population changes, and ancestor-descendant relations between different human groups (Bernal et al., 2010; Moraga et al.,

2010; Bodner et al., 2012; de Saint Pierre et al., 2012a, 2012b; Motti et al., 2015; Llamas et al., 2016; Postillone, 2016; Galland and Friess, 2016; Crespo et al., 2017a, 2017b; Nores et al., 2017; among others). However, due to the fact that the European conquest of the region caused migratory processes and genetic admixture during the last centuries (O'Fallon and Fehren-Schmitz, 2011; Avena et al., 2012; de Saint Pierre et al., 2012b; Postillone, 2016; Crespo et al., 2017a, 2017b), it seems difficult to study processes of such temporal depth using the information obtained from contemporary urban and rural populations (de Saint Pierre, 2017). For this reason, the study of ancient DNA obtained from archaeological remains has become an important tool, not only to analyze issues related with past demographic dynamics and the possible actions of microevolutive processes, but also to perform a comparison with the lineages present in contemporary native populations (Moraga et al., 2010; de La Fuente et al., 2015; Postillone, 2016; Crespo et al., 2017a, 2017b), allowing us to measure the impact of the last centuries historical changes.

The purpose of this research is to establish the existence of population's differentiation and continuity that could have exist among human groups of the region and infer the microevolutionary processes that could have affected the genetic structure of these populations.

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Finally, the results obtained will be compared with the different peopling and biological variability hypothesis outlined from archaeology and morphology.

1.1. Model from archaeology

Considering archaeological terms, Patagonia can be divided into three macro-regions: a northern one between latitudes 39°30' S and 44° S; a southern one between latitudes 44° S and 52° S (Magallanes Strait); and an insular region, represented by Isla Grande de Tierra del Fuego and archipelagos, between latitudes 52° S and 54° S (Borrero, 2008). The earliest Patagonian site is Monte Verde, with a chronology based on multiple evidence of human activities between 18,500–14,500 cal BP (Dillehay et al., 2015). Whereas the eastern slope has different areas with early dating around 15,500–13,900 cal BP (Prates et al., 2013). In this last region, the central Deseado massif area, the eastern and Magallanes basins are the ones with the oldest temporal depth (Prates et al., 2013).

Borrero (1989–1990) was the first one to propose a peopling model from a biogeographical and metapopulation perspective that depended on environmental productivity and on the spatial and temporal distribution of the archaeological record. He suggests that the Patagonian occupation would have taken place in three phases (exploration, colonization and effective occupation of the space), based on environmental changes, resources and water availability. The Deseado river, Magallanes basin and the North of Tierra del Fuego (still joined to the continent) would have been the first settlements in the Argentinean Patagonia throughout the first phase (Borrero, 1999, Salemme and Miotti, 2008, Prates et al., 2013; among others). The dispersion pattern must have combined groups fission processes with the expansion of hunting radius giving rise to metapopulations, founder effects and evolutionary divergences (Borrero, 1999).

It is throughout the mid and mainly the late Holocene when the archaeological signal rises significantly, this supposes an increase of demography and decreased mobility (Martínez et al., 2013, García-Guraieb et al., 2015, Zubimendi et al., 2015, among a number). Also, some long-distance contacts are found in some regions, evidenced by certain types of raw material and artifacts that link different regions (Gómez Otero and Stern, 2005, Favier Dubois et al., 2009, Pérez and Reyes, 2009, Silveira et al., 2013, among a number).

Recent research based on simulations with radiocarbon and mitochondrial DNA (mtDNA) sequencing data, partly supports these assumptions as it concludes that the first occupation of Patagonia would have probably taken place between 17,000–14,000 cal BP (Perez et al., 2016), with a slow population growth throughout the first millennium, and a faster period throughout the mid Holocene, reaching a maximum approximately 1000 cal BP.

1.2. Biological records of human groups

Until the present, the archaeological record of human remains of the first period of occupation in Patagonia throughout the Pleistocene-Holocene transition is scarce. It is from the mid and late Holocene when this type of record first appears in different sectors of this region (Borrero, 2008).

Lahr (1995) recognized robust cranial features as typical in this region, product of the preserved morphology of its first inhabitants and certain population homogeneity when compared with other groups in the Americas. Later investigations confirmed this morphological trait being Tierra del Fuego groups the most differentiated, possibly due to geographic isolation (González-José et al., 2001; González-José et al., 2002). Genetic drift, random and non-random factors and/or local differentiation processes have been recently postulated as the main modeling mechanisms for biological diversity present in these populations (González-José et al., 2008; Perez et al., 2009; Menéndez et al., 2015). Low demographic density and the relative biogeographical

isolation may have created suitable scenarios for the generation of serial founder effects, which would explain the correlation between biological and geographic distances also found in the analysis of dental pieces from the late Holocene (Bernal et al., 2010). This last model suggests multiple expansions and successive dispersals of small hunter-gatherer groups featuring low demographic densities in fragmented environments, that's why every one of these would only reflect part of the genetic and morphological variation of the original group, thus explaining the morphological variation patterns observed.

Recent cranial morphometric research has tested these hypotheses with the use of 3D computer axial tomography (Galland and Friess, 2016). The groups from Tierra del Fuego proved to be the most differentiated in the continent, with significant differences among the insular groups (Selk'nam, Kaweskar, Yamana) and continental groups. According to the authors, these populations would have a single recent origin and their differences would be explained by drift effect, isolation and adaptation to the environment.

1.3. Model from population genetics

Different lineages have been identified in South American native populations, which would reflect early dispersion in the continent. Subclades defined as D1g, D1j and D4h3a have a Pacific coastal scattering (Perego et al., 2009; Bodner et al., 2012) and are highly frequent in native Patagonian populations, thus showing the entry path of the first people. For the D1j clade, however, a possible origin at the center of Argentina has been postulated, as in the present time it is there where its higher frequency has been found in extant populations and it has also been seen in ancient populations in Cordoba Province, meanwhile gene flow events must not be ruled out (García et al., 2012; Nores et al., 2017). D1g has a wide distribution, whereas D4h3a would seem to be confined to areas located more towards the south, a fact that would prove a larger drift in the south.

Additionally, de Saint Pierre et al. (2012a, 2012b) have conducted a re-analysis of the sequences available in the region and managed to define two additional subclades (B2i and C1b13), which would only be present in Patagonia, thus suggesting a clinal distribution; A2, B2 disappear to the south, as C1 and D1 increase. Different research on skeletal remains of the late Holocene have detected a high frequency of clades C1, D1, D1g and D4h3a (Lalueza et al., 1997; García-Bour et al., 2004; Moraga et al., 2010; de La Fuente et al., 2015; Motti et al., 2015; Raghavan et al., 2015; Crespo et al., 2017a, 2017b), which also suggest the impact of drift as a main micro-evolutionary process in the region. The discovery of clade B2 at the Baño Nuevo 1 site in the Chilean Patagonia, with temporalities close to ca. 10,000 cal BP (Reyes et al., 2012), could indicate the loss or very low frequency of this lineage through time or a sampling bias.

2. Materials and methods

Hypervariable region 1 (HVR-1) sequences of mtDNA from 70 pre-Columbian and historic individuals (see Supplementary material 1.1, Table S1), plus 306 sequences of native extant groups (see Supplementary material 1.1, Table S2) were gathered from the literature, which yields a total number of 376 individuals, covering a time range of ca. 3100 years BP up to the present time (Table 1, Supplementary material 1.1 Tables S1 and S2). They were aligned, polymorphisms were identified and for each sequence the haplotypes were defined (see Supplementary material 1.2). Ancient individuals reviewed were grouped into six populations: Andean northern Patagonia (ANP), coastal northern Patagonia (CNP), Santa Cruz coast (SCC), Chilean archipelagos (CA), North of Tierra del Fuego (NTDF) and Beagle Channel (BC).

Genetic variability was calculated for each population (haplotype number, haplotype and nucleotide diversities) so as to compare diversity in both pre and post-Columbian groups. Variability was also

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