



Antiquity of mtDNA lineage D1g from the southern cone of South America supports pre-Clovis migration



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ARTICLE INFO

Article history:

Received 3 October 2016

Accepted 2 May 2017

Available online 13 June 2017

Keywords:

DNA mitochondrial

Peopling

Coastal route

ABSTRACT

The southern cone of South America has been an important source of information regarding the early peopling of the Americas. The discovery of the Monte Verde site was revolutionary; it led to wide acceptance of the pre-Clovis hypothesis and its corollary, the coastal migration route. Although numerous additional pre-Clovis sites have been reported in South America, debate continues about the timing of the earliest human migration. Perhaps because of the paucity of very early sites in North America, researchers there are increasingly focused on the genomic evidence.

The mitochondrial subhaplogroup D1g described in 2012 and found in Amerindian populations of southern Chile and Argentina, represents today as Monte Verde did before, an interesting paradox that has not yet received much attention. The age calculated for D1g, between 25,000 and 19,000 cal yr BP is extremely old for a South American mitochondrial subhaplogroup. The anomalous age of this haplogroup does not fit the currently accepted framework for the other mtDNA haplogroups in the Americas. In this article I compare D1g old age with those from other published D phylogenies, using the rho calculation methodology in order to test the reliability of this older age estimate. Might this lineage be evidence for an early pre-Clovis migration?

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1. Introduction

In the complex history of human migrations, it is widely accepted that America was the last continent colonized by humans, most likely from Asia through Beringia (Goebel et al., 2008; Tamm et al., 2007; Powell, 2005). Although many colonization hypotheses for the early peopling have been proposed, two remain the most supported by the scientific community today; the Clovis hypothesis (Tankersley, 2004) and its counterpart, the coastal route, or pre-Clovis migration (Gruhn, 1988). The Clovis hypothesis, predominant in the latter half of the 20th century, was supported by the discovery of Clovis and Folsom sites in central North America (Haynes, 1964). This hypothesis proposes that America was first settled by migrants coming from Beringia who crossed through an ice free corridor between the Laurentide and Cordilleran ice sheets about 13,500 cal yr BP. These migrants quickly populated the contiguous United States, and their descendants then rapidly populated Central America and reached southernmost South America by 12,800 cal yr BP (Haynes, 1964). In the years since the

discovery of the Clovis and Folsom sites, many additional Clovis-related sites have been found, making the Clovis complex, with its distinctive lithic, bone, and ivory tools, one of the best-represented cultural groups in North America, (Tankersley, 2004; Waters and Stafford, 2007).

In 1989 Dillehay reported archaeological materials from Monte Verde, in southern Chile, that dated older than any Clovis site. This discovery shocked the archeological world; for the first time the status of the Clovis people as the first American migrants was seriously questioned. Monte Verde offered support for the previously proposed alternative hypothesis (Fladmark, 1979; Gruhn, 1988) that envisioned an early entry of migrants by a coastal route along the Pacific Ocean. Besides its older age, the lithic assemblage discovered at Monte Verde also reinforced the idea of a pre-Clovis migration because they show no affinities with the characteristic Clovis lithic industry. Additional ¹⁴C dates for t, for Monte Verde II indicate a calibrated age of ca. 14,100 yr B.P. (Dillehay et al., 2008).

After Monte Verde, other sites with distinct non-Clovis lithic industries have been reported. However only the sites with ages younger than ~15,500 cal yr BP have wide support from the scientific community (e.g., Waters and Stafford, 2013). All sites older than ca. 16,000 cal yr BP, such as Cactus Hill, La Sena, Lovewell,

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Topper, Tlapacoya, or Pedra Furada, have been questioned for different reasons: the possibility of post-depositional mixing; secondary association of dated charcoal and artifacts; or of the dubious anthropogenic character of the putative artifacts (Haynes, 2002, 2005; Waters et al., 2009). So, all the pre-Clovis sites with supported ^{14}C dates are roughly contemporaneous with Monte Verde. In North America, these include Debra L. Friedkin, 15,500 cal yr BP (Waters et al., 2011); Meadowcroft Rockshelter, perhaps 15,200 yr BP (Adovasio and Carlisle, 1988); Schaefer and Hebior, ca 14,800 yr BP (Joyce, 2006); Bluefish Caves, 15,000 yr BP (Cinq-Mars, 1979), Page-Ladson, 14,500 yr B.P. (Halligan et al., 2016), and Paisley Caves, ca. 14,300 yr BP (Jenkins, 2007; Jenkins et al., 2013). In South America, besides Monte Verde, sites dated earlier than 14,000 yr BP include Huaca Prieta in coastal Peru, ca. 14,200 yr BP (Dillehay et al., 2012) and Arroyo Seco 2 in Argentina, with an ostensibly human-modified bone dated recently to ca. 14,100 yr BP (Politis et al., 2016). Very recently Bourgeon et al. (2017) dated human presence in Bluefish Cave at ca. 24,000 yr BP. If this date is later confirmed, the problem of the contemporaneous dates between North and South America archeological sites could be dismissed.

Apart from the similar ages of both North and South American archeological sites, the genetic evidence provided by mitochondrial DNA (mtDNA) has become critical for those authors who support pre-Clovis ages for settlement of the Americas (Fagundes et al., 2008; Schurr, 2004). Mitochondrial DNA is a maternally inherited, small, circular molecule frequently used in studies of human population history. Unlike nuclear DNA, the non-recombinant mtDNA allows the reconstruction of molecular phylogenies once the 16,569 base pairs of the genome are sequenced. The improved techniques of the last decade have enabled the complete sequencing of thousands of mtDNA genomes (mitogenomes), resulting in a very complete worldwide phylogeny, with a complete description of haplogroups (named with letters from A to V), sub-haplogroups and haplotypes of populations from all continents (www.phylotree.org). In the Americas, four major continental haplogroups (named A–D) have been defined, as well as a minor North American haplogroup named X (Bailliet et al., 1994; Forster et al., 1996; Horai et al., 1993; Torroni et al., 1993). All A–D mtDNA lineages have Asian counterparts, confirming previous findings of the ancestral origin of the Native American population in Asia. For X haplogroup, instead, a close molecular counterpart for specific American X2a has not been found in Asians, suggesting that its X2 ancestor became lost in Asians after entry in Beringia, most probably because of genetic drift (Perego et al., 2009).

In recent years, in parallel with the refinement of the worldwide mtDNA phylogeny, the resolution of Native American-specific haplogroups has improved. Today, the overall number of recognized founding maternal lineages has gone from just the five mentioned before to a current count of 15 (Perego et al., 2010). Among these, seven haplogroups – A2, B2, C1b, C1c, C1d, D1 and D4h3a – are pan-American, as they are distributed across the double continent (Bandelt et al., 2003; Behar et al., 2012; Fagundes et al., 2008; Schurr and Sherry, 2004; Tamm et al., 2007), while the remainder are less frequent and generally are restricted to North America (A2a, A2b, C4c, D2a, D3, D4e1, X2a and X2g) (Fagundes et al., 2008; Kashani et al., 2012; Kumar et al., 2011; Malhi et al., 2010; Mizuno et al., 2014; Perego et al., 2009; Schurr and Sherry, 2004). Other molecular phylogenies have been completed for the geographically specific haplogroups in South America, C1b13 and B2i2 (de Saint Pierre et al., 2012b), D1g and D1j (Bodner et al., 2012).

As for the pan-American haplogroups, they all reveal, with the exception of C1d, entry times estimated as 15–18 thousand years ago (kya); these ages are too old to accommodate the Clovis-first hypothesis but instead offer support for the proposed coastal route and migration just after the LGM (Rothhammer and Dillehay,

2009). The geographically specific clades have a time range of 11.3–19.7 kya. The wider time range is expectable, because specific demographic histories can have implications for the lineages' ages. However, one geographically specific sub-haplogroup, D1g, has an older age than all of the pan-American haplogroups. Haplogroup D is one of the better-characterized lineages in the literature, represented in present-day populations throughout northern, eastern, and central Asia and America. It evidently originated around 50–30 kya in eastern Asia, from whence D-bearing group subsequently expanded northwards to southern Siberia, and then farther into northern Asia and finally into the Americas (Kong et al., 2003; Metspalu et al., 2006). In current populations, the oldest D lineages are present in the eastern Asia. This haplogroup has two principal branches, which reflect major migrational movements; D4, which is spread all over East Asia, Southeast Asia, Siberia, Central Asia and America (in the form of derivate lineages D1, D2a, D3, and D4h3) and D5/6 which is found mainly in East Asia and Southeast Asia, with minor frequencies in Siberia, Central Asia and India (Derenko et al., 2010; Tanaka et al., 2004; Zheng et al., 2011).

Bodner et al. (2012) analyzed and described the D1g sub-haplogroup together with D1j, both geographically restricted to the southern cone of South America. In view of their apparently similar distribution, the authors minimized a number of issues such as the difference of their ages (D1g is ~4.6 kyr older than D1j) and their differing geographic locations in the native populations (D1g in southern Chile–Argentina, D1j only in central Argentina). Interestingly, Bodner et al. proposed a single migration model for both clades; however, in doing so they ignored the older age of D1g and the further implications that this could have for the peopling of the Americas.

My aim in this article is to reanalyze the D1g phylogeny with an updated version (de Saint Pierre et al., 2012a), and to apply the evidence to the early peopling scenario. For this purpose, I will compare the age of D1g with those of other published D phylogenies. I intend to address the reliability of this older age estimate for a geographically restricted lineage and the implications it could have for the dating of the earliest peopling of South America.

1.1. Methodology

The D1g phylogeny was first published by Bodner et al. (2012), but later de Saint Pierre et al. (2012a) published an updated version, adding three new mitogenomes from Chilean Amerindian populations. The construction of the phylogeny was performed by hand using the polymorphisms shared by individuals to construct clades, following the maximum parsimony criterion. The mutational site 16519 was not taken into account because it was considered highly homoplastic (Soares et al., 2009). The ages of D1g and other D clades were estimated by means of calculating the rho (ρ) index. The statistic rho, as an approach to molecular dating, was first proposed by Forster et al. (1996) and it is defined as the average number of polymorphisms l observed along m unique lineages (weighted by sample size) stemming from a given ancestral node in a resolved genealogical tree. The confidence intervals on the obtained date can be derived from the expected variance of ρ (Saillard et al., 2000). After rho methodology was criticized by Cox (2008), Soares et al. (2009) proposed a corrected rho-based molecular clock which has been used extensively for the calculation of divergence ages of mitochondrial phylogenies. For the other D haplogroups used in the comparison (see Table 1 for references), the ages originally estimated by authors were not used; instead, they were recalculated using the same methodology described before, in order to avoid problems associated with particular modes of estimation. In Table 1 are listed the re-estimated divergence ages. Rather than resuming the debate about the methodology itself, with this exercise I intend to explore the ages of other D mitochondrial haplogroups and to

Table 1
Divergence times of haplogroup D mitochondrial phylogenies.

Haplogroup	Date ^b (kyr)	reference
D4b ^{a,c}	30.8 ± 13	Volodko et al., 2008
D4e ^{a,c}	24.7 ± 8.6	Volodko et al., 2008
D2	10.4 ± 5.9	Kumar et al., 2011
D2	9.8 ± 5.9	Derenko et al., 2010
D2a	8.9 ± 6.9	Derenko et al., 2010
D4h3a	17.6 ± 3.7	Perego et al., 2009
D1g	22 ± 7.7	de Saint Pierre et al., 2012a
D1j	16.7 ± 9.4	Bodner et al., 2012

^a With a Japanese cluster.
^b Age estimates using the corrected molecular clock proposed by Soares et al. (2009).
^c The names don't match with those from the article because they were changed for those names in the phylogeny.

examine the D1g clade in a broader context, to determine if this methodology regularly produces over-estimated ages.

2. Results and discussion

Haplogroup D1g was described in 2012 in two articles; first, Bodner et al. (2012) published the complete phylogenies of D1g and D1j using Chilean and Argentinian urban samples obtained from the Sorenson (SMGF) Database (today maintained by AncestryDNA since its acquisition of SMGF). Shortly afterwards de Saint Pierre et al. (2012a) published a populational analysis of the D1g haplogroup within native populations, using the hypervariable region of mtDNA. However, a complete phylogeny of D1g, using Bodner's D1g sequences plus the three additional samples, was included in

the supplementary information. Each article reached a different conclusion with respect to D1g; Bodner et al. propose a common migration route for D1g and D1j, while de Saint Pierre et al. propose a shared migration route for D1g and B2i2, but not for D1j since this haplogroup is absent in Chile. This disagreement might be explained by the different sources of the analyzed samples; urban dwellers from Chile and Argentina in Bodner's study, and rural natives from Chile and Argentina in de Saint Pierre's. While the use of urban samples to analyze mitochondrial haplogroups can be very useful where it is difficult to obtain native samples, one must be extremely cautious in analyzing the results. Because of the massive migrations from rural world to cities in the Americas over several centuries, it is very difficult to determine the original places of origin of urban haplotypes, which could generate inaccurate population models. In Bodner's article, this lack of geographic precision led them to confuse the locations of D1g and D1j. A more cautious observation of native population frequencies reveals that D1g is restricted to populations in the south of Chile and Argentina; it occurs in high proportions in Mapuche, Pehuenche, Huilliche and in minor frequencies in Patagonian populations, the Yamana, Aoni-kenk and Kaweskar (Moraga et al., 2000; Garcia-Bour et al., 2004; de Saint Pierre et al., 2012a). In contrast, D1j is found in north-central of Argentina but is virtually absent from Chile (García et al., 2012).

The early divergence age estimated for D1g has been largely ignored and inadequately discussed. Bodner's paper reports ages of about 18.3–19.7 kyr, according to two different methods used for age calculations, maximum likelihood and rho, respectively. Interesting, when one adds to the D1g phylogeny the three new sequences reported by de Saint Pierre Fig. 1, the rho estimated age

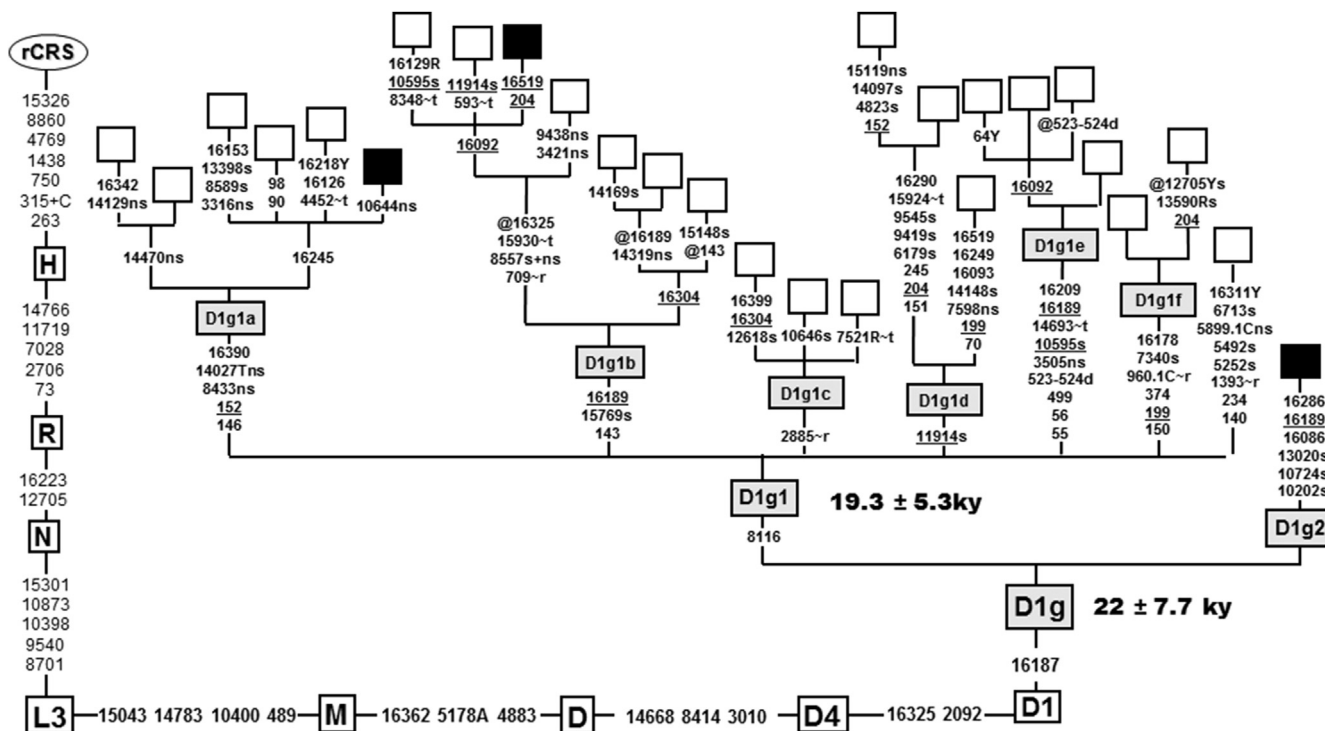


Fig. 1. Phylogenetic tree of southern South American haplogroup D1g. This tree includes 23 sequences reported by Bodner et al. (2012) and 3 complete mtDNA sequences from de Saint Pierre et al. (2012a), and illustrates subhaplogroup affiliations. The position of the revised Cambridge Reference Sequence (rCRS) (Andrews et al. 1999) is indicated for reading off sequence motifs. All SNPs and indels are shown on the branches except for cytosine insertions at np 309. In the case of transversions, insertions, or heteroplasmic mutations, the base is indicated according to the IUPAC nucleotide code. The prefix@ indicates the reversion of a mutation occurring earlier in the phylogeny. The suffixes "s" and "ns" indicate synonymous and nonsynonymous substitutions, respectively, while "t" and "r" indicate affected positions in tRNA and rRNA loci, respectively. Recurrent mutations within the phylogeny are underlined. White squares are Bodner et al. (2012) sequences, black square are from de Saint Pierre et al. (2012a). Coalescence times shown are rho estimates, and have been obtained by including all sequence changes (except 16519, 16182C, 16183C and 16194C) from the respective root according to Soares et al. (2009).

increases from 19.7 to 22 kyr. The explanation for this is that one of the new samples, a Yamana, lacked one of the two basal polymorphisms reported in Bodner's phylogeny; site 8116. Due to its absence, in the new phylogeny the polymorphism 16187 is the only basal one for D1g. Remarkably, no other D1g individual without the 8116 mutation has ever been found, except the aforementioned Yamana (see de Saint Pierre et al., 2012a, pp 2). This can be explained by the biological and cultural factors of the population in which this haplotype was found. The majority of the Amerindian D1g-8116 population (Mapuche, Pehuenche and Huilliche) is located near from Monte Verde area, between 38° S and 40° S. The Yamana, although part of the same population substrate, are in fact very isolated geographically from the rest of the D1g population (by ~1000 km). They were marine hunter-gatherers who inhabited one of the most isolated and climatically challenging places on earth, the fjords of Tierra del Fuego. The vast extent of the territory covered by D1g populations and the antiquity of the migration process might explain the conservation of an old and rare D1g haplotype in one population and its complete absence from the rest. Archeological data show that Patagonia was populated very early, beginning with Monte Verde (14,200 cal yr BP) and Arroyo Seco 2 (14,100 yr BP). The rest of Patagonia was occupied after 12,900 yr BP (Miotti and Salemme, 2004; Steele and Politis, 2009) and Tierra del Fuego was completely settled by 9000 cal yr BP as represented by the site of Tres Arroyos (Massone, 1987). This chronology allows enough time for genetic drift to act and is concordant with a model of the phylogeny of Patagonian D1g as the result of a very old migration and peopling process.

Although there is widely accepted evidence of the early settlement of Patagonia by ca. 14,000 cal BP, these archeological dates are still ~5000 years later than the estimated molecular age of the D1g clade, and they are still too young to fit the calculated age of arrival of D1g in the Patagonia. This inconsistency might be attributed to flaws in the molecular estimates, which are less reliable than direct dating of artifacts or skeletal material. The inaccuracy of molecular dates based on assumed constant mutation rates has been discussed by many researchers (Fu et al., 2013; Green and Shapiro, 2013; Ho and Larson, 2006; Loogvali et al., 2009; to name just a few). Molecular age estimates must be derived from a nucleotide substitution rate; various studies have employed quite different rates, resulting in very discordant ages. As an example, with respect to early peopling of the Americas, a single data set has produced ages differing by around 5000 years only because different mutation rates were used (Fagundes et al., 2008; Ho and Endicott, 2008). However, despite criticism of molecular dating relative to archeological dating, the molecular clock has proved to be extremely valuable in imposing credible chronological frameworks on peopling events that would otherwise be difficult to date. In America, given the ostensibly similar dates obtained for archeological sites both South and North America, molecular dates appear roughly accurate and therefore have assumed pivotal importance in discussions role respect of the earliest peopling.

Of the phylogenies analyzed (Table 1), the oldest age, of 30.8 kyr, correspond to the D4b haplogroup which is found mainly in Siberian populations but also in a Japanese cluster (it was also described in one Canadian Inuit). This divergence age is consistent with a hypothesized date for the peopling of eastern and northern Asia. The D4e haplogroup, which is also Asiatic-American, has an age of 24.7 kyr. This lineage has mainly Siberian and Japanese clusters, but also has a greater presence in North American populations belonging to the sub-clade, D2a. This age, slightly lower than that of D4b, is also consistent with the origin of a hypothetical ancestral population that ultimately would be the source of different populations found today. The last Asiatic-Amerindian lineage analyzed, D2, has a notably lower divergence age than those of D4b and D4e.

This clade is more restricted; it is found in Siberians in Asia and Aleuts and Eskimos in America. Its age, ~10 kyr, is probably associated with a later migratory event in the Arctic. There is agreement that Aleut, Eskimo and Na-Dene populations descend from later, different migrations, after the one that gave rise to the Native Americans south of Canada (Reich et al., 2012; Flegontov et al., 2016).

Of the exclusively Amerindian haplogroups, D4h3a has an age of 17.6 kyr. This is a good candidate to date the early peopling, since considerable evidence has shown it to be an ancestral haplogroup. D4h3a has been recovered from the late Pleistocene (12,707–12,556 cal yr BP) Anzick child (Rasmussen et al., 2014) and from a skeleton of an early Holocene individual from Alaska (Kemp et al., 2007), which is empirical evidence of the presence of this lineage in Paleoamericans. Also, D4h3a has a wide geographic distribution, being found low frequencies in populations across the continent, including the most southern native populations, the Patagonians (de Saint Pierre et al., 2012a; Moraga et al., 2010).

Finally, there are the Southern Cone-restricted haplogroups D1j and D1g. The age of D1j is 16.7 kyr. Today this haplogroup has a very restricted location in the north of Argentina (García et al., 2012), although it was reported in an ancient Taino from Venezuela (Lalueza-Fox et al., 2001). So, although today D1j is restricted only to Argentina, it could be part of an ancient continental migration wave that peopled the eastern side of the Andes Cordillera (Rothhammer and Dillehay, 2009). There is some archeological evidence of early occupation of this part of South America, e.g., Taima-Taima in Venezuela, perhaps at ca. 16,000 cal yr BP (Bryan, 1973), Pedra Furada and other sites in northeastern Brazil, perhaps pre-dating 40,000 cal BP (Santos et al., 2003) Arroyo Seco 2 in Argentina, arguably as old as 14,100 yr B.P. (Politis et al., 2016).

In comparison to the previously discussed haplogroups, the divergence age for D1g (22 kyr) appears too old, even considering that the rho methodology may have produced somewhat over-estimated divergence ages. In this regard, it must be noted that the ages calculated by Behar et al. (2012) for these haplogroups are much more recent: 23,530 (+2137) for D4b, 18,606 (+3586) for D4e, and 12,954 (+2580) years for D4h3a. As Fiedel notes (this volume), selection of a different, faster mutation rate could radically reduce the ages of D1g and D1j, even to fit within the Clovis/Fishtail-first chronological framework he advocates. Nevertheless, I still think the rho-based chronology is reliable, and I wish to further explore its possible ramifications.

The archeological evidence shows that the Southern Cone was effectively settled at least by 14,100 cal yr BP (Dillehay et al., 2008), but that date is still separated by ~7000 yr from the rho-estimated origin date for the D1g clade. However, even though D1g is restricted today to Patagonian populations, this may not always have been the case. D1g perhaps could have originated farther north of its present-day location and simply by genetic drift, it may have disappeared from the rest of the continent. Something similar seems to have happened to the D4h3 clade, which was apparently much more widespread in the early Holocene (Lindo et al., 2016; Diaz-Matallana et al., 2016). Interestingly, Patagonian populations have some particularities relative to other Amerindian populations that suggest that they may be direct descendants from a coastal Paleoamerican migration and thus good candidates to examine for genetic evidence of the first migration. Morphologically, cranial studies suggest a greater affinity between Patagonian populations and Paleoamericans than is seen in other recent Amerindians; this has been interpreted as the result of long isolation with consequent retention of ancestral traits (Lahr, 1995; Gonzalez Jose et al., 2001). Patagonian languages are also enigmatic. Various authors have classified the Selk'nam, Yamana and Kaweskar languages as isolates divergent from all other Native American languages, (Civallero,

2008; Sanchez, 1993; Viegas, 2005). Traditionally, the Mapuche language, Mapudungun, has been considered a branch of the Andean stock; however, an analysis by Viegas (2005) overturns this hypothesis and shows that it is also an isolate. With respect to their genetics, Patagonian populations also have high frequencies of D4h3a (de Saint Pierre et al., 2012a; Moraga et al., 2010), which linked them to the North American Paleoamericans (Rasmussen et al., 2014; Lindo et al., 2016). Patagonian populations may have retained ancestral traits from the first migrants that were lost in other contemporary populations; D1g could be part of this legacy and thus an ancestral haplogroup, notwithstanding its limited geographic distribution.

This analysis does not prove that the estimated age of 22 kyr for D1g is accurate; nevertheless, to fit the D1g evidence within a peopling model, one may propose a scenario in which the first migration to America occurred much earlier than most researchers currently consider (e.g., Potter et al., this volume). However, how much earlier might this first migration have been? A recent analysis of ancient South American mitochondrial haplogroups by Llamas et al. (2016) dated the first migration south of the ice sheets to ~16 kyr cal BP. This scenario rules out Clovis as the first migrants, but it is not early enough to explain the antiquity of D1g. Recently, a study by Perez et al. (2016) placed the start of Patagonian settlement between 18 and 16 kyr B.P., which is more congruent with the ancient origin of D1g proposed here, but contradicts the age calculated by Llamas et al. (2016). Genetic anthropologists have generally accepted archaeologists' relatively conservative interpretation of the evidence, which puts first peopling south of the ice sheets around 16 to 15,000 cal BP (e.g., Waters and Stafford, 2013). To accommodate both the Anzick genome and the archaeological record, they postulate a migration to South America just barely early enough to account for the occupation of Monte Verde ca. 14,200 cal BP. Researchers have not yet acknowledged the profound implications of new archaeological evidence reported from the vicinity of Monte Verde (Dillehay et al., 2015): stones interpreted as artifacts, associated with charcoal assumed to represent anthropogenic fire, date from at least 18,500 cal yr BP, and possibly as early as 25,000 cal BP. These putative remains of human activity appear no less convincing than most of the widely accepted materials from MV II. A date of ca. 18,500–25,000 cal BP for human occupation of southern Chile would, of course, fit perfectly with my proposed chronology for appearance of the D1g clade.

A topic not often considered explicitly in discussions of early peopling is the likely rate of advance of migrants. A feasible rate must underlie any realistic scenario. So, how much time would be necessary for migrants to cross the ~14,000 km that separates Monte Verde from a potential entry point in Beringia? Henn et al. (2012) propose a rate of 0.5 km/yr, taking into account the archaeological dating of the Out of Africa expansion from its origin to its conclusion: a route of 25,000 km over a period of 50,000 yr. Rasmussen et al. (2011), in an article about Asian dispersal, allow 12,000–15,000 years for the journey of ~11,000 km between south Middle East to Australia. Although they never actually calculate a possible rate of advance for this migration, a simple estimation would give us 0.9–0.7 km traveled in a year. Using an estimated rate of advance of migration based on these two examples, the time required for migrants to arrive at Monte Verde ca. 14,100 cal BP is at least 14,000 yr, which should give a potential time of 28,000 cal yr BP for the beginning of American migration. Most researchers would doubtless regard this potential age as too early. Both the known archaeological record and the molecular dating recently proposed by Llamas et al. (2016) allow only about ~2000 yr to reach Patagonia. However, to make this journey in 2000 years, the American migrants must have advanced at a rate of 7 km/yr, which is between 8/10 times and 14 times faster than the rates of

advance for Eurasian migrations inferred from the data of Rasmussen et al. and to Henn et al., respectively. *Homo sapiens* were moving into already occupied territories in Eurasia, which would surely have affected the speed of their expansion. While American migrants could have moved much more rapidly into an uninhabited continent, I consider 7 km/yr as too fast to be realistic. Doubling the duration of the Beringia–Patagonia journey to ca. 4000–5000 years, gives a rate ~4/5 time faster than the Middle East–Australia migration, so, it is still high but more realistic. Fix (2005) in a computational simulation model gave 3000 years for the spread of the founding lineages through North America, a rapid dispersion but consistent with the early peopling model I propose.

In the scenario supported here, the first migrants would have traversed the Pacific coast of the Americas prior to 21,000–20,000 years ago. Recent reports provide archaeological evidence of marine adaptations in Hokkaido, Japan, 24,000 yr ago (Otsuka, 2016), and in Okinawa at 35,000 yr ago (Fujita et al., 2016). Therefore, an effective coastal adaptation by the first migrants can be realistically projected (see Faught, this volume). A continental interior route or any variant of the Clovis-first hypothesis is dismissed here in view of the absence of an ice-free corridor between the ice sheets at LGM (Mandryk et al., 2001; but see Dawe & Kornfeld, this volume). In my preferred scenario, the Clovis people would have been one of the first cultural groups that developed *in situ* in America, but they were derived from some early coastal group that eventually ventured into the interior, while others continued on to southern territories.

Acknowledgments

I would like to thank the late Professor Donald Jackson (†), my first contact with the archeological world. My thanks to Drs. Julie Morrow and Stuart J. Fiedel, for organizing the “After Anzick” symposium in the SAA 81st Annual Meeting, and for all their collaboration during the writing process for this manuscript. Finally, thanks to the Universidad de Chile VID project for granting me the funds to attend the SAA 81st Annual Meeting (Orlando, Florida - 2016).

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