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Towards a reconciling model about the initial peopling of America

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ABSTRACT

The last two decades have seen numerous debates in the field of the initial settlement of America and noteworthy was the disagreement between physical and molecular anthropologists. Recently, it has been pointed out that this discordance could partly originate from the description methods and classification labels used in craniometry, which did not account fairly for the within-sample and within-group variance. From there, a federative model for the initial peopling of America has been designed which could now explain the biological variability found at both the craniofacial and genetic level. This is a major step in the study of the initial settlement of America, which deserved to be highlighted. The present paper recalls the two conflicting models that prevailed for the last 20 years of anthropological studies in America before browsing the newly accepted hypothesis about the origin of the first Amerindians as seen by its authors. Lastly, the article evokes some areas of investigations, which could furnish significant fallouts about the dynamics of the peopling of Americas in the future.

1. Introduction

Since the 16th century, the American continent has always gathered an uninterrupted interest from an anthropological and archaeological point of view. The origin of the ancestors of the present-day Native populations of America – namely Native Americans or Amerindians – was mentioned in the very first times of exploration of the Americas by Jesuit Jose de Acosta (1589) and by French naturalist Georges-Louis Leclerc de Buffon (1749), completed in the 20th century by the use of skeletal and biological investigations in extinct and extent Amerindians. Based on the dental [1], cranial [2], classical (i.e. red cell and protein) genetic systems [3,4], prior anthropological studies about the dynamics of the initial peopling of America highlighted grades of allele frequencies as well as shared biological features between Amerindian and Asian populations, which strengthened Jose de Acosta's assumption which can be summarized as the incoming of the first Amerindians from Asia.

The first interdisciplinary scheme for the initial settlement of America has been proposed in the mid-1980s as elements of linguistics, dental morphology (28 crown and root traits) and genetics (serological genetic systems) [5]. Their theory relied on a convergent classification of the Amerindian languages, dental traits and blood groups and protein genetic systems into three separate groups. Under their view, the present-day Amerindian populations originated from three distinct waves coming from Asia at the Pleistocene-Holocene transition (~12,000–10,000 years before present [YBP]), by way of the now-submerged Bering land bridge, Beringia, that could have emerged by a fall of the sea level of about 120 m from presently during the Last Glacial Maximum (LGM; 21,000–10,000 YBP) [6].

Briefly, Greenberg et al. [5] assumed that a first group of populations would have left Siberia, crossed Beringia and entered the Americas about 12,000 years ago to spread into

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most of the New World. These first Americans, also called Paleoindians, would have introduced the Amerind language family, nowadays widely spoken from North to South America (e.g. Cherokee, Maya or Quechua). Then, the Na-Dene speakers would have entered secondly to inhabit the interior of Alaska, the northern Pacific coast to the southwestern states of USA, Arizona mainly (e.g. Navajo, Apache). Lastly the Eskimo-Aleut speakers would have arrived to occupy the Arctic periphery of America (e.g. Inuktitut). Interestingly, a first entrance into the Americas dated by 12,000 YBP found agreement in previous archaeological evidences from North America. Indeed, by the time of Greenberg et al.'s [5] hypothesis and years after, the fluted stone tool technology named "Clovis" and ^{14}C calibrated by about 11,000 YBP (11,050–10,800 ka BP [7]) was viewed as the oldest human manufacture of America. For the two last decades, Greenberg et al.'s [5] tripartite assumption remained thus the starting point for all subsequent works about the initial colonization of the Americas.

With the advent of improved methods of data exploration and treatment – increasing number of population genetic markers and longer DNA sequences, use of variance/covariance matrices, time divergence estimation, population structure analysis and the Bayesian approach among others – abundant anthropological attempts have scrutinized the morphological and gene diversity found in past and present Amerindians. The main dataset encompasses skull and face remains [8] and two uniparentally inherited DNA: the mitochondrial DNA, or mtDNA, transmitted by women and the non-recombining portion of the Y-chromosome (NRY), only possessed by men [9–11]. Later, additional information was provided by HLA genes [12,13], the X and autosome chromosomes [14,15] completed with archaeological evidences from North, Central and South America, and microbiology studies of bacteria *Helicobacter pylori* [16] and intestinal parasites (i.e. helminths [17]); living forms that co-migrated with the human populations. As expected, undoubtedly clustering of the Amerindian to the Asian populations was found together with an unanimous challenge of Greenberg et al.'s [5] assumption putting forward: (a) a plausible earlier colonization than 12,000 YBP in agreement with the recognition of a pre-Clovis occupation (e.g. Paisley Cave, Cactus Hill, Valsequillo, Taima Taima, Monte Verde, Pedra Furada [18–21]); and (b) controversies about the delimitation of the Amerind/Na-Dene/Eskimo-Aleut linguistic phyla into exactly three distinct biological stocks.

2. The craniometric/genetic discrepancy

The first molecular studies using the maternally inherited DNA (mtDNA) revealed that past and present-day Native Americans belong to five major distinct phylogenetic groups designated haplogroups A, B, C, D, and X, also present in populations from Siberia and parts of Asia [22]. The four American A–D mtDNAs are spread amongst North, Central and South Amerindians belonging to either the Amerind, Na-Dene and Eskimo-Aleut linguistic family as defined by Greenberg et al. [5] while X is restricted to North Amerindians [23]. Relatedness comparisons have showed closer mtDNA genetic similarities amongst the Amerind, Na-Dene and Eskimo-Aleut populations present than with any Mongolian and East Asian ethnic group while coalescence time estimates for the age of the autochtonous mtDNAs indicated a simultaneous occurrence for all five Amerindian female lineages (between 19 and 15,000 YBP [24]). Hence, mtDNA data pointed towards a unique migratory event for all Amerind, Na-Dene and Eskimo-Aleut populations which would have brought all Amerindian founding lineages from Asia, probably before 18,000 YBP [25–27].

Noteworthy are the geographic distributions of the minor X maternal lineage exclusively in North Amerindians (Ojibwa, Navajo, Nuu-Chah-Nulth and Sioux populations) [23,28] and the Clovis lithic culture, also exclusive to North America. Given that X represents ~4% of the European mtDNAs [29] and the resemblance between Clovis and the Solutrean "bay leaf" industry (southwestern Europe; 22,000–17,000 YBP), the possibility of an additional settlement of North America from Europe has risen [30]. Nevertheless, inadmissibility of a putative European ancestry for North Amerindians has commonly been accepted because of the wide 10,000-year chronological gap between the Clovis and Solutrean cultures, dental and many other morphological similarities between Native Americans and East Asians not Europeans, and finally recent studies of the mtDNA that clearly distinguished the European from the Native American founding X lineage, namely X2a [22,31].

For analogous heritability properties to the mtDNA, the NRY represents a very useful tool to trace back the male lineages of the human populations. Former studies of the initial peopling of America using the NRY reported in Amerindians the predominance of one lineage, Q, absent in any African, Asian or European populations [10,32,33]. The Amerindian-specific Q lineage is made of the ancestral Q* haplogroup, the Y-chromosome lineage that could actually reach America, which afterwards derived into the predominant Q1a3a* lineage, which then evolved very locally into the most derived haplogroup Q1a3a1, found in populations from the western part of South America (59% of the Ticuna, Brazilian State of Amazonas, and 10% of the Wayuu, Guajira peninsula, Colombia [32,34,35]). Q and especially its sublineage Q1a3a* represent the majority of the Amerindian Y-chromosomes in North, Central and South America (up to 100% in many populations), belonging to either the Amerind, Na-Dene and Eskimo-Aleut linguistic family of Greenberg et al.'s [5] classification. Besides the Q lineage, [36] detected a second male founder, C*, a very sporadic Y-chromosome haplogroup found in Asian (Korean and Japanese) and Plains Native American populations of North America (Cheyenne and Keres).

Such a distribution coupled with an average age of the ancestral Q* haplogroup estimated at 15,000 YBP [35] fit with the model of a major migratory event into America circa 18,000–15,000 YBP, which is similar to what was observed for the mtDNA [24]. Afterwards, minor gene flows would have occurred between the Northernmost