

Genetics of Modern Human Origins
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**Hypothesis Compatibility,
Hypothesis Testing
and Evidence Measurement:
Genetic Evidence for the Origins of Native Americans**

Introduction

The purpose of the present paper is to develop a methodological procedure of determining the evolutionary history of any human population, to generate a plot of principal hypotheses about the origins of Native Americans based on the existing archaeological, paleobiological and linguistic information and to test this plot with the currently available molecular (mtDNA and Y chromosome) evidence.

In the following, I will briefly go over the current archaeological, (paleo)biological and linguistic controversies about the relationships between the Old World and the New World and their directionality.

Archaeologists are markedly divided into three groups: a conservative majority sticking to the 12,000 BP (¹⁴C) [13,500 calendar years BP] limit of human occupation of the Americas associated with the efflorescence on the continent-wide scale of projectile points of the Clovis type and related lithic technologies; a staunch minority voting for the dates up to 40,000 years; and a small group of romantic outliers that are ready to see human touch in geological facts dating back to 100,000-250,000 years (see overviews and discussions in Meltzer, 1995; Crawford, 1998: 16ff; Dillehay et al. 1992; Dillehay and Meltzer, 1991a). The recent acceptance of the Monte Verde site in southern Chile dated to 12,500-13,500 (¹⁴C) [13,600-14,400 BP [cal.] [Dillehay, 1989; Dillehay, 1996; Fagan, 1997; Fiedel, 1999) raises the probability that other pre-Clovis sites such as Cactus Hill in southern Virginia (ca. 16,000-15,000 BP [¹⁴C]), Meadowcroft Rockshelter Stratum II in Pennsylvania (ca. 15,000-13,000 BP [¹⁴C]), Pendejo Cave in Arizona (25,000-12,000 BP [¹⁴C]), Monte Verde I (ca. 33,000 BP [¹⁴C]), Pedra Furada in Brazil (40,000 BP [¹⁴C]) indeed mark the presence of early inhabitants on the American continent.

The archaeological picture of the human presence in the Americas remains inconclusive in view of the total absence of technological parallels between highly conspicuous Clovis points and bifaces and Late Pleistocene Siberian and/or East Asian assemblages. Alternatively, the microblade tradition that distinguishes the Siberian Paleolithic beginning from 23,000-20,000 BP (Chard, 1974; Slobodin, 1999: 490ff; Kuzmin and Orlova, 1998) is not found in the Americas. The paucity of archaeological materials coupled with oftentimes bad stratigraphy and unreliable radiocarbon dates in Northeast Asia (Kuzmin and Orlova, 1998) do not provide sufficient documentation for the process of the peopling of the Americas from this part of the Old World. The situation is

further complicated in view of the fact that Clovis-type industries tend to become younger and decrease in diversity and frequency in British Columbia and Alaska along the putative ice-free corridor. Some archaeologists (Müller-Beck, 1967; Clark, 1991; Dixon, 1993: 119; also Bryan, 1969: 342; Bryan, 1991: 21) suggest that a reverse south-to-north population movement from transglacial Alaska is no less, if not more possible than the traditional conception of Siberian hunters entering the New World from the northernmost tip of East Asia. The recent discovery of an Americanoid fluted point at the Uptar site in northeast Siberia dated to 8,300 BP [¹⁴C] (King and Slobodin, 1996) together with several other complexes from the Northeast and the Amur River Basin (Ushki VII-VI (possibly no earlier than 10,500 BP (Kuznetsov, 1994: 142)), Osipovka, Serdyak, Avlondya, Ust-Belaya, Novopetrovka, etc.) featuring bifacial points typical to the earliest American cultures (including the diagnostic fluting !) (Tolstoy, 1958; Derevianko, 1969), not observed in earlier Siberian sites and dated to the Pleistocene-Holocene boundary (ca. 11,000-10,000 BP) made archaeologists hypothesize a reverse migration from America into Siberia in the early post-Pleistocene (Tolstoy, 1958; Chard, 1959; Willey, 1966: 34; Bryan, 1978: 309; Dikov, 1979a; Dikov, 1979b; Slobodin, 1999: 487). A similar idea was initially put forward by Franz Boas and other members of the Jesupian expedition, who considered the Chukchi, Koryak, Nivkh, Itel'men and Yukagir an "offshoot of the American race" (Boas, 1905; Boas, 1910), and recently supported in (Hicks, 1998).

The emerging startling controversy in American archaeology is therefore that Clovis culture long believed to have originated in the New World (Krieger, 1964: 55) shows not a population expansion from Asia but a migration from America into Asia along the Bering bridge. Paradoxically, the Clovis First paradigm is in need of pre-Clovis sites in order to sustain the claim that America was actually peopled from the Old World. The lack of reliable archaeological sites in the pre-14,000 America is consistent not only with the lack of human occupation but equally with small population size, isolation and certain patterns of mobility among the earliest Americans. Even a single archaeological site on a continent occupied by small isolated demes would count more than a series of sites left by a rapidly growing or stable large population. Thus, the sudden proliferation of sites throughout the Americas around 12,000 years may represent the upper part of a sigmoid curve, with the base of the curve lying well back in the Late or Middle Pleistocene (Whitley and Dorn, 1993; Gruhn, 1997: 30). The diversity of well-adapted cultural contemporaries of Clovis (Dillehay et al. 1992: 147; Roosevelt et al. 1996; Wright, 1999; Gruhn, 1997) makes it unlikely that the Clovis technological phenomenon represents the earliest migration from the Old World.

If Asia shows no traces of a culture that could be considered the technological progenitor of Clovis, Europe appears to provide the missing parallels. Profound technological similarities between Solutrean assemblages in the Iberian peninsula (20,000-17,000 BP) and the Kostenki culture in European Russia (33,000-27,000 BP), on the one hand, and the Late Pleistocene American bifacial points, on the other, are interpreted by some archaeologists (Greenman, 1963; Bradley et al. 1995; Pearson, 1997; Stanford, 1999) as suggesting a migration of a small European population either by an Atlantic sea route or via the Verkhoyansk range in the Ural Mountains. If the former route looks less plausible on biogeographical grounds but is supported by some

chronological correspondence, the latter scenario is more solid in terms of geography but appears unlikely because of the huge discrepancy in the dates. Alternatively, if America was initially peopled in the Southeast by a small group of sea adventurers carrying Solutrean technological characteristics, their emergence in the early Holocene Siberia may well be a part of an extensive northward-southward colonization of the Western Hemisphere. However one could also recall the Lewisville site in Texas with good stratigraphy, major Wisconsin interstadial flora and bone and charcoal dates of 38,000-37,000 BP (^{14}C) that featured crude stone tools, a Clovis-like projectile point, hearths and burned animal bones (Willey, 1966: 29-30; Krieger, 1964: 45). If a similar technological innovation could occur thousands of years before Clovis as far away as European Russia or the Iberian Peninsula, one can hardly guarantee that it could not happen in the same continental cultural context thousands of years before its major outburst. Monte Verde shows that stemmed points may have been present in the Americas prior to the Clovis horizon. However both in the case of Lewisville and Monte Verde the intrusion of later strata may account for the early appearance of this technological feature.

Science has greatly benefited from the series of recent skeletal finds in America that belong to the Late Pleistocene and Early Holocene period. Although it has long been acknowledged that modern Native Americans demonstrate morphological affinities with aboriginal Siberians, Paleoindian samples from South and North America (Lagoa Santa, Lapa Vermelha, Kennewick man, Spirit Cave man, Wizard Beach man, Buhl woman, Minnesota woman, and others) exhibit extensive heterogeneity. They are generally characterized by pronounced development of supraorbital ridges, low frontals, marked post-orbital constriction, prominent occipital tori, long crania, small mastoids, small bizygomatic breadth and prominent facial angle fall outside of the range of modern human variation and sometimes (Minnesota woman) demonstrate phenomenal divergence from living humans in multivariate and principal component analyses (Powell et al. 1999). The greatest proximity is found not between Paleoindians and modern Siberians and American Indians but between Paleoindians and the Ainu, Europeans, Southeast Asian, Australians and even Africans. The remarkable morphological difference between Paleoindians and modern Amerindians was initially interpreted as showing two waves of migration from Asia (Neumann, 1952) – an idea that received prominence in public circles after the recent dating of Kennewick man. However more evidence seems to favor a continuity-and-rapid-morphological change interpretation rather than a replacement hypothesis (Powell et al. 1999).

Thus, paleoanthropologists are inclined to locate the source population for Amerindians as well as for living northern Mongoloids, southern Mongoloids and Australians in Sundaland between 60,000-20,000 BP (Neves and Pucciarelli, 1989; Neves and Pucciarelli, 1991; Powell, 1993; Steele and Powell, 1992; Lahr, 1995: 167-169; Jantz and Owsley, 1997; Neves et al. 1999). The only Asian skull that can be firmly ascribed to this proto-population and that shows consistent parallels to the Paleoindian sample is hominid 101 from Zhoukoudian Upper Cave dated to 10,600 BP [^{14}C] (Kamminga, 1992; Neves and Pucciarelli, 1998). Certain archaic traits from this proto-population, including robusticity, have survived in living Australians, Ainu and Patagonians (Lahr, 1995; Lahr, 1996). Experts hypothesize that this proto-population represents an early migration into (South-)East Asia of anatomically modern

humans found in Africa around 100,000 BP (Neves et al. 1999). However the unique ancestral relationship of African and Near East fossils from Border Cave, Skhul and Qafzeh to proto-Asians/Amerindians and Upper Paleolithic Europeans has never been established on morphological grounds (Fruyer et al. 1993: 37). Surprisingly, the aforementioned non-Mongoloid highly heterogeneous proto-population that gave rise to living humans in Asia, Oceania and the New World is paleobiologically better circumscribed not in Southeast Asia (Lahr, 1995: 167-168) but in the Americas (Powell et al. 1999).

From the point of view of odontology, modern Amerindians together with Siberians and East Asians belong to the Sinodonty pattern (Turner, 1992; Scott and Turner, 1997). The Sinodont dental pattern marked by high frequencies of shoveling and double shoveling, enamel extensions and 3-rooted lower first molars is treated as the most complexly differentiated and specialized human type (Turner, 1992: 427-428). It is immediately related to the Sundadont pattern found in Southeast Asia and Oceania, which is distinguished by less pronounced character of those features. Sundadonts represent a more generalized dental configuration and occupy an intermediary evolutionary niche between Sinodonts and Euroafricans on the scale of dental complexity and robusticity. Australians demonstrate conspicuous local peculiarities but nevertheless are grouped by Turner and others into the synthetic proto-Sundadont or Australaisan category. The generalized nature of the Sundadont pattern has led Turner to believe that it represents the ancestral human dental type (Turner, 1992: 429). Developed in Southeast Asia between 40,000 and 20,000 BP and represented in the Minatogawa remains (17,000 BP), ancient Jomonese and modern Ainu the Sundadonty pattern was replaced during the Late Pleistocene-Early Holocene transition by the Sinodonty pattern that was carried over into the Americas. Thus, Turner suggested a late migration of Northeast Asians into the New World.

However, in agreement with craniological data, prehistoric Amerindian dental samples demonstrate higher variability than modern samples and approach the Sundadonty profile (Haydenblit, 1996; Powell, 1993). This is interpreted as indication of an earlier (pre-Clovis?) expansion in the New World, with dental similarities in modern Amerindians and Siberians/East Asians resulting from converging evolution (Lahr, 1995). The Sinodonty-Sundadonty heterogeneity of Paleoindian dentition does not match any particular Eurasian Upper Paleolithic dental plan. Some researchers find striking resemblance between certain Paleoindian specimens and the teeth from Siberian Neolithic burials (ca. 7,000 BP) (Haessler, 1999), which may not be accidental in view of the archaeological evidence for the presence of Amerindians in Northeast Siberia in the early Holocene (see above) and the presence of specifically Amerindian cranial features in Okunev and Sopka samples from South Siberia dated to 5,000-4,000 BP (Kozintsev et al. 1999).

Finally, the classification of American Indian languages remains a vexing puzzle after the vast majority of linguists (Campbell, 1997; Goddard, 1996; Heath, 1998: 143; also Morell, 1990) have dismissed the prodigious lumping effort of Joseph Greenberg (Greenberg, 1987). Greenberg believes that some 2,000 American Indian languages can be most parsimoniously grouped into three families: Eskimo-Aleut, Na-Dene and Amerind that represent three independent migrations from the Old World. Chronologically Greenberg correlated the earliest migration that gave rise to the Amerind family with the

Clovis bottomline of 11,500 BP and received support from some genetic and dental interpretations (Greenberg et al. 1986), while his opponents estimate the linguistic diversity between those American Indian languages that does not fall into the uncontroversial Na-Dene family as going back to 35,000-50,000 years (Nichols, 1990). On the global scale, American Indian languages exhibit profound phylogenetic and structural diversity that far exceeds language diversity in Africa but is overall lower than in the Old World (Nichols, 1992; Heath, 1998; Nettle, 1998).

Alternatively the Greenbergians meet Nichols' historico-typological approach to linguistic diversity (Nichols, 1992) with equally harsh criticism (Ruhlen, 1994b). Long-range comparisons have led researchers to postulate genetic connections between Na-Dene and Sino-Tibetan-North-Caucasian-Basque superphylum and between Amerind and Nostratic (Greenberg's Eurasiatic) languages (Ruhlen, 1994a). A first series of sound correspondences has been detected between Na-Dene and the Ket language in Central Siberia (Ruhlen, 1998). The fact that Amerind and Na-Dene are related to different Eurasian superphyla is interpreted as a significant evidence for multiple migrations into the New World.

Statement of Methodology

As reproduced in one of the latest issues of *Discover* (Wright, 1999: 63), the epigraphic lamentation of a National Museum of Natural History physical anthropologist was a direct response to the current crisis in the studies of the history of human presence in the Americas. The history of no other population has instigated such deep epistemological and social cleavages in the academia as the history of American Indians. Alternatively, since the discovery of the first Folsom points in 1926 and the first Clovis points six years thereafter, no significant advance in our understanding of the origins of Native Americans, the timing of their appearance in the New World, the location of their putative Old World source population or the earliest demographic parameters of Native Americans has been accomplished. Whilst the academic fights are hot, the American prehistoric "questionnaire" stays blank.

It appears that there are very few things pertaining to the origins of Native Americans that are currently known with a full degree of certainty and that are demonstrable in a multivariate system of evidence. First, humans are known to have been present in the Western Hemisphere as far south as Chile for at least 14,000 years. Second, the earliest known inhabitants of the Americas were anatomically and behaviorally modern *Homo sapiens sapiens*. Third, no pre-human hominids identified in the Old World paleontological record were present in the New World. Fourth, Native Americans remained separated from the Old World for a long period of their existence on the continent due to the post-glacial submergence of the vast Beringia landmass. Their population size at the time of European colonization amounted to only 2-8 % of the world population (ca. 10-40 million Native Americans vs. ca. 500 million as the world total in 1650). Fifth, the earliest known Native Americans demonstrate diverse intercontinental connections being morphologically associated with East, Southeast Asia and Australia, technologically – with Europe, and linguistically (if one trusts long-range comparisons) – with the whole conglomerate of Eurasian languages. The implications of the

multidisciplinary data are exceedingly complex. There are deep gaps in our understanding of the origins of Native Americans. Why the bifacial point culture so extensively represented on the whole continent has no roots in the Siberian Paleolithic but may signal the opposite: a migration of an American population into Northeast Asia in the Late Pleistocene-Early Holocene? If Clovis was not the earliest culture in the Americas, why is it so hard to detect any pre-Clovis assemblages, while archaeological signatures in Siberia are found in abundance starting from 43,000 BP? If the population size of the putative migrants in the New World was exceptionally small as compared to their source population in Asia, why skeletal remains similar to the non-Mongoloid Paleoindian populations are not found in Siberia and very rarely found in East Asia? If the first Americans were numerous and culturally diverse, why no traces of the microblade technology is found in the Americas? If humans arrived in America by only 14,000 BP, how could they develop exceptionally great language diversity in such a short period of time? If it was the consequence of a dramatic population bottleneck, what triggered, first, the rapid colonization of the whole continent by the initially small group of hunters and second, the 1000-4000-fold demographic outburst that led to the XV century Native American population size of some 40 million individuals (Crawford, 1998: 32ff; Salzano and Callegari-Jacques, 1988)?

Before embarking on genetic evidence for the origins of Native Americans, it seems necessary to construct a coherent interpretative framework that would be oriented on testing multiple hypotheses and considering multidirectional population movements. The construction of an interpretative framework involves several levels or clades: each level is organized as an opposition between its own null hypothesis and its own marked hypothesis. For every level, null and marked hypotheses exist as the only possible alternatives to each other and they should be properly identified as showing more relevance to each other than to the hypotheses belonging on a different level. Evidence for every model is measured in terms of qualitative probability that its marked hypothesis successfully rejects its null hypothesis. If evidence favoring the null hypothesis or the marked hypothesis remains inconclusive for a particular interpretative level, it cumulatively increases the evidential basis for the interpretative clade of a higher order.

This methodological idea will ensure the procedure of hypothesis testing rather than hypothesis compatibility and theory building rather than assumption collecting.

“There remains, however, a wide gap between the available theory and data; too often we fail to draw firm conclusions because our interpretation of analytic results requires that we make myriad assumptions about our data.... Often these assumptions are implicit, invisible to most. How then are we to make any progress?” (Mountain, 1998: 21).

It will also help to clearly understand, first, what is actually known and abundantly demonstrable in the evolutionary history of a population and what is simply implied for the sake of decision making in the face of uncertainty; and second, what questions and from what interpretative level any piece of information can potentially address. The ultimate aim of the cladistic interpretative analysis is to reach such a level of abstraction from which the

highest resolution of controversial information coming from different disciplines can be exercised. The point of a cladistic interpretative analysis is not to reject one hypothesis and give credence to another but to organized various hypotheses in a structure within which the best of their respective explanatory potentials can be integrated in a coherent whole.

Taking into account that no living or prehistoric Old World source population(s) for Native Americans has yet been conclusively identified and the timing of the emergence of humans on the American continent is subject to considerable controversy, I propose as the null hypothesis of the highest level the idea that Native Americans are not derivative of any Old World population. A null hypothesis serves not as an idea to be proved but an idea to be disproved: if taken into account, it allows one to see what major issues remain unresolved and what possible assumptions hamper the progress in understanding. As Meltzer and Dillehay have rightly emphasized, instead of trying to prove or disprove early dates of human presence in the Americas,

“it is more profitable to discuss the ways in which we approach and attempt to resolve this problem” (Meltzer and Dillehay, 1991: 3).

The accumulation of evidence on the evolution of *Homo sapiens* in the Old World has always been accompanied by the assumption that humans could not evolve in the Western Hemisphere. Although everything that we know about the origins of modern humans gives the idea of humans evolving in the Americas little positive weight, I believe that independent evolution is a valid null hypothesis for the discussion of the history of any continental population known to have been occupied by humans for a considerable period of time. The belief in humans colonizing the Americas from Asia became firmly established in European consciousness well before any scientific evidence could give it any empirical or theoretical support. In 1797, a land commissioner, Gilbert Imlay (Imlay, 1969: 365-366), stated that, on the basis of “familiarity, or rather identity, of the persons and manners of the Americans and those of the Tartars of the north-eastern parts of Asia”, “the more reflecting part of mankind” was inclined to think that Indians peopled America from Northeast Asia. Imlay then continued with a statement that was destined to become the cornerstone of the anthropological and folk conceptions about Amerindian prehistory.

“We may now therefore conclude that no further inquiry will ever be made into the general origin of the American tribes”.

Two hundred years later Michael Crawford (Crawford, 1998: 3-4) offers an almost exact replica of the XVIII century way of thinking.

“Since the initial European contact with the native peoples of the New World, a considerable body of scientific evidence has been compiled about the origins of these populations. This evidence indicates extremely strong biological and cultural affinities between New World and Asian populations and leaves no doubt that the first migrants into the Americas were Asians, possibly from Siberia”.

Needless to say, “strong biological and cultural affinities” have little bearing on the rejection of a null hypothesis: similarities are irrelevant to the problem of the directionality of evolution.

The failure of many American archaeologists to give credit to the null hypothesis prevents them from observing that the distribution of the earliest culture on the American continent shows a northward movement of people into Alaska and Northeast Asia and not a southward expansion of an Old World population. Thus, little common effort is invested in constructing a paradigm that would bring together all the diffused signals of pre-Clovis occupation of the continent (Alsoszatai-Petheo, 1986) – a paradigm in the absence of which the null hypothesis cannot be rejected.

As a matter of fact, current debates around Multiregional or Out-of-Africa scenarios of human evolution implicitly center around the problem of how successfully one can reject the null hypothesis for Asia, Africa and Europe. Despite the increasing dissatisfaction with the course of this debate expressed in the following commentary

“The debate has persisted and shows no sign of resolution despite the incorporation of new data and dates during the past decade” (Smith and Harrold, 1997: 113),

there are important lessons to be gained from the arguments of the Out-of-Africa proponents. For instance, it seems possible that progressive modernization of morphology observed in Asia and Africa does not automatically imply the relevance of this evolutionary process for the emergence of the ancestors of modern humans. Neanderthals persisted in Europe until 30,000-25,000 BP coexisting there with *Homo sapiens sapiens*, transitional or archaic fossils are found in China in the late Middle Pleistocene (Dali, Yunxian), Ngandong remains in Java date to 50,000-27,000 BP (Swisher et al. 1996) but neither of these populations, according to the Rapid Replacement theorists, developed into the ancestors of living humans. What, then, makes it necessary that African archaics’ or the so-called anatomically modern humans’ modernization resulted in the emergence of living human diversity? As long as living and prehistoric human populations are arguably genetically closer to one another than to any other species and anatomically-behaviorally closer to one another than to any “archaic” or “anatomically modern” groups (Howells, 1989), evidence coming from living and prehistoric human variation has a methodological priority over any interspecific comparisons. As Niles Eldridge and Stephen Gould argued,

“No theory of evolutionary mechanisms can be generated directly from paleontological data. Instead, theories developed by students of the modern biota generate predictions about the course of evolution in time” (Eldridge and Gould, 1972: 93).

The lack of conclusive evidence for the peopling of the Americas is coupled with continuing uncertainty about the origins of living humans in the Old World to the effect that the discussion of the origins of Native Americans should be more sensitive to the necessity of uncontroversial rejecting of the null hypothesis for this region.

It is worth mentioning that American Indian intellectuals and communities unanimously reject the idea of the peopling of the Americas arguing, on the basis of their oral traditions, that “Indians have always been

here” (Deloria, 1995; Riding In, 1992; Echo-Hawk, 1994; Mihesuah, 1996: 46-47). The inability of scientists to make a solid theory out of the persistent but never tested assumption that America was peopled results in various undesirable backlashes from the Native American public such as the unavailability of skeletal remains for proper long-term examination and the reluctance to provide blood samples for population genetic studies.

The marked hypothesis of the highest order boils down to the idea that the Americas were peopled from one or several locations in the Old World. It further bifurcates into two hypotheses known as “Out-of-Asia” and “Out-of-Europe”. The first one should be treated as a null hypothesis insofar as the concept of an adventitious landing of a handful of late Pleistocene would-be sailors or of a lost population from European Russia discovering an ice corridor into the New World is far less plausible on commonsensical grounds than that a group from a well populated Siberia or East Asia separates from its parent stock and expands into a newly deglaciated territory.

Within the “Out-of-Asia” interpretative level three major clades can be discerned. Specifically which location is the most likely source area for Paleoindians: Siberia and Northeast Asia or East and Southeast Asia? Was America peopled by a small group of individuals involved in a transient (leapfrogging) migration pattern (island model of colonization) or by a large body of paleo-demes involved in a demic expansion (stepping-stone model of colonization) (see, Beaton, 1991)? If a new territory is colonized from an immediately adjacent area (Northeast Asia), it is more likely that the expansion involved a large body of migrants unless there are significant geographical or climatic barriers; if a new territory is colonized from a distant area (East Asia), populational leapfrogging seems to be a more likely scenario. Finally, was America colonized by several independent migrations from different geographic areas in the Old World or from a single locale? This issue may equally belong to an “Out-of-Europe” interpretative level.

It is customary for population genetic studies to follow the trodden path provided by archaeology and paleobiology. I have only tried to expand this route by constructing a plot of different models and accentuating the necessity for a thorough testing of the null hypothesis for the origins of Native Americans. However I believe that neither archaeological, nor paleobiological perspectives can have a veto right on the models coming from genetic evidence. The continuing failure of the former disciplines to give reliable and non-subjective answers to the questions of the timing of human presence in the Americas, the demographic structure and patterns of mobility of Paleoindians, the number of waves of expansion and the location of the source population for the earliest known archaeological and paleobiological elements in the Americas leaves us with a hope that genetic data is more suitable for yielding answers to these crucial queries.

Implications of the Global Pattern of Genetic Differentiation: A Demographic Alternative to the Out-of-Africa Model of Human Evolution

Genetic evidence seems to overwhelmingly favor a single origin model of modern human origins. It is important that, in the course of the past decade, genetics has given the major impulse to the Replacement model of the origin of modern humans, which is shown by the palebiologists’ use of genetic evidence

to favor African rather than Asian fossil record (Lahr, 1996). A consistent signal of a rapid human expansion has been observed in several polymorphic loci (Cavalli-Sforza et al. 1988; Reich and Goldstein, 1998). The distribution of coalescence dates from multiple loci consistently shows the time depth of modern human genic variation on the order of 250,000-200,000 BP and not 1,8 million years as the Multiregional Candelabra model predicts (Ruvolo, 1996). Mitochondrial DNA, a minisatellite (VNTR) locus and short tandem repeat polymorphisms (STR) demonstrate that the diversity outside of Africa represents a closely related subset of the African diversity, which is unexpected if several independent lines of human evolution existed outside of Africa (Mountain, 1998: 14; Tishkoff et al. 1996; Tishkoff et al. 1998; Armour et al. 1996).

Several features in the global genetic variation point to a special position occupied by Africans: first, they possess greater diversity as compared to non-African populations has been detected for mtDNA (2.32 vs. 0.95-1.65), Y chromosome (0.878 vs. 0.718-0.779), STR markers (80.7 vs. 58.8-73.0) and a minisatellite locus (D16S309) (37 vs. 13) (Mountain, 1998: 31; Bowcock et al. 1994: 456); second, Africa harbors more distinct lines of descent in mtDNA, Y chromosome and minisatellites than is found outside of Africa, while non-Africans share a limited number of lineages (Cavalli-Sforza et al. 1988; Hammer et al. 1998; Li Jin et al. 1999; Armour et al. 1996: 156). This often appears on phylogenetic trees in the form that some Africans (usually the Khoisans and the Pygmies) comprise one branch, while other Africans and non-Africans comprise the other branch. The depth of the outlying African lineages is interpreted as evidence for their belonging to a clade ancestral to non-Africans. The greater diversity in Africa is interpreted as indicating greater time depth and greater long-term effective population size. If humans started to differentiate first in Africa and then a migration carried a subset of African lineages outside of the continent, then Africans greater effective population size automatically means greater time depth.

However this model does not cover the whole range of molecular evidence and allows alternative interpretations. First, many genetic systems do not indicate greatest diversity within Africa: 16.3 for Africans vs. 13.7-20.2 for non-Africans in classical markers, 29.7 vs. 27.5-37.9 for RFLPs, 2.11-3.1 vs. 3.09-4.41 for the level of heterozygosity and 1.61-3.5 vs. 2.41-3.48 for the number of segregating sites in the B-globin system (Mountain, 1998: 31; Bowcock, 1994: 456). Africans tend to show greater diversity in high mutation systems and not in low mutation systems, which is incompatible with the idea of a bottleneck that separated two populations in the course of the exodus out of Africa and can be explained as a response to rapid population growth resulting in large effective population size (Templeton, 1999: 637-638). Great genetic distances separating the Khoisans and the Pygmies from both other Africans and non-Africans or phylogenetic trees showing Africans and non-Africans on different sides of a neighbor-joining tree can be a function of geographical distances in the Wright model of isolation by distance with restricted gene flow (Templeton, 1999: 638-640). Long branches that usually appear in dendrograms for the Khoisans and the Pygmies can result from a past bottleneck with subsequent isolation (Livshits and Nei, 1990).

Templeton (1999) suggested that the patterns of modern human genetic variation can be better explained as reflecting recurrent gene flow between Africa and Eurasia during the whole time period marked by coalescence

estimates. Rogers and Jorde (1995) suggested that, if Africa was colonized from Asia earlier than Europe, this would be consistent with the pattern of greater African diversity and separation. One can also hypothesize that several chronologically distinct migrations into Africa with various degrees of isolation between the constituent groups and their source population(s) and between the constituent groups within Africa could result in the observed pattern of African variation. At least three distinct population clusters in Sub-Saharan Africa defined linguistically as the Khoisan, the Nigero-Kordofanian and the Nilo-Saharan families oftentimes appear on genetic maps (Cavalli-Sforza et al. 1988; Watson et al. 1997: 695). Early admixture between initially distinct groups can easily be expected for the Khoisans and Nilo-Saharans in East Africans, between the Bantu and the Khoisans in South Africa, between Nigero-Kordofanians and the Pygmies in Central Africa (Excoffier et al. 1987).

Distinctive features (or implications) of the single origin scenario include cladogenesis (in contrast to anagenesis in the Multiregional model), multiple species in the Old World that became extinct or replaced by *Homo sapiens sapiens*, small disjunctive isolated demes, small effective population size (ca. 10,000 breeding individuals per generation in contrast to 100,000 individuals in the Multiregional model), bottlenecks, rapid expansions, patchy geographic distribution (Howell, 1999: 202).

I believe that the interpretative clade of the Recent Single origin of modern humans bifurcates into two alternative hypotheses as to the location of the homeland. The two alternatives within the Single Origin interpretative clade can be discerned in the two types of interpretations of phylogenetic trees constructed on the basis of the global mtDNA variation. The earliest cladogram of restriction site morphs offered in (Johnson et al. 1983) showed highest diversity in Africans and several distinctive lineages within Africa. The authors suggested two possible roots of the tree. One is based on central types, namely the types that demonstrate the highest worldwide frequencies. According to the neutral theory, the highest frequency of a type equals the probability of it being the oldest. The other is based on the midpoint estimate and shows the main clade comprising Orientals, Amerindians, Caucasians and the Bantu, and a separate clade embracing the variation among the Khoisans. The first interpretation locates the root outside of Africa, the second interpretation locates the root within Africa (**Fig. 1**). In 1989, Excoffier and Langaney (Excoffier and Langaney, 1989: 127) and, in 1990, Excoffier (Excoffier, 1990: 75) arrived at essentially the same tree and, on the basis of a frequency analysis, located the root (type 1) outside of Africa (**Fig. 2**). If Oriental and Caucasian variation derived directly from the ancestral type, the African variation stemmed mostly from more peripheral types 7, 10, and 2. Templeton (1993: 60-64) corroborated the Excoffier-Langaney interpretation with his nested cladistic analysis and located the root in the clade 3-1, i.e. outside of the range of African haplotypes. Students of the Y chromosome and B-globin variation have encountered the same controversy in the global tree interpretation and suggested a compromise in the form of the initial Out-of-Africa expansion with a subsequent return of Asians to Africa that accounted for the majority of African Y chromosome diversity (Hammer, 1998; Li Jin, 1999; Harding et al. 1997).

This asymmetry inherent in the majority of dendrograms has led several researchers to postulate the departure of the human genetic variation from

neutrality or from the mutation drift equilibrium (Excoffier, 1990; Merriwether et al. 1991). Excoffier (1990: 134-135) suggested that the departure from neutrality stems from the overly high frequencies of the ancestral type in Caucasoids and Orientals resulting from some selective pressure. However it seems counterintuitive that the high frequencies of the ancestral type represent aberrance. Quite on the contrary, if all human types coalesce to the ancestral one, then at the time of coalescence the latter must have been close to fixation. Merriwether et al. (1991) proposed exactly the opposite explanation to the departure from equilibrium, namely the excess in the number of segregating sites as compared to the overall level of diversity (**Fig. 3**) due to the long-term rapid growth of human populations. It appears that the excess in the number of segregating sites in the human genome derives largely from its excess in African populations (especially in high mutation systems) that leads to the “primary split” between Africans and non-Africans observed in a number of dendrograms. One could see a reason in believing that the lack of equilibrium in the human genome stems from the excess in frequencies of the most common type(s) only if the specifically African (Khoisan and Pygmy) rare types were found at high frequencies in Eurasia. This would have signaled a dramatic bottleneck in non-Africans as compared to Africans (Watterson, 1984). However actually one observes exactly the opposite: typical Eurasian alleles are found in slightly lowered frequencies in Africa, while rare African alleles are not found in Eurasia. It may be that Africans, or at least a portion of them, have experienced a severe prolonged bottleneck followed by a rapid population growth that fixed certain private variants (see, Neel and Thompson, 1978) not found in Eurasia.

Rare African haplotypes can be considered ancestral to the human tree only if they represent lineages retained from the *Homo erectus* stage. This is hard to test in the absence of DNA from *Homo erectus* but, if it were the case, then the earliest human population did not pass through a bottleneck, or, in other words, the speciation was phyletic and not lineage-splitting. This, however, contradicts the overwhelming evidence for reduced genetic diversity in humans and their genetic and morphological isolation from other species.

The aforementioned characteristics of the modern human demographic history as seen through the Recent Single Origin lens conceal two possibilities: either the initially large human population experienced steady growth in size without fissioning into small isolated demes, then a rapid demographic outburst that after a lengthy period of time resulted in an expansion outside of the homeland; or the initially small human population remained constant in size (or experienced a slow growth) and differentiated into small isolated demes with little gene flow among them; then a number of demes from a certain area left the continent and experienced rapid demographic growth with continuous expansion into different areas, with multiple bottlenecks, isolation by distance, gene flow and fusions; the isolation between the parent population and the source population resulted in no gene flow between the small parent population and the exponentially growing daughter population.

If one accepts the former scenario, then Africa indeed figures as the most likely source for the modern human expansion. The greatest diversity and divergence of African lineages implies that non-Africans emerged as a result of a bottleneck that occurred when a significant amount of genetic diversity has already accumulated in their parent population and that this large parent population has already become significantly distinct from other large

populations on the continent. However this evolutionary pattern is exactly what constitutes the core of the arguments of the proponents of Multiregional developments (large population size, no bottlenecks (in Africa), natural selection, etc.).

If one is willing to consider the other scenario, then Africa appears as the least likely candidate for the origin of modern humans, with its excessive diversity resulting from several continuous migrations of groups that at various times experienced bottlenecks of different duration and that some of them have been connected by gene flow with different populations outside of Africa. Ultimately the African genetic specificity will boil down to the retention of large effective population size *after* the initial rapid population growth. Thus, in the second model, modern humans' homeland will be marked by limited genetic heterogeneity, while the increase in genetic diversity and distance will be proportionate with the increase in geographic distance from the homeland. Since the level of diversity is different for different loci in different populations, this scenario could also affect different genetic systems in some non-African populations.

The first scenario (Out-of-Africa) will also imply the general northward decrease in genetic diversity, while the second scenario will imply the general increase in genetic diversity with latitude. Humans tend to sustain greater population size in tropical areas that results in greater genetic and linguistic diversity there (O'Rourke et al. 1985; Nettle, 1999). Multiple migrations are also likely in a southward direction, as the demographic history of demic expansions in Southeast Asia, Australasia and Africa (Bantu), with few migrations in northern Europe and Asia, seem to suggest (Renfrew, 1992).

Amerindian populations have long been considered good examples of early human demes (Neel, 1970; Neel, 1978), and it is not unlikely that they may provide important clues to what should be expected from a small population expanding to colonize a vast geographic area, from a population that evolves in isolation or from a series of populations coming from different locations at different times to reconnect through gene flow and admixture – questions that are so relevant to the contemporary discussions of modern human origins. As Rick Ward states,

“...Amerindian populations have mostly evolved without experiencing the mass population movements that occurred on the Eurasian and African continents. Consequently, Amerindian populations not only offer an exceptional opportunity to study the effects of evolution in situ, but may also provide a paradigm for much of the evolutionary history of modern *Homo sapiens*” (Ward, 1997: 37).

The rapidly growing scale of molecular penetration into the origins of Native Americans can hardly be grasped in a single paper, so the following discussion will be restricted mainly to the mtDNA and Y chromosome variation. The emphasis will be laid on the former genome, with the Y chromosome variation used to test the patterns observed in the mtDNA.

Mitochondrial DNA Studies of Native Americans: History and Current Perspectives

Johnson et al. (1983) provided the first global distribution of mtDNA haplotypes defined through the utilization of a number of restriction endonucleases, *HpaI*, *BamHI*, *HaeII*, *MspI*, *Avall*. Thirty-two fragment patterns yielded 35 different combinations (haplotypes). For four restriction sites, American Indians demonstrated ancestral combinations at 100% frequencies. The fifth restriction site was not informative because of the deficiency of the sample. The overall pattern involved progressive increase in the frequencies of the ancestral type from Africa to Europe, Asia and America with the concomitant reduction of diversity of mtDNA types (**Fig. 4**). American Indians demonstrated the least departure from the ancestral state and the least mean distance.

Wallace et al. (1985), Excoffier and Langaney (1989) and Schurr et al. (1990) offered essentially the same picture of the position of Amerindian variation in the global pattern and provided information about the state of the *HaeII* morph in Amerindians that Johnson et al. failed to elucidate (**Table 1**). Morph 1 showed at 90% frequencies in the Ticuna (South America), at 100% frequencies in the Maya and at 92% - in the Pima (North America). All values for the ancestral type were higher in America, than in Asia. The Pima contained greater diversity in this site than Asians and other Amerindians. An additional restriction site identified by Wallace et al. and Schurr et al., *HincIII*, showed a similar pattern: the Maya had morph 2 at 89%, the Ticuna - at 58% and the Pima - at 55.4%, with four other morphs. Asians gave also a high value for the ancestral fragment pattern (83.4%) and diversity lower than among the Pima. Morph 6 at this site was found at high frequencies in the Pima and Ticuna and at low frequencies in Asians, which made the researchers propose a “dramatic founder event” that occurred in the course of the colonization of America. Four founding lineages were detected from which all the observed Amerindian diversity could be derived by a minimum number of nucleotide substitutions. These four lineages defined by 1) *HincII* morph 6 (site loss at np 13259) and an *Alu* site gain at np 13262), 2) COII-tRNA^{Lys} intergenic 9-bp deletion and the lack of the *HincII* morph, 3) *HaeIII* site at np 663, 4) *AluI* site loss at np 5176 were initially referred to as respectively AM2, AM6, AM10 and AM1 haplotypes and later renamed C, B, A, D haplotypes. AM1 was put in the center of the overall phylogeny in accordance with Johnson et al.’s ancestral morph (Schurr et al. 1990: 618). All four founding sequences were also observed in Asia, although neither Asia, nor America yielded the haplotype that would connect AM 1, AM 6 and AM 2 with AM 10.

A more extensive analysis with 14 endonucleases of 17 Amerindian populations confirmed the presence of the four founding lineages that accounted for 96.9% of Amerindian mtDNA variation (Torrioni et al. 1992; Torrioni et al. 1993a; Torrioni et al. 1993b). The fifth founding lineage, X, characterized by a *DdeI* site loss at np 1715 and np 10394 has been recently identified in the representatives of seven linguistic families in North America, with the highest frequency (25.7%) in the Chippewa and the overall position in Amerindian variation of 3% (Brown et al. 1998; Smith et al. 1999). Unlike the other four lineages, lineage X is absent in Asia but is present at low frequencies in virtually every European group (Indo-European and Basque) and at 40% frequency in the Caucasoid Druze (T. Schurr, personal communication). The reduced median network of Amerindian lineages is shown in **Fig. 5**.

The distribution of the five Amerindian haplotypes is non-random: lineage A shows a trend of increasing frequency from south to north; the frequency of lineage B increases from north to south in North America and Central America and from south to north in South America and Central America; lineages D and C generally have higher frequencies in South and North Americas, with a decline in Central America (Merriwether et al. 1995: 418-421). In Siberia, lineages C and D are found at slightly elevated frequencies (e.g. 58.1% of C₁ in the Evens, 59.3% of C₁ in the Yukagirs; from: Easton et al. 1996: 218). Lineage A rises to high frequencies in some Na-Dene and Eskimo groups in America and in the Siberian Chukchi.

Surprisingly, lineage B has not been found in Siberia. In America it displays a radiation pattern of distribution, with zero frequencies in the extreme north (among the Eskimos and the Northern Athabascans) and extreme south (Tierra del Fuego) (Merriwether et al. 1995: 420; Fox, 1996: 866). In the Old World, the 9-bp deletion is found in one North Altai individual, in the Yukagirs (although against a lineage C background, i.e. with presence of the *HincII* 13259 site loss and the absence of *HaeIII* 16517 site gain) (Merriwether et al. 1996: 205), among the Mongolians (2.38%) (Merriwether et al. 1996), Chinese (7%), Japanese (19%), Koreans (15%), Ainu (1,5%), Malays (3%) (Fox, 1996: 867, percents read from a chart), Negritos, Coastal New Guineans, eastern and western Micronesians, Filipinos and Vedda, and in high frequencies among the Maori, Fijians, Samoans (90%), Cook Islanders, Tonga (100%), Nieu, Hawaiians (95%) (Harihara et al. 1992; Lum et al. 1994; Melton et al. 1995; Cann and Lum, 1996). The cases of a 9-bp deletion representing two independent origins – one from the Asian clade, the other from local development – were reported from Western Australia (Betty et al. 1996). A 9-bp deletion is further reported in the Pygmies (Mbuti 30%, Efe 30.3%), Malawian (26.7%), Lemba (26.9%), Sotho-Tswana (20.4%) and other Bantu and in the Nilo-Saharan Luo (1.7%) (Soodyall et al. 1996: 595). It was found in a single European individual but against a different haplotypic background (Soodyall et al. 1996: 603).

Soodyall et al. as well as argue for possible independent origin of the African and European deletion, although length mutations are far more rare compared to simple point mutations. There is evidence for a 9-bp deletion with the typical Asian-Amerindian sequence pattern in West Africans (Merriwether et al. 1995: 424). In other parts of the world, the deletion is also thought to have arisen multiple times but it nevertheless implies a “single ancient [deletion – G.D.] event” (Wallace and Torroni, 1992: 408; Santos et al. 1994: 971). The presence of a 9-bp deletion against a different lineage in the Yukagirs, who live between the areas of the “classical” Asian deletion, suggests that this marker may stand in a phylogenetic relationship to other variants of the deletion in Asia and America (comp.: Fox, 1996: 868).

The mtDNA genome among the Amerindians shows diverse links with Old World populations: lineages A, C and D are found in Siberia, at low frequencies in South East Asia (Ballinger et al. 1992), A and C were observed in several European individuals; lineage B is found in East Asia, Southeast Asia, Oceania and, possibly, in Australia and Africa; lineage X relates Amerindians to Europeans. Although, in terms of the number of polymorphic sites, Native Americans are extremely homogeneous and comprise the smallest portion of the global diversity (comp. 50 haplotypes encompassing 68 sites in the Americas vs. 106 haplotypes encompassing 191 site in Asia (Wallace and Torroni, 1992: 408-

409, with the sampling limited to that time) (**Fig. 6**), which is consistent with them having the smallest continent-specific population size; their lineages appear in all major world clusters – a situation opposite to that of Caucasoids with very narrow range of sequence divergence and limited number of segregating sites, on the one hand, and to that of Africans with very specific and divergent lineages (Horai et al. 1993: 40-41). Africans and Australians appear to be most divergent from Amerindians, which appears to be correlated with their greatest geographical separation. The presence of the 9-bp deletion in Amerindians, Asians, Australians and Africans may represent either an ancient mutation event or several independent developments. The highly divergent African clade found mostly in the Khoisans and the Pygmies is the only clade that does not include Amerindian lineages (Horai et al. 1993: 42).

Africans are also exact opposites of Amerindians in terms of site diversity, which correlates with them having the greatest long-term effective population size. What also appears to be true is that the paucity of informative restriction sites in Amerindians means that they display ancestral monomorphic states for the sites, which are polymorphic in the Old World – an observation that first emerged in the works of Johnson et al. and Excoffier and Langaney. Meanwhile the small fraction of the mtDNA genome, which is polymorphic in the Americas, displays diverse associations with other continental populations.

Control region (CR) analyses that usually duplicate global phylogenies with higher resolution reveal a different situation in the Amerindians. Average nucleotide diversity among Amerindian lineages (1.30%) approximates the worldwide value of 1.44. A number of Amerindian groups even exceeds the latter value (Cumbal 1.50, Yaldad 1.58, Paraquina 1.75) (Horai, 1993: 29). The Nuu-Chah-Nulth (Nootka) from British Columbia has become the classical case of an Amerindian tribal group with phenomenal mitochondrial diversity. In their early report (1991), Ward et al. mention 28 lineages defined by 26 variable positions, with average sequence divergence of 1.49%. This amount of diversity corresponds to 81% of diversity in urban highly heterogeneous Japan and 62% of diversity among 57 Sub-Saharan lineages. Direct comparisons with the !Kung (Vigilant et al. 1989) showed that the Indian tribe was twice as diverse as the African group (1.09% divergence in the !Kung). Ward et al. (1993) reported similar values of nucleotide diversity for other North American Indian tribal groups. Subsequently Ward (1997) identified additional 9 variable sites and 5 lineages in the Nuu-Chah-Nulth. The total of 35 sites and 33 lineages exceeds by the order of magnitude micro-differentiation among the !Kung (16 sites) and the Pygmies (17 sites in the Biaka) and approximates the nucleotide variation in such African groups as the Kanuri, the Songhai and the Hausa, whose population size is 100 times greater than that of the Nuu-Chah-Nulth (Watson et al. 1996: 439) (**Table 2**). Native Americans demonstrate that intertribal diversity (6.5 substitutions) is only marginally greater than intratribal diversity (5.8 substitutions), whereas in Africa the intertribal divergence (9.95 substitutions) is twice as great as the average intratribal sequence variation (6.1.) substitutions (Ward, 1997: 46). Greater population size of Sub-Saharan Africans can account for the slightly higher values of sequence variation than in the Americas. It has been noticed that in Africa greater diversity is found among food-producing and not hunting-gathering societies (Watson et al. 1996; Templeton, 1999).

Extensive mitochondrial micro-differentiation within Amerindian tribes echoes the situation with classical nuclear markers (Crawford, 1998). For instance, genetic differentiation among Yanomamo villages as measured by the fixation index (F_{st}) is greater than among the three major continental groups in the Old World (Hartl and Clark, 1989: 302). As in the case with nuclear markers (Neel, 1978; Neel, 1973; Chakraborty, 1988), the frequency of occurrence of rare mitochondrial lineages in Amerindian tribes is extremely high, i.e. on the order of 75% of the total number of lineages (Richards et al. 1999: 525). The situation is remarkably similar to the pattern of Amerindian linguistic differentiation: long-range comparisons detect a certain unity within the Amerind cluster, while short-range comparisons identify high variability among the languages and the lack of demonstrable lexical and grammatical relationships.

Another important characteristic of the American Indian mitochondrial variation is mutation-drift equilibrium suggested in (Chakraborty and Weiss, 1991) and supported by Ward et al. (1993) and Bailliet et al. (1994). Thus, the idea put forward by Excoffier (see above) that the whole human genome demonstrates a departure from neutrality was challenged for Native Americans. Previously mutation-drift equilibrium was demonstrated for the Native American nuclear variation. The immediate implication of this finding is the constant size of the Native American populations, which is observed also in non-unimodal distribution of pairwise sequence differences (Horai, 1993; Stone and Stoneking, 1998: 1163; Rienzo and Wilson, 1991: 1600) and in positive or insignificantly negative values of Tajima's D (Stone and Stoneking, 1998: 1159) in most tribal groups. Mutation drift equilibrium also complicates the establishment of founder sequences and coalescent times and marks the absence of a departure from selective neutrality. The correlation between coalescence dates in the Old World and the New World populations may not be very consistent. Interestingly enough, mutation-drift equilibrium was not observed in the Haida that belongs to the Na-Dene linguistic cluster (Ward et al. 1993).

Interestingly enough, Tajima's D estimates for the four principal founding lineages in the Americas consistently yield large negative values (Stone and Stoneking, 1998: 1166, with -1.9694 for A, -1.9873 for B, -1.8047 for C and -2.1172 for D; Bonatto and Salzano, 1997a: 1418, with -2.363 for A, -2.359 for B, -2.226 for C and -2.060 for D in the hypervariable segment I), which signals large haplotype expansion. It is unclear why the highly differentiated polyphyletic Amerindian populations that supposedly carry along their diversity from the time of their occupation of Asia do not show population growth, while haplotype expansion is statistically very significant. Updated coalescent times for the four haplotypes are shown in **Fig. 7**. All of them fall within the range 35,000-50,000 BP (10.3% mutation rate) or 25,000-40,000 BP (15% mutation rate). The lack of difference in the distribution of coalescence times for all haplogroups is equally strange taking into account the prediction that in exponentially growing populations coalescence times for different lineages are different (Slatkin and Hudson, 1991: 559). If the statistically detected expansion of haplotypes means rapid population growth, then one would expect to observe excessive variability in segregating sites in Amerindians but this is far from being the case. However it was observed (Bonatto and Salzano, 1997: 1416) that, in an Amerindian sample, polymorphisms exist only in one sequence or

are shared by a small fraction of sequences, with no substitution occurring in more than 20% of the haplogroup sequences. In other words, the polymorphisms at individual sites consist of one mutant and the rest of the sample will have the ancestral nucleotide at the site. This marks exponential growth from a single ancestral sequence (Slatkin and Hudson, 1991: 559).

The emerging picture derived from the studies of mitochondrial and nuclear variation in the Americas presents Native American populations as slowly expanding from a single small source located either in the Old World or in the New World around 40,000-50,000 BP. No rapid expansion associated with the putative arrival of Clovis hunters around 12,000 BP is supported by the mtDNA evidence. Even if the mutations occur at a faster rate, the demographic parameters visible in modern Native Americans seem to rule out any late expansive entry into the uninhabited continent.

The mitochondrial pattern outlined above creates continuous puzzles for the geneticists who try to determine the relationships between the Old World and the New World populations. A well-known paper that attempted to bring together linguistic, genetic and dental information on the origins of Native Americans advance a hypothesis about three waves of colonization of the New World, namely the Amerind, the Na-Dene and the Eskimo-Aleut expansions (Greenberg et al. 1986). On the basis of reduced sequence diversity in Na-Dene, Torroni et al. (1992) suggested two independent migrations into the Americas. Horai et al. (1993) argued for four migrations basing on the diverse relationships between the four Amerindian haplotypes and the Old World clusters. Merriwether et al. (1995) and Kolman et al. (1996), Forster et al. (1996), Karafet et al. (1997); Stone and Stoneking (1998), Novick et al. (1998), Bonatto and Salzano, 1997a; Bonatto and Salzano, 1997b) convincingly showed, both from the point of view of mtDNA and Y chromosome, that the Amerindian genetic variation represents a unity of diverse lineages. It was pointed out that all four principal Native American mtDNA haplotypes are evenly distributed throughout the Americas and are found in the Amerind, Na-Dene and Eskimo-Aleut clusters and that it was unlikely that the same combination of lineages entered the Americas in three or two chronologically separate waves. Since the 9-bp deletion is absent in Siberia, Mongolia, or broader East Asia/South Siberia was proposed as a likely source territory for human expansion into the New World. It is in this area that the four primary haplotypes was recorded at noticeable frequencies (Merriwether et al. 1995; Kolman et al. 1996).

The discovery of the fifth founding lineage, F, undermines this interpretation, since the X haplotype is not found in Siberia, Mongolia or East Asia. The simplest explanation is that this lineage was lost in Asia but this is not convincing because, assuming greater population size in Asia, lineages like X or B had a greater chance of being preserved there and not in America. However the reverse is true. Furthermore, in Mongolia, the four other lineages do not show monophyletic clustering (Kolman et al. 1996: 1326).

If lineage X was brought to North America with a separate wave of migrants from Europe, why it is not found in northern Na-Dene or Eskimos. If it somehow figured into the New World via an Atlantic sea route, why no other typical European marker has been brought along. Furthermore, no correspondence exists between molecular dates for the peopling of the Americas and the Clovis horizon: mtDNA times of diversification consistently point to an

early pre-Clovis emergence of humans on the American continent. Nucleotide diversity values from Mongolian groups show little difference from the diverse Amerindian lineages ($\pi = 0.018$ for all Mongolian samples, 0.016 for the Dariganga and 0.018 for the Khalkha vs. 0.014 for the Japanese and Southeast Asians, 0.014 for Siberians, 0.017 for the Altai, 0.016 for the Nuu-Chah-Nulth, 0.018 for the Mapuche, 0.015 for the Yakima, Bella-Coola and prehistoric Oneota (Kolman et al. 1996: 1328; Stone and Stoneking, 1998: 1159)). Kolman et al. (1996) used the $E(\nu)$ parameter to measure long-term nucleotide diversity. It gave significantly higher values for the Mongolians as compared to Siberians, the Kuna and the Embera. However, first, these American Indian tribes have reduced overall diversity in the Americas and, therefore, may not be representative, and second, $E(\nu)$ estimates diversity on the basis of restriction site differences (Excoffier and Langaney, 1989: 76), which may be not reliable in view of the disequilibrium state of the Old World variation. No sign of a population bottleneck has been detected in Amerindian variation. In Siberia, lineages A, C and D are no older, if not younger than in the Americas (Starikovskaya et al. 1998: 1486), while the other Siberian haplotypes are of a more recent origin.

Available data seems to indicate that the distribution of Amerindian haplotypes in Eurasia may be equally explained as the migration of a highly micro-differentiated Amerindian group into the Old World. The absence of a well circumscribed source population for Amerindians in Eurasia contrasts with the existence of this population within America itself, and it may be more parsimonious to view the distribution of Amerindian lineages in Eurasia as an admixture from America. Having this hypothesis in mind, one can settle down several vexing contradictions: the detection of the expansion of lineages A, B, C, D in American samples and the absence of bottleneck traces and the constant population size in modern Amerindian variation; the unity of the Amerindian cluster and the variety of connections between its constituents and the Old World clusters; a similar pattern of variable linguistic relations between Amerind and Nostratic/Eurasiatic and Na-Dene and Sino-Tibetan; the greater diversity of the Amerind cluster as compared to Na-Dene, Eskimo-Aleuts and Siberians and the departure from mutation-drift equilibrium among Na-Dene indicating a movement northward and not southward. In this case, Mongolia/East Asia/South Siberia would figure as an important springboard for the spread of the 9-bp deletion further south into Sundaland and Oceania (comp. Ballinger et al. 1992). The presence of Paleoindians in East Asia can be further seen in the Zhoukoudian skull coming from the period, which is ca. 1000 years later than the age of Clovis. An Amerindian group carrying lineage X could contribute to the genetic pool of Caucasoids. In this case, one does not need to ponder about an adventitious penetration of a European group into the Americas but instead takes this connection as having its roots in a wider expansion event.

However outlandish this perspective may seem, it is a possible reading of the available genetic and archaeological data on the contacts between America and Siberia in the Late Pleistocene. At least the Chukchi that are mitochondrially closer to Native Americans than to other Siberians (Starikovskaya et al. 1998) may represent remnants of the expansion of Paleoindians into Alaska and Northeast Asia. Y chromosome clearly shows the

presence of the major Native American haplotype DYS 199 T in the Chukchi (Karafet et al. 1997; Santos et al. 1999).

The search for the origins of Native Americans should be placed on a deeper chronological level: archaeological and genetic evidence seems to agree that, for the Late Pleistocene, the null hypothesis for the Americas can not be successfully rejected. America may not be a recent offshoot of an Asian population but a continent that participated in the making of the modern human genetic variation. Unfortunately, I am not able to review the Y chromosome information pertaining to the origins of Native Americans but it appears to give additional support to the possibility of an Amerindian expansion into the Old World.

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