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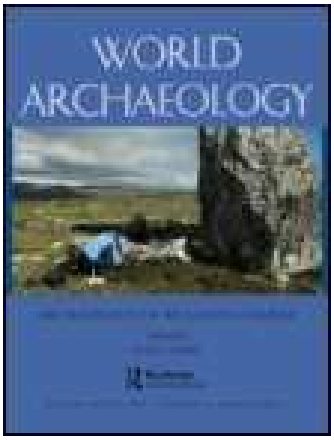

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Solutrean hypothesis: genetics, the mammoth in the room

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Solutrean hypothesis: genetics, the mammoth in the room

Stephen Oppenheimer, Bruce Bradley and Dennis Stanford

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Abstract

The Solutrean hypothesis for the origin of the Clovis archaeological culture contends that people came from south-western Europe to North America during the Last Glacial Maximum. This hypothesis has received numerous critiques, but little objective testing, either of cultural or genetic evidence. We contest the assertion that there is NO genetic evidence to support this hypothesis, and detail the published evidence, consistent with a pre-Columbian western Eurasian origin for some founding genetic markers, specifically mtDNA X2a, and some autosomal influence, found in ancient and modern Native American populations. The possibility that the inferred pre-Columbian western autosomal influence came more directly than through Siberia is not even considered in such studies. The mtDNA X2a evidence is more consistent with the Atlantic route and dates suggested by the Solutrean hypothesis and is more parsimonious than the assumption of a single Beringian entry, that assumes retrograde extinction of X in East Eurasia.

Keywords

Archaeogenetics; migrations; Solutrean hypothesis; Palaeo-Americans; mtDNA; aDNA.

Introduction

In the past decade there has been a significant shift in our general understanding of how, when and by whom the Americas may have first been 'settled'. We have gone from a relatively simple model of a group of Siberian hunters following large animals into the North American continent and marking their presence with a distinctive set of artefacts and behaviours (Clovis First) to the proposition that there were earlier peoples that may have come from different places at different times (Collins et al. 2013). That there were people in the Americas before Clovis (13,500–12,800 BP), is now generally accepted as proven (e.g., Gilbert et al. 2008). What is still very contentious is who these people were and where they came from. There is still a tendency to

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emphasize a one route entry model, specifically from Northeast Asia (single or multiple, coastal and/or inland). Yet these hypotheses have yet to be well articulated. An additional route has long been proposed, which suggests that Pleistocene people came to the Americas not only from north-eastern Asia but also across the Atlantic from south-western Europe during the last glacial maximum circa 22,000–17,000 BP (Bradley and Stanford 2004; Stanford and Bradley 2012). While this proposition has been clearly presented as a hypothesis (Stanford and Bradley 2012), it has elicited strong opposition, based on some specific critiques, both of the ideas and evidence (Straus, Meltzer, and Goebel 2005; Eren et al 2013). There have been four main 'objections': (1) the distance between the proposed origin point (the region where the Pyrenees meet the Bay of Bisque) and the entry point in what is the now submerged Grand Banks off of Newfoundland; (2) the *perceived* difficulty of making a North Atlantic crossing during the LGM; (3) the time gap between the originating archaeological culture (Solutrean) and Clovis; and (4) the claimed lack of genetic evidence of this proposed founding population. There have of course been other challenges to the model, such as the suggested dissimilarities between the artefact assemblages (Straus, Meltzer, and Goebel 2005), etc. Some of these are published debates and will rightly continue to be points of discussion. This article is specifically focused on the issue of the genetic evidence, based mainly on the long-standing, mitochondrial evidence for the anomalous phylogeography of Native American haplogroup X2a and its most recent common ancestors in West Eurasia and North Africa (data in Reidla et al. 2003; Fernandes et al. 2012). This evidence is phylogeographically most-parsimonious with a specific additional Pleistocene West Eurasian entry to Northeast America.

But we also discuss recent analyses, here, that we feel have either: (1) ignored that possibility (e.g., Reich et al. 2012); or, (2) led to over-interpretation of evidence to reject it (Fagundes et al. 2008; Hooshiar Kashani et al. 2012; Rasmussen et al. 2014), or (3) have interpreted their own/new autosomal evidence for pre-Columbian, West Eurasian influence in the Americas, *assuming* it came in via Beringia, without formally testing that route against the alternative Atlantic route (Rasmussen et al. 2014; Raghaven et al. 2014; Patterson et al. 2012).

Archaeological discussion

Recent archaeo-genetic developments discussed here include genetic-inference claims of three Late Pleistocene human remains (two skeletal and one faecal) in Siberia (Mal'ta), Oregon (Paisley Cave) and Montana (Anzick Clovis Cache). While our focus is on the DNA results, a few comments about their archaeological contexts are in order. The Mal'ta site (Raghavan et al. 2014) has been studied off and on since the 1920s and, based on the dates and artefact assemblages, especially the mobiliary art, it may be interpreted as related to the Gravettian, which spread from West into Central Eurasia, west of Lake Baikal. That the aDNA results from the single Mal'ta individual in Central Eurasia show some connections to West Eurasia, in having a basal U mtDNA haplotype and a Y haplotype basal to R is therefore of no particular surprise. That there are also autosomal traits shared with Native Americans is also not unexpected since Mal'ta is indeed in East Eurasia (Fig. 1). However, the Mal'ta remains, at ~24 ka, are geographically closer to the origins of the Gravettian in Eastern Europe than they are to the Bering Strait (Fig. 1). That the Mal'ta individual has something important to contribute to the debate is without question, but the interpretation that the pre-Columbian West Eurasian

admixture (14 to 38 per cent) into Native Americans (Raghavan et al. 2014) that they estimated, could only have entered the Americas via Beringia rather than by some other route, e.g., trans-Atlantic, seems unsubstantiated. The latter route was not mentioned let alone tested/excluded as a model in that analysis. In any case, there is no established Western Eurasian archaeological trail east of Mal'ta, and into Alaska (as implicit in the archaeo-genetic Upper Palaeolithic route claim in the Mal'ta paper), early enough or archaeologically congruent enough to be ancestral to the older-than-Clovis cultural remains in eastern North America (Collins et al. 2013). The other site mentioned (Afontova Gora) is even further west than Mal'ta and Soviet researchers interpreted that if anything the directionality indicated by Mal'ta to Afontova Gora is to the northwest not toward Beringia.

The mtDNA results (A2 & B2) of the analysis of older-than-Clovis (circa 14,500 BP) reported human coprolites from Paisley Cave in Oregon clearly show East Asian affinities (Gilbert et al. 2008) consistent with re-calibrated estimates for the ages of those branches (Soares et al. 2009). This is also supported by the non-Clovis archaeological materials that have been found associated with them. How this may or may not relate to the origin(s) of Clovis remains to be debated and cannot be asserted.

Finally, we have some real concerns about how the Anzick Cache results (Rasmussen et al. 2014) have been used to support a single western entry, and more specifically how the 'genome analysis' has been used to decide that the study 'refutes the possibility that Clovis originated via a European (Solutrean) migration to the Americas' (Rasmussen et al. 2014, 228). We are not challenging the aDNA results but we do have concerns about the way they have been over-interpreted towards one single migration model (see below) and the confident representation of the site archaeology and stratigraphy. We question the interpretation that the analysed human remains 'were found in direct association' with Clovis artefacts (Rasmussen et al. 2014, 225). We have two concerns. First, the association was not confirmed by controlled archaeological excavation and recording. A subsequent archaeological investigation of the site did not confirm the association (Taylor 1969, 149). While a later site examination also found no intact deposits, and other arguments were used to assert an association (Owsley et al. 2001, 117–18). Second, the directly dated human remains (14c cal 'average' 12,707–12,556 BP) and Clovis antler artefacts (14c cal 'average' 13,039–12,763 BP) (Rasmussen et al. 2014) yielded non-overlapping dates (at 2 sigma [95.4% probability]) indicating that the artefacts are older than the person. At a minimum there is a 56-year gap but it could be as much as 483 years. To simply say that the age difference was because the artefacts were heirlooms is unsupported speculation and assumes that the 56-year gap is the best estimate. However, even if a direct association is accepted, this still doesn't demonstrate that the child's genetic makeup was specifically indicative of the origins of Clovis culture or inform on the geographic origins of Clovis and cannot be used to refute the Solutrean hypothesis (see below).

Genetics and culture

Archaeological literature critiquing the Solutrean hypothesis (SH) has come most vociferously from Clovis-Firsters (e.g., see Fiedel and Morrow 2012, 382; Morrow 2014). Surprisingly, in view of this and the mitochondrial X2a geographic anomaly (data in Reidla et al. 2003; Fernandes et al. 2012), mentioned above, some recent autosomal studies confidently ignore or dismiss the SH route on summary evidence. For instance, one recent autosomal-based publication (Reich et al. 2012),

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reconstructing the genetic prehistory of the first Americans from modern populations, relies on a solely-Beringian ancestry route as a given and ignores a possible *supplementary* ancestral population-source route for their four selected First Nations groups in Canada, who collectively form a separate phylogenetic branch from other mainland Native Americans they analysed (Reich et al. 2012, Fig 1c). Another autosomal study on a ~13 ka aDNA sample (Rasmussen et al. 2014) in western Montana claims 'our genome analysis refutes the possibility that Clovis originated via a European (Solutrean) migration to the Americas' (Rasmussen et al. 2014, 228), but omits to test for trans-Atlantic sources of West Eurasian Pleistocene gene flow to the Americas, which is inferred in their own analysis (see below).

Migrating groups of people carry their culture, language and genes, but rarely do these markers survive in the same proportions unless, perchance, they were the only settlers. All three proxy records of the past leave some record in the soil and/or among descendant societies, in different strengths, accuracy and precision of dating. So, it is essential that each proxy should be explored *and dated* independently before inferences on interdisciplinary congruence are made (Oppenheimer 2004). Further, while predictions from hypotheses derived from one proxy can, without prejudice, be tested for independent support from another, items of evidence selected from one, cannot simply be used to 'disprove' or, alternatively, patch-up narrative deficiencies in the other. Most importantly genetics should not be used, as in the past, to find support for the current most influential archaeological paradigm; rather it should objectively test all testable migration-models.

Material culture and languages can change dramatically with small intrusions of new people. Linguists even have a name for it: *language switch* (Vasek 1983). Genes also mix, but leave long-lasting records, both in individuals and in populations. The importance of the individual lineage record applies particularly to non-recombining uniparental lineages, which give an uncorrupted record of their own history, have phylo-geographic continuity and persistence and, unlike culture, offer direct proxy records of discrete prehistoric population migrations. Uniparental lineages (mtDNA & NRY) each have one quarter the effective population size of any autosomal locus. Their consequent greater tendency to local extinction than autosomes means that modern persistence and lack of recombination, increases rather than decreases the *phylogeographic* specificity of surviving founding lineages and their descendants.

So, multidisciplinary reconstruction, requires a separation and enforced independence of each proxy dating for the past, in order to avoid self-referential circularity of arguments (Oppenheimer 2004). Advocates of the SH accept the mitochondrial evidence that the majority (4+/5) of founding lineages (i.e., A–D, with the exception of X2a) arrived in Alaska from Beringia at least before the Holocene, i.e., allowing plural (e.g., both east and west) Palaeolithic routes and entries with subsequent genetic and cultural admixture. The possibility of multiple colonizations unfortunately increases that risk of confusion. The implications of this, in determining which ancestors brought which early tool traditions and who ended up using them, are more complicated than testing a single-entry scenario. Perhaps unsurprisingly, critics of the SH often implicitly couch their dispute in terms of either Beringia/or SH.

Anzick study: a cultural or genetic refutation of the Solutrean hypothesis?

The risks of relying on one-to-one direct links between material culture and genes can, perhaps best, be illustrated with reference to a recent, important archaeo-genetic publication in *Nature*

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(Rasmussen et al. 2014), which offers an extraordinary genetic window into the Pleistocene, only ~1,500 years after the current earliest evidence of human occupation in the American Northwest. Implicit conflations of the culture-genes bond linked-with the either/or argument are introduced in the introductory abstract (Rasmussen et al. 2014, 225):

> … the people who manufactured Clovis tools remain under debate. It is generally believed that these people ultimately derived from Asia and were directly related to contemporary Native Americans. An alternative, Solutrean, hypothesis posits that the Clovis predecessors emigrated from southwestern Europe during the Last Glacial Maximum.

The authors did extensive genome sequencing on a male infant, deposited approximately 12,680 years ago in proximity of Clovis artefacts at the Anzick site in western Montana. They inferred (Rasmussen et al. 2014, 227) that the 'Anzick-1 sample is genetically more closely related to Central and South Americans than to any other populations'.

They later argue further (Rasmussen et al. 2014, 228) that the infant

> … is closely related to all indigenous American populations. As such, contemporary Native Americans are effectively direct descendants of the people who made and used Clovis tools and buried this child. In agreement with previous archaeological and genetic studies, our genome analysis refutes the possibility that Clovis originated via a European (Solutrean) migration to the Americas.

The first of these claims confirms a reliance on the validity of claiming a *direct bond* of descent between material culture and genes as proof, which is weak in the context of their 'refutation', both generally and specifically, in this case. For the claim to hold more water, would indeed require only a single-source American entry, which is duly asserted a few sentences later, or if plural-entries, that Clovis was the earliest culture and this site was near the founding date, neither of which apply. The former, singular, assertion is unproven and is not confirmed by the combination of diverse East Eurasian mtDNA founders and West Eurasian X2a (see below). For the latter, i.e., with plural entries, the site would have to be coincident with the earliest directly dated settlement of northwest America or at least with the earliest finding of Clovis tools, neither of which it was.

By their own estimate (Rasmussen et al. 2014), the Anzick child was actually around 1,500 years younger than the first confirmed American human remains (Gilbert et al. 2008; Fig. 2) showing directly dated human coprolites from Paisley Cave in Oregon, over 14,000 years old and pre-dating Clovis technology by over 1,000 years, thus directly refuting the old *Clovis First* claim. The coprolite paper shows various Clovis dates tightly clustering around 13,000 kya (Gilbert et al. 2008; Fig. 2), the oldest antedating the Anzick human remains (average 12,680 kya) by 320 years, the latter post-dating the coprolites by around 1,500 years.

The dates of appearance of Clovis points across Northern USA (Waters and Stafford 2007) are also surprisingly synchronized, so there is no clear West-East or East-West direction. If, as the SH argues, East Coast Atlantic settlement occurred before the evolution of hallmark Clovis technology and Clovis spread material culture from East to West (but not necessarily with many people – see Bradley and Collins 2013), it would have reached pre-existing settlements in Montana well before the Anzick child was born. At that time people in the West *were* indeed

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likely to be largely of Beringian origin, consistent with Anzick – also inferred from lower modern-western X rates in mtDNA studies (Fig. 1; see also, e.g., Malhi et al. 2008, Fig. 2; Perego et al. 2009, Fig. 3). However, by analogy, guns and horses spread from the East early in the colonial period, but fairly soon they were not just used by Europeans; so the genes of the final owner could not, therefore, identify the ultimate origins of the animal or artefact type.

Concerning the second claim above – 'our genome analysis refutes the possibility that Clovis originated via a European (Solutrean) migration to the Americas' – it is difficult to see which part of their genome analysis specifically tests, let alone refutes the SH, given the complete absence of any further mention of the SH, or any supplementary Atlantic route, elsewhere in the paper and online material. Furthermore, as discussed in more detail below, their own study actually finds evidence of pre-Columbian West Eurasian admixture.

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Separating genetics and culture and testing model predictions

Given the risks of reading too much into associations of genes and material culture, when cultural and genetic admixture resulting from putative multiple entries both tend to confound inferences and conclusions, it is important to ask what unique, uncontaminated biological insight genetics has to offer, for what is largely an archaeological-cultural argument about geographic sources and dates of migration. To focus on this, some details of the archaeological discourse need to be put to one side, as opaque to genetic enquiry. These include technological sources, lithic evolution and chronological gaps and the question of whether *independent evolution*, from any convincing ancestral Pre-Clovis source point style in northeast Asia, trumps a phylogeny connecting it to Solutrean technology at the LGM on the other side of the Atlantic.

Having done that trimming, the only clear relevant directional message that currently remains is genetic and even stronger with complete sequencing and recent data (Reidla et al. 2003; Fernandes et al. 2012), namely that one of the five oldest Pleistocene founding American mitochondrial lineages, X2a, is unlikely to have come from East Eurasia on phylogeographic parsimony grounds, with the only possible alternatives being West Eurasia and North Africa. Currently, the SH is the only archaeological model which predicts or offers any credible geographic parallel for this directional anomaly which has remained as the elephant (or mammoth) in the room for over sixteen years.

Testing predictions of hypotheses is a useful tool of the scientific method. Ignoring anomalous evidence, not testing it objectively, rather retesting current dogma, lacks balance. American X2a does not of course 'prove' the specifics of the SH, but does oblige geneticists looking at other parts of the genome, to test available hypotheses to explain the substantial presence of pre-Columbian West Eurasian genetic signatures found in Native American populations, rather than assuming they all arrived from Beringia (e.g., Reich et al. 2012).

The key genetic questions and predictions arising from the SH are: (1) is there non-cultural evidence for a Palaeolithic migration from the western Old World across the Atlantic to the Americas; (2) if so, from where and (3) when? As mentioned above, non-recombining uniparental genetic lineages (mitochondrial DNA and the Y chromosome), do each have an uncorrupted, cumulative record of their own prehistoric origins. Unlike material culture, and the rest of our vast genome, they preserve direct, unambiguous proxy-source sequence-records of discrete prehistoric population migrations. For, unlike the rest of the genome, they do not

recombine (the genome-wide splicing and dicing which happens after every ovum fertilization, when different populations meet), and each chromosome retains its own ancestral record intact. New, random, non-lethal mutations on these chromosomes occurring over thousands of years allow a detailed lineage tree to be reconstructed, on which fresh mutations are geographically highly-specific, allowing the migration of new branches (mutations) to be inferred phylogeographically, and dated, using formal methods of founder analysis (Avise 2000; Richards et al. 2000). It is important to realize that while uniparental markers can only partly inform on population admixture history and relative size, the distribution of their branches in time and space are specific markers of migration in their own right.

Mitochondrial DNA evidence

That modern uniparental lineage branch-distributions have far greater regional and intercontinental geographic specificity than individual autosomal loci has been amply demonstrated over the past twenty-seven years. Evidence for the modern human out-of-Africa migration was first demonstrated unambiguously in 1987 using mitochondrial DNA phylogeography (Cann, Stoneking, and Wilson 1987). It was later confirmed to be a single migration, with all non-Africans belonging to one founding 'L3' African lineage (haplogroup) entirely confined within its two non-African branches M & N, while all the rest of the L tree haplogroups remain in Africa (reviewed in Oppenheimer 2003, 2012).

For the handful of American founding mitochondrial lineages it could be nearly that simple. It has been agreed for twenty-one years that the four main Palaeolithic founding lineages in the Americas are derived from four ancient haplogroups, which are well represented in East Eurasia generically as A, B, C and D (Torroni, Schurr, et al. 1993; Torroni, Sukernik, et al. 1993). These four haplogoups clearly evolved in East Eurasia long before the LGM and are absent in West Eurasia (Soares et al. 2009, Fig. 6). Furthermore, with a couple of minor back-flow-exceptions across the Bering Strait, the American *derivative*-branches of these four haplogroups are *only* found in the Americas, though with relatively different geographic distributions. The five deepest branches (specifically A2, B2, C1a&b & D1) date genetically in America around 14-kya (Soares et al. 2009, Fig. 6), consistent with the dates of the 14-kya coprolites from Oregon which, neatly, feature A2 and B2 aDNA haplotypes (Gilbert et al. 2008).

So much is common ground, but there is a fifth Palaeolithic American haplogroup: X2a, derived from West Eurasian 'X' (Brown et al. 1998; Reidla et al. 2003). This uniquely-American founder lineage 'X2a', is a sub-clade of X2-225 (Fernandes et al. 2012), and is of Pleistocene age: 14,080 yr; (10,321–17,914) by Maximum Likelihood (ML) and 21,289 yr (11,040–32,035) by Rho, on complete mtDNA sequences (Fernandes et al. 2012). Although these estimates are clearly Pleistocene, with one of possibly greater *local* antiquity than those of haplogroups A-D in America, X2a has a completely different ancestral source and distribution, originating near the Mediterranean region, and is near-absent from East Eurasia (Figs 1 and 2: see also Reidla et al. 2003; Fernandes et al. 2012).

The X haplogroup is clearly West Eurasian in origin, as is X2-225 (Figs 1 and 2). Along with two other early relict primary branches of ex-African macro-group N (N1 & N2), X most likely originated 'within the Arabian Peninsula' (Fernandes et al. 2012, 347) close to

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the out-of-Africa movement to Southwest Asia, and evidently never made it past the Indus Valley towards East Eurasia (Fernandes et al. 2012). The largest, but not oldest, X branch, X2, most likely originated in the eastern Mediterranean region around 22 kya, rapidly expanding in diversity and geographic distribution at that time (Fernandes et al. 2012). X2 has many primary branches distributed throughout West Eurasia, most sharing a further mutation at np 225 (Fig. 2; Fernandes et al. 2012). The unique phylogeography and Palaeolithic founding age of X2a in America, means it physically separated near to the founding age of its parent X2a'j around the LGM in West Eurasia. Three large X2-225 branches (X2e, X2a'j and X2b'd) also expanded at that time (22–18 kya) and spread mainly west. Confusingly, np 225A subsequently reverted independently in both sub-clades X2e2 and X2a1 (Fernandes et al. 2012: Fig. 1), but this does not of course alter the West Eurasian ancestry of X2a nor affect the Altai X2e2 red herring (next paragraph).

The most geographically conservative of these three branches X2e, expanded locally in the Levant and into the Caucasus and eventually, during the historic period, to the Russian Altai (Derenko et al. 2001, 2007), where it is only represented as a single highly-derived closely-related founding-cluster (a unique derivative of X2e2: Fig. 2) of three similar haplotypes dating to ~2.6 kya (Fernandes et al. 2012). This recent, derived and geographically isolated clade on the south-western verge of East Eurasia, is the most easterly representative of X and is clearly not ancestral to X2a, nonetheless is regularly promoted as such, by SH critics (e.g., Straus et al. 2005; Bamforth 2013, Morrow 2014) as evidence that the X2a ancestor travelled from the Mediterranean, through Siberia, leaving no trail, half-way round the globe, to Beringia. Even if the phylogeny could miraculously be 're-arranged', it is wishful and misleading to argue that the Russian Altai is remotely close to Beringia or even integral to East Eurasia, let alone that X2a and X2g went east to America and then went extinct in East Eurasia.

The most western European distribution among these three large X2-225 branches is seen in X2b'd (Age: 18,983 yr (14,856–23,191) by ML), which spread west along both the north and south Mediterranean coasts to Morocco, Spain and up the Atlantic coast and widely throughout Europe, including the British Isles (e.g., Orkney). X is present in Basques, both in Mid-Holocene aDNA (Izagirre and Rua 1999, Table 2) and X2b & X2c in modern populations. It would of course be helpful to know if the X2-225 sub-clade was present in relevant parts of Pleistocene Europe as well as in the Mid Holocene. However, given the small handful of Iberian samples analysed for that period (Brandt et al. 2013; Skoglund et al. 2014), and the fact that, although X2 is widespread in West Eurasia, even modern rates of X2 in Western Europe are low ($\leq$3%) and heterogeneous (Fig. 1), with higher rates in the Mediterranean region, so absence of Hg X in relevant Late Pleistocene aDNA analyses in West Eurasia cannot be taken to indicate absence at that time. Unfortunately, little high-resolution X data is available for Iberia for any period. There is, however, a recent report from the Franco-Cantabrian region noting a 'great diversity and high frequency for subhaplogroup X2' (García et al. 2011, 39). In particular 6/91 samples (6.6 per cent) from the Vizcaya province in the northern Basque Country were characterized as X2 (based on HVS-1 markers) mostly X2b & X2c, one X2b sequence having a near HVS-1 match in Morocco (García et al. 2011, Table S1). South Portugal has an X frequency of 3.6% (González et al. 2003), and Spain an X2 rate of 4.2% (Crespillo et al. 2000). Orkney also represents an Atlantic X2 hotspot with 7.2% X2 (Helgason et al. 2001).

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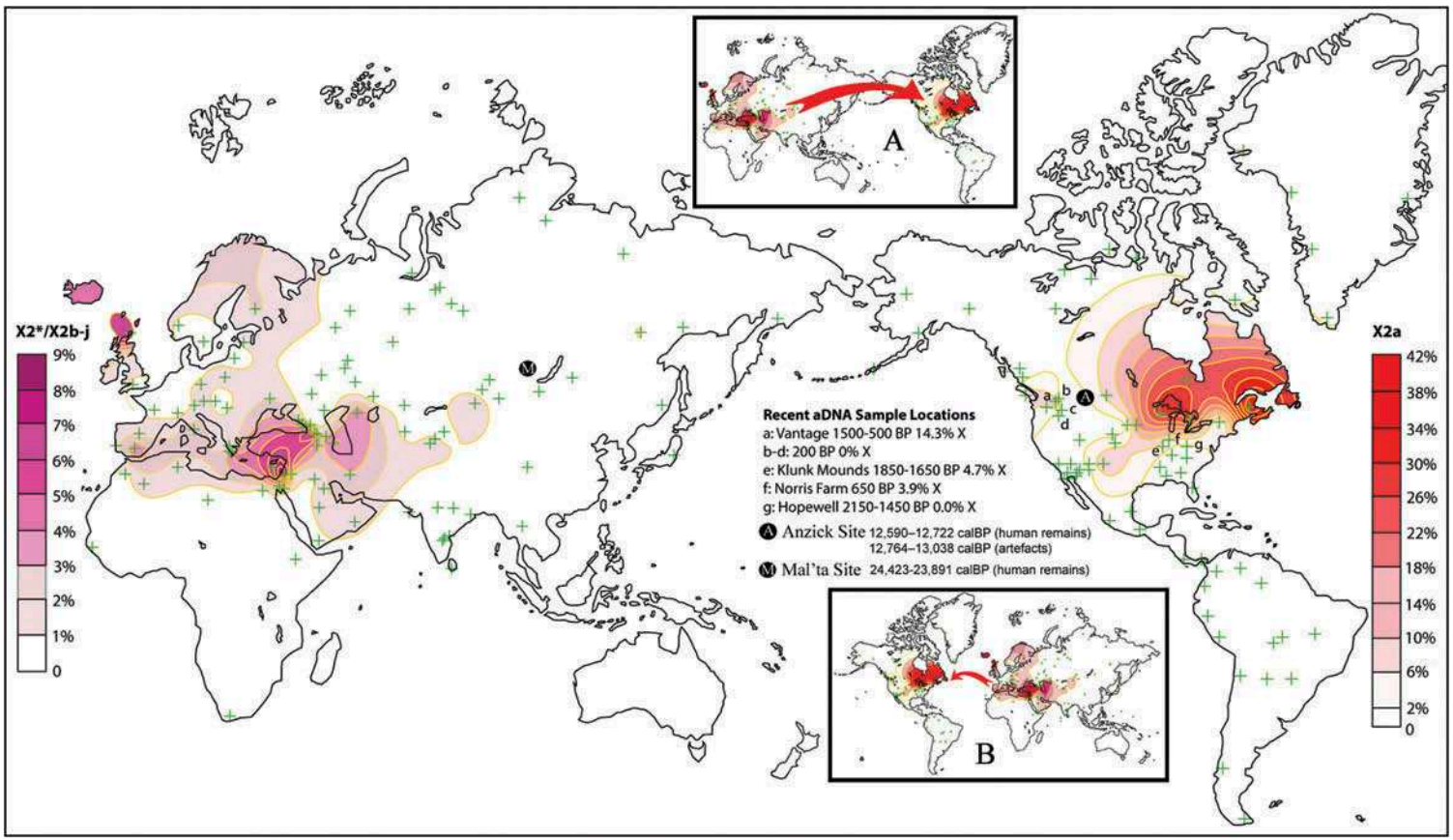

Figure 1 Worldwide distribution of Mitochondrial Haplogroup X2. © Stephen Oppenheimer, Bruce Bradley and Dennis Stanford, 2014. All Rights Reserved. Insets: (A) Across Asia hypothesis; (B) Across the Atlantic hypothesis (same scale). Collated and corrected for repeat citations from all sources cited in: Table 1, Reidla et al. 2003; Table S4, Perego et al. 2009; Table 3, Helgason et al. 2001; Table 3, Bolnick and Smith 2007; Scozzari et al. 1997; Malhi and Smith 2002. Anzick dates: (Rasmussen et al. 2014) and Mal'ta dates: (Raghavan et al. 2014).

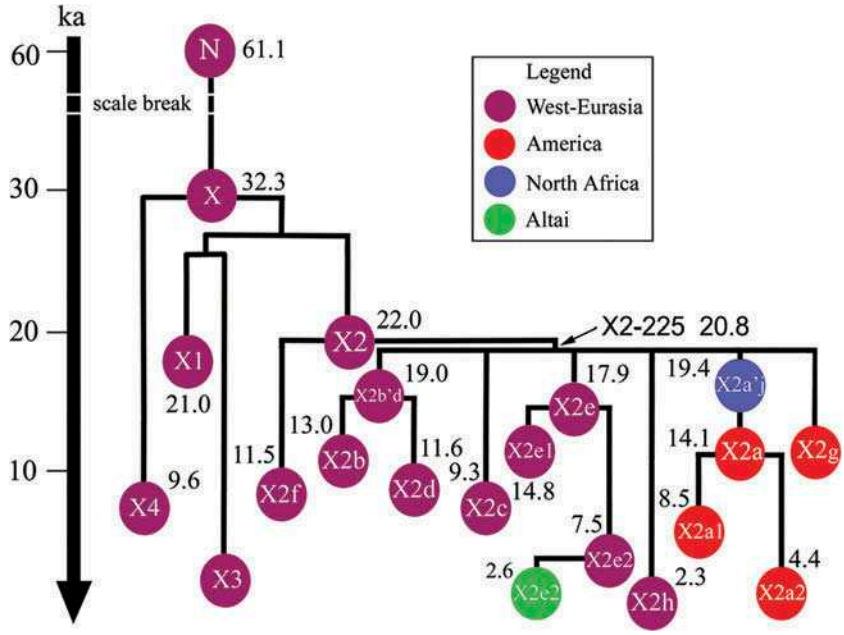

Figure 2 Schematic tree of Mitochondrial Haplogroup X.
Ages indicated are maximum likelihood estimates obtained with the complete mtDNA genome (in ka). (Redrawn and modified with permission from Fernandes et al. 2012, Fig. 1.)

This apparently rapid coastal spread of X2b'd from the Levant to the Atlantic is consistent with the Pleistocene use of boats by modern humans there and elsewhere. The Pleistocene antiquity of such maritime skills is well-attested archaeologically elsewhere in Oceania, using radiocarbon and luminescence-dating (reviewed in Oppenheimer 2012), thus clearly does not preclude such spread further along the edge of Atlantic pack ice at the LGM. For Melanesia, the first archaeological evidence of occupation of the island of New Guinea has been radiocarbon dated to 49 ka BP (Summerhayes et al. 2010) and 40 ka BP to the east, in New Britain island (Leavesley et al. 2002). For Australia, the carbon ceiling has been increased to around 48 ka using the ABOX-SC method (Turney et al. 2001). Non-carbon dating techniques, however, suggest an earlier human colonization of Australia by 50–60 ka (Roberts et al. 1994; Roberts and Jones 2000; Bird et al. 2002, 2004). One need not look only to Southeast Asia for evidence of early watercraft. There has been much discussion of their use in the colonization of western Scandinavia during and after the final glacial retreat (Bjerck and Breivik 2012; Bonsall, Pickard, and Groom 2013).

The third, and most diverse, primary X-225 branch is X2a'j (Fig. 2; 19,409 yr; 15,547–23,342, by ML), which includes X2a in the Americas and has several relict X2j branches found in 3 Egyptians (Fernandes et al. 2012) and a single haplotype from Iran (Reidla et al. 2003). The latter shares two further mutations with the north-African X2j cluster as well (at np sites 16,179 and 16,357), thus confirming X2a'j as a solid Old World common ancestral node for the American X2a branch with its nearest relative X2j being located in Egypt on the opposite side of the globe from Beringia across the North Pole. To critics, a possible Most Recent Common Ancestor for X2j and X2a in North Africa or Southwest Asia, might fail to confirm an Iberian cast-off point for X2a *en route* to the Americas but, as mentioned, 'proving the specifics

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of the SH' is not the purpose of this discussion. Given the absolute paucity, and reality of X2j, it simply confirms Western Eurasia/Mediterranean as the home of the X2-225 clade and its relevant branch X2a'j and certainly gives no support to a Beringian route for X2a.

In addition to the X2a branch, there is another Native American X2-225 branch represented by a single haplotype 'X2g' unique to the Americas and the Ojibwa Nation who also possess the greatest X2a diversity in the Americas. In their definitive review of X origins, Fernandes et al. (2012, 352) remark:

> The rare X2g, also found only in Native Americans, indicates that the spread from the Near East toward the Americas could have begun as early as the emergence of the X2-225 clade (~21 ka), given that this root could have been the only founder sequence.

This glacial age of X2-225 (20,786 yr; 17,358–24,269 by ML) is significantly older than the founding age estimates for American A-D at ~14 ka, using the same calibration method, and thus appears to inflate the potential founding date of X2 in the Americas. In our view this statement can also be taken not to exclude the more direct and shorter route from the Near East across the Atlantic (Fig. 1B). The hypothetical transit of the Atlantic would necessarily have taken a shorter time than Egypt to Alaska overland.

In spite of its unique antiquity, X2a has a focused distribution in the Americas. It is limited to North America and to groups speaking 'Northern Amerind' languages in Greenberg et al.'s (1986) tri-partite American language classification, as referred to in the autosomal studies discussed here (exceptions being Navajo and Apache, both southern Athabaskan (Na-Dene) and Pueblo Jemez who speak a Central Amerind language). X2a has not otherwise been found in Greenberg's other two northern language macro-groups Na-Dene or Eskimo-Aleut. More specifically, among defined First Nations groups X2a is found at highest frequency (Fig. 1), branch antiquity and diversity (Fernandes et al. 2012, source data in Fig. S1 and SOM) in Northeast America. The highest frequencies and lineage diversity are among the Algonquian-speaking (Northern Amerind) First Nations of the Great Lakes region (Fernandes et al. 2012: tribal affiliations sourced from Fig. S1, tree). Three such groups (Wisconsin Chippewa, and N. & S. Ojibwa) have X2a frequencies between 25 to 30 per cent, while another three Algonquian-speaking groups range from 4 to 7 per cent (Perego et al. 2009, Table S4). Indeed the two primary branch nodes of American X2a (X2a1 ~8.5 ka & X2a2 ~4.4 ka) and also X2g (Fig. 2), are predominantly represented among Algonquian-speakers, as are 7/10 tertiary branches of X2a (data in Fernandez et al. 2012, Tree S1). Pre-Columbian aDNA evidence for X2a1a has also been found in the same modern linguistic region (in Illinois: Norris Farm in Fig. 2) at 4 per cent (Stone and Stoneking 1998). X was also tested for in six other archaeological site aDNA collections (data in Mahli et al. 2004; Bolnick and Smith 2007), dating between 200 BP and 2,150 BP in sufficient numbers to make frequency estimates, including a total of three pre-Columbian sites with X present at frequencies from 3.9 to 14.3 per cent (Fig. 1).

Eastern Canada and the Great Lakes region thus currently appear to have the highest regional frequencies, modern branch-diversity and aDNA support, consistent with an eastern primary region of X2a dispersal. The same cannot be said for the Northwest of the continent (Fig. 1). The only other modern Native American groups that have significant frequencies of X2a are three other widely-separated, culturally-unrelated, phylogenetically-derivative clusters (see below) to the west and south (Fig. 1), in order of proximity to the Great Lakes: (1) Nearer –

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to the southwest of the Great Lakes: Sioux (Siouan: 7.3 per cent), (2) Far west – Vancouver Island and Washington State: Yakima (Sahaptin: 4.8 per cent) and Nuu-Chah-Nulth (Wakashan: 8.8 per cent); Pre-Columbian aDNA evidence for X, from 500–1,500 BP, has also been found at Vantage in Washington State (1/7; Malhi and Smith 2002; Malhi 2004), (3) Southwestern USA – Navajo (3 per cent) and Apache (0.5 per cent) (both southern Athabaskan languages) and Jemez (Pueblo Kiowa-Tanoan: 10 per cent).

Extensive surveys of X2a traces found in the *general mixed* populations of North American States (Perego et al. 2008, Fig. 3, lower left; Table S3), *excluding* autochthonous Native American groups, show a distinctive distribution, mostly very low rates (≤ 3 per cent), with the highest rates (1.74–2.52 per cent) focused in a moderate but distinct shift-to-the-west from the Great Lakes region to formerly Siouan-speaking regions. This shift centers on North Dakota-South Dakota, Montana-Wyoming with lower rates in the mainly Algonquian-speaking Canadian Prairie Provinces of Manitoba, Saskatchewan and Alberta (1.80 per cent). X2a is also found in former Apache territory (Oklahoma: 0.68 per cent). Exceptions to this non-tribal western-shift pattern are, perhaps unsurprisingly, found in other north-eastern, formerly Algonquian-speaking areas (Minnesota 0.93 per cent; Wisconsin 0.52 per cent; Pennsylvania 1 report: Perego et al. 2008, Fig. 3, lower left; Table S3).

Complete sequence phylogeny (Fernandes et al. 2012, Fig. S1) of X2a shows that identified haplotypes from Native Americans of the three non-Algonquian-speaking regions (above), belong mainly to just one of the seven subgroups of X2a1 (namely X2a1a, age: 7,689 yr; 4,835–10,592 by ML). The other six X2a1 subgroups all include Algonquian-speakers as the majority, while X2a1b has 2/8 haplotypes located away from the Great Lakes (Pennsylvania and Montana) and X2a2 has 1/4 types from Navajo (Fernandes et al. 2012, Fig. S1). Both of the two X2a1a embedded subgroups include Sioux, while one of these (X2a1a1 ~4.3 ka) has Jemez and Nuu-Chah-Nulth on one branch and Sioux on the other (the same Washington cluster from Nuu-Chah-Nulth in Vancouver Island, inferred as X2a1a1 from HVS sequence/RFLP in Brown et al. 1998). A south-eastern United States aDNA dispersal location is Florida, where pre-Columbian (~ 8 ka) aDNA evidence for X (inferred from sequence as X2a1a1*) has also been found (Smith et al. 1999), consistent with the implied Early Holocene date of expansion of X2a1a.

As mentioned, the Great Lakes Algonquian-speaking region encompasses the highest frequencies and the oldest and deepest X2a (and X2g) branch-ancestry. The default phylogeographic inference would therefore be that the derived cluster X2a1a, and its haplotypes currently found in the three geographically-dispersed Native American Groups, ultimately derives from an ancient dispersal event towards the south and west of the Great Lakes, in the early Holocene, flagged by X2a1a, best represented among Sioux. However, more sequences would be required to explore this inference. There is, however, no phylogeographic support for a west-to-east spread of X2a.

This new evidence-based perspective that the region of greatest antiquity of American X2a appears to be in northeast Canada and that the three other younger more-derived X2a regions in North America may have been colonised by more recent Early Holocene dispersals to the south, east and west, suggests an ultimately eastern introduction of X2a and X2g to the Americas consistent with an additional trans-Atlantic migration suggested by archaeological evidence (Stanford and Bradley 2012).

Since the Lakes region would have been largely covered by periglacial lakes adjoining the Laurentide Ice sheet before the Holocene, this raises the logical questions of where the putative first east coast settlements most likely occurred and which rivers they might have used to

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migrate to the Great Lakes area. The St Laurence River is certainly an access possibility and X2a (X2a1 as inferred from HVS sequence in Smith et al. 1999), has been found in 50 per cent (3/6) of a small sample of Algonquian-speaking Mi'kmaqs who live around its estuary (Malhi, Schultz, and Smith 2001). Moreover X2a1 has been identified in aDNA from the extinct Beothuk of nearby Newfoundland (Kuch et al. 2007).

Finally, there are other European mtDNA lineages among first Nations, but they have been ignored, routinely left out of reports and certainly not studied (Malhi, Schultz, and Smith 2001, 23). One of the earlier sources (Scozzari et al. 1997), however, surveyed Ojibwa living on Manitoulin Island and reported an X frequency of 25.7 per cent and an H frequency of 5.7 per cent, which was assumed to be of recent European maternal origin.

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Arguments made for X2a arriving via Beringia

It is difficult to find formal arguments in favour of X2a arriving via Beringia, rather than summary-dismissive contra arguments to the Atlantic source of X2a. Two recent genetics papers have argued in favour of X2a arriving via Beringia with the other four haplogroups (A-D).

One of these (Fagundes et al. 2008), claims to refute the SH on the basis of theoretical modelling of a single entry because, on their estimates, American X has a similar age and diversity to the other American mtDNA founders. They argue it could have gone through a similar LGM bottleneck to the other lineages in Beringia and thus claim their

> results strongly support the hypothesis that haplogroup X, together with the other four main mtDNA haplogroups, was part of the gene pool of a single Native American founding population; therefore they do not support models that propose haplogroup-independent migrations, such as the migration from Europe posed by the Solutrean hypothesis. (Fagundes et al. 2008, 589)

No other support for a shared (X2a + A-D) migration history is given, and no comparative likelihood tests of alternative 'haplogroup-independent migrations' are offered. The fact that the LGM would have had similar effects on groups arriving on the east coast of America, with similar date constraints is not mentioned. Twelve of the eighty-six mtDNA complete genomes used for age estimates were X2a, compared with the twenty-four used in Fernandes et al. (2012). In fact their overall estimate for the transition period within Beringia/America was fairly broad at 5,000 years:

As for the absence of X in East Eurasia, the reverse of the Old World A-D distribution which is exclusively found there, this is surprisingly not seen as a parsimony constraint, simply asserted, with no other discussion, as the expected result of drift:

> It is likely that this haplogroup is absent in eastern Siberian populations because of drift effects, which impact rare variants more strongly. Thus, its probability of being lost through random effects would be high. (Fagundes et al. 2008, 589)

Drift and extinction of X2a & X2g ancestry in East Eurasia (Fig. 1) cannot simply be invoked as highly likely (unlike A-D), in this way, without considering phylogeographic parsimony cost to their underlying hypothesis. If X2 was so liable to extinction to start with, how did it manage to cross Eurasia, with multiple bottlenecks and still achieve substantial frequency in Northeast

America? No evidence or similar example is given from the mtDNA phylogeographic literature for the assumption of high probability of retrograde land-based lineage extinction nearly half way round the world. It would be difficult to find one. The cost in phylogeographic parsimony to their core hypothesis is not considered, in comparison to a transatlantic founder migration of X2a and the single X2g haplotype, both of which have the same MRCA in the West Eurasian/ Mediterranean region and obviously have no need to invoke retrograde drift-extinction in the Atlantic (inset A vs B: Fig. 1).

In spite of such theoretical claims, long-distance uniparental lineage migration nearly always leaves, not only a trail, but progressive, geographically-defined mutational branch markers. One of the best examples of such trail-persistence, can be found in the progression of B4a1a from SE Asia through the Melanesian islands to Eastern Polynesia in the Pacific. In spite of serial founding effects and drift a progressive genetic trail can be traced along the island chain evolving through B4a1a1, to B4a1a1a to B4a1a1a1. In spite of evident drift, nowhere is the trail actually lost en route (Fig. S1 in Soares et al. 2011). If a phylogeographically specific genetic trail can be left across the Pacific Islands in spite of serial founder effects, it is more likely, than not, to be left somewhere in the landmass of East Eurasia or at least have left specific traces.

Another recent article (Hooshiar Kashani et al. 2012) also argues against the SH on the basis of modelled shared population genetic histories within America as summarized in the abstract (below) but, surprisingly in this case, their argument is based on claimed simple associations between two uncommon founders, being very similar to each other in America and different from the other founders:

> Taking into account that C4c is deeply rooted in the Asian portion of the mtDNA phylogeny and is indubitably of Asian origin, the finding that C4c and X2a are characterized by parallel genetic histories definitively dismisses the controversial hypothesis of an Atlantic glacial entry route into North America. (Hooshiar Kashani et al. 2012, 35)

Their parallel evidence that X2a & C4c together formed a dual founding migration within America (thus by inference discrete from the other A-D lineages) is based on three types of association between mtDNA X2a and C4c in North America (clearly not on their lack of association in NE Asia): (1) rarity, (2) co-distribution restricted to the North American continent, and (3) similar founding age. While simple associations may sometimes be considered as suggestive, they are not normally accepted as definitive evidence. However, the genetically unlinked regional/temporal associations offered here seem too non-specific even for suspicion, let alone for the above refutation. To enlarge:

1. **Firstly, shared rarity**: C4c is indeed very rare (total sixteen complete sequences, three in Canada in their Table 1), being first discovered in Columbia in 2007, and much rarer than X2a, which achieves frequencies up to 30 per cent in several Great Lakes First Nations (Fig. 1). Moreover shared-rarity is present in many multiple haplogroup migrations and is not regarded as a feature indicating unique common ancestry as a separate migration within the same timescale as other co-founders, in formal uniparental Founder Analysis (e.g., in Richards et al. 2000);
2. **Co-distribution restricted to North America**: While, with the exception of two basal C4c instances in Columbia, South America (Tamm et al. 2007), both haplogroups are

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restricted to North America, they do not closely co-distribute regionally within that continent. While X2a is clearly most frequent and diverse in the Canadian Great Lakes region with phylogeographic evidence of some minor spread southeast from there (Fig. 1), C4c has only three Canadian instances (one in British Columbia and two in Manitoban mixed/Metis groups), with the rest widely scattered further south in the USA, excepting the US west coast (their Fig. 1).

3. **Parallel/dual Founding Ages of X2a & C1c**: Using the current complete mtDNA sequence calibration method (Soares et al. 2009), they estimated the root age of C4c to be 13.8 +/– 3.8 ky (by Maximum Likelihood) and 12.3 +/– 2.9 ky (by Rho), which are statistically indistinguishable from the Soares et al. (2009) ML estimates for five other American founding lineages with ultimate East Eurasian ancestors (A2:14.6 ky; B2: 14.6 ky; C1a:13.0 ky; C1b: 14.5 ky; and D1: 13.5 ky). By contrast, the estimates Hooshiar Kashani et al. (2012) make for the age of American X2a (table 2) were older: 18.6 +/– 5.5 ky (ML) and 18.4 +/– 5.2 ky (Rho), and could not thus be described as more parallel to C4c than to any other founding lineage.

To conclude on mtDNA, our discussion of evidence from the X2a/X2g lineages suggests that there is a case to explore for those predictions of Pleistocene gene flow from West Eurasia to the Americas, most parsimoniously by the direct route across the Atlantic. If so, it would seem appropriate to look at other parts of the human genome for such influence. Such questions have not been formally addressed, at least not in relation to the Atlantic route suggested independently by the SH and the phylogeography of X2a/X2g lineages. There is indeed some recent evidence for pre-Columbian West Eurasian autosomal admixture but it is not clear why this is presumed to have travelled across Siberia, as discussed in the next section.

Autosomal evidence for pre-Columbian West Eurasian admixture

Moving first to the Rasmussen et al. (2014) claim introduced above: 'our genome analysis refutes the possibility that Clovis originated via a European (Solutrean) migration to the Americas.' While not explaining the basis of their SH genomic refutation, the authors do actually find evidence *for* Pleistocene West Eurasian autosomal admixture in the Americas, which would be predicted by the SH.

They make this inference by several analytic approaches. First they acknowledge a relative genetic affinity of Anzick to Western Eurasians (Rasmussen et al. 2014: Supplementary Information Sect. 15.6), suggesting admixture and gene flow 'prior to the first migration into Beringia and the Americas'. However, while this relative West Eurasian affinity may have arrived via Beringia, as they have presumed, they did not formally explore the alternative direction of gene flow, namely that the minor, apparent evidence for West Eurasian affinity that they detected, might have come more directly via the Atlantic (e.g., before Clovis tools evolved), and subsequently admixed with the Siberian co-ancestors of all Americans. This omission of any comparative test of direction weakens rather than strengthens their claim to refute the SH.

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Furthermore they also found that the ancient population that Anzick represented, was not basal to that for modern Northern Amerinds (NA), analysed from further east in Canada, although otherwise closely related with them (Rasmussen et al. 2014, 226–7 and SI Sect. 15.4). A basal relationship of Anzick to modern Northern Amerinds should have been expected from the sole Beringian entry hypothesis, given the relative proximity of NA to the *east* of the Pleistocene Anzick child, and also since Anzick was actually basal to all other Native American groups further south. This picture, of the ancestry of NA (and Chipewyan) groups distinct from all other mainland groups, finds echoes in the modern genetic population phylogeny (Reich et al. 2012, Fig 1c) mentioned above.

One of the possible explanatory models Rasmussen et al. (2014) tested for this anomaly of NA ancestry was articulated as: 'The NA groups carry ancestry from a previously undocumented stream of gene flow from the Old World.' Testing the model of 'undocumented stream of gene flow', they looked for and found 'no evidence for Siberian gene flow into the Northern Amerinds' (Rasmussen et al. 2014, SI Sect. 15.4, 27). But, again they did not explore the alternative explanatory possibility of an earlier trans-Atlantic stream of gene flow which, by virtue of geography, would influence the NA in East Canada to a greater extent than the SA populations, in this context. These omissions of testing predictions of, or of evidence for, or against, the SH hardly help to confirm their refutation of it.

Similarly to the Anzick report the Mal'ta paper (Raghavan et al. 2014) infers pre-Columbian West Eurasian admixture in mainland Native Americans. The Mal'ta paper abstract states: 'Our findings reveal that western Eurasian genetic signatures in modern-day Native Americans derive not only from post-Columbian admixture, as commonly thought, but also from a mixed ancestry of the First Americans' (Raghavan et al. 2014, 87).

The genetic affinity they noted between Native Americans and the Pleistocene Mal'ta sample was also detected to a significant extent using modern-day Western Eurasian populations instead, with West Europeans (Orcadian (highest), French Basque, French, North Italians and Russians) having greater affinity than the Middle East or Central and South Asia (Raghavan et al. 2014; Fig 3b; SI Sect 14.5). In spite of this the Northeast Asian route was still presumed for these West Eurasian affinities, with no mention of an Atlantic route.

From such D-statistic analyses, they inferred 'that Native Americans have mixed origins, resulting from admixture between peoples related to modern-day east Asians and western Eurasians' (Raghavan et al. 2014, 89). They also modelled past population admixture history in relation to the Mal'ta sample using *MixMapper* v1.0 and modeled 'Karitiana as having 14–38% western Eurasian ancestry and 62–86% east Asian ancestry' (the Karitiana are an isolated South American group with no other apparent genetic evidence of recent European admixture). Again, the trans-Atlantic possibility of gene flow was ignored as indicated by the statement: 'it is likely that populations related to MA-1 [Mal'ta] mediated the mixture event between western Eurasians and Native Americans' (Raghavan et al. 2014: SI Sect. 12).

Ancient admixture between Europeans and Karitiana and other groups was also explored by Patterson et al. (2012), using f3-analysis on 'population triples' from the HGDP dataset. Without going into detail, an extract from a key section entitled 'Evidence for Northeast Asian-related genetic material in Europe' again reveals the assumption of Beringian route for such admixture:

> We single out from Table 5 the score for French arising as an admixture of Karitiana, an indigenous population from Brazil, and Sardinians. The Z-score of –18.4 is unambiguously

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> statistically significant. We do not of course think that there has been substantial gene flow back into Europe from Amazonia. The only plausible explanation we can see for our signal of admixture into the French is that an ancient northern Eurasian population contributed genetic material to both the ancestral population of the Americas and the ancestral population of northern Europe. This was quite surprising to us, and in the remainder of the article this is the effect we discuss. (Patterson et al. 2012, 1083)

We are concerned that it is presumed in all these analyses that the inferred pre-Columbian west-Eurasian admixture into Native Americans arrived via Beringia and there was no mention of the possibility that this pre-Columbian west-Eurasian admixture could, alternatively, have come across the Atlantic. There was nothing in the analysis, which formally or explicitly determined the geographic direction of inferred, shared West Eurasian population ancestry, from Siberia or from the Atlantic.

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Y chromosome

The SH and a high frequency of X2a in northeastern Native American groups, might both predict unexpectedly high 'European' or at least high West Eurasian Y haplogroup frequencies there (e.g., Straus et al. 2005, 522). That is indeed the case overall (e.g., Hammer et al. 2005, Fig 3D). In geographic plots, R1 frequencies in native populations, of the Great Lakes/Algonquian-speakers stand out as the *great majority*, having among the highest worldwide R1 rates (e.g., Malhi et al. 2008; and World frequency map as of 1 June 2014), even higher than non-western Europe and far higher than other Native Americans (c. 0–10 per cent). When further characterized in the USA (Hammer et al. 2005), 97 per cent of R1 had the M269 SNP (unambiguous Single Nucleotide Polymorphism), which defines R1b1b, the main West European Y-haplogroup, which possibly originated there before the LGM (Morelli et al. 2010). The less-reliable P25 was used in an earlier US study (Zegura et al. 2004).

The main problem with interpreting unusually high Y-R1 frequencies in Northeast Native Americans, is that the published SNP characterization is still too poorly resolved in all studies to differentiate ancient migration from post-Columbian introduced R1. STR (Short Tandem Repeats – more rapidly mutating, but less reliable than SNPs) characterization of R1, however, indicates a substantial proportion of derived, STR-haplotypes *not* shared with Europeans (Bolnick, Bolnick, and Smith 2006, Fig 6b; Zegura et al. 2004, Fig. 5). This would not be expected if those R1 STR types were all recent European introductions, and could be consistent with being derived from more ancient founders. While better phylogenetic resolution is needed, these results, far from refuting the SH, are more consistent with its predictions than solely with massive recent male replacement.

Conclusions

The Solutrean hypothesis (SH) currently offers an archaeological explanation for the origins of the majority of pre-Clovis cultural assemblages and their *in situ* evolution into Clovis; no such credible cultural-evolutionary sequence has been offered for Palaeolithic East Eurasia as their cultural

source. In parallel, the SH offers the only credible route-explanation for the unique, substantial presence of West Eurasian-derived X2g and X2a in the Great Lakes region of north-east America, and their antiquity. The East Eurasian ancestry of 4/5 major American founding mitochondrial lineages (A-D) is undisputed, but does not affect the above inferences.

As predicted by X2a, West Eurasian Y haplogroups have much higher absolute rates in north-east Native Americans than those in the rest of the Americas. Three recent autosomal studies have all found substantial evidence of pre-Columbian, West Eurasian autosomal admixture in Native American populations. While this has all been presumed to have arrived via Beringia, the alternative trans-Atlantic route for such gene flow was not considered or tested.

Genetic critiques of the SH and the X2a/X2g evidence for an additional Atlantic migration, including the Rasmussen, Fagundes and Hooshiar Kashani 'refutations', are argued in the form of counter-assertions, including hypothetical summary-descriptive similarities of X2a with A, B, C and D and a presumed high likelihood of extinction of X in East Eurasia, rather than hypothesis-testing and rules of evidence. However, while the SH prediction of the X2a/X2g phylogeographic-evidence continues to attract controversy, much more work is required for the rest of the genome, including balanced model-testing.

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