

## **Part 2. The Interdisciplinary Context for Dene-Yeniseian**

### **GENES ACROSS BERINGIA: A PHYSICAL ANTHROPOLOGICAL PERSPECTIVE ON THE DENE-YENISEIAN HYPOTHESIS**

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#### **1.0. INTRODUCTION**

In the Boasian triad of race, language and culture (Boas 1940), anthropologists have long acknowledged that the process of change, or evolution, accelerates as one moves from biology, to language, to culture. Deducing deep historical relationships based on cultural elements is difficult, given the ease of borrowing (diffusion) and the rapidity of developing and adopting new ideas (innovation) or losing old ones (cultural drift/selection). Despite its comparable potential for horizontal as well as vertical transmission, language is still much more conservative than culture. Linguistic ties can often be perceived over many millennia, though there is no consensus among historical linguists on the temporal limits of establishing 'genetic' relationships. Given the well known case of Indo-European languages, most would agree that recognizable linguistic similarities can persevere for at least 5000 years. Beyond that temporal limit, the consensus among linguists falls apart. Manning (2006) sets the range from about 5000 to 10,000 years. Biology, in the form of observable (cf. skin, hair, eye color), measurable (cf. stature, cephalic index), morphological (cf. shovel-shaped incisors, fingerprint patterns), and genetic traits (red blood cell antigens, serum proteins, red cell enzymes, DNA polymorphisms), is much more conservative than language. Biological affinities are evident among populations whose linguistic ties are entirely obscured. For example, there is no obvious connection between Indo-European and Caucasian, but the biological similarities of speakers from these two language families is observed consistently across many biological systems. Eskimo-Aleuts and American Indians, whose linguistic affinities are blurred by the passage of time, also have biological ties that are clearly discernible. For these examples and more, see Cavalli-Sforza et al. (1994) for genetic markers and Scott and Turner (1997) for tooth crown and root trait frequencies.

The linguistic similarities between members of the Na-Dene and Yenisei language families demonstrated by Edward Vajda, Merritt Ruhlen (1998), and others (i.e., Dené-Yeniseian hypothesis), can only be fully appreciated by those with training in linguistics. Our goal is to survey the literature in physical anthropology and genetics that has some bearing on the linguistic hypothesis linking Dené and Yenisei speakers. In the case of Na-Dene, that involves populations from Alaska and western Canada who are referred to as northern Athapaskans (e.g., Kutchin, Tanana, Koyukon, Ahtna, Ingalik, Tanaina, Dogrib, Slave, Tutchone, Beaver, etc.), recent migrant populations to the American Southwest who are called southern Athapaskans (Navajo, Apache), and the more distantly related Tlingit on the coast of southeast Alaska. There are few biological data available for Athapaskan groups from California (Hupa), the Plateau (Nicola) and northern

Plains (Sarsi). While the Na-Dene family is represented by several dozen distinct groups in North America, the only surviving speakers of Yenisei are the Kets of central Siberia.

In reviewing the literature, we found only one instance where geneticists tested explicitly the Dené-Yeniseian hypothesis (Rubicz et al. 2001). Most research deals more broadly with peopling of the New World, genetic differentiation among Siberians in a broader Asian context, or the interrelationships among Native American populations. Out of a substantial, albeit relatively recent literature, we focus primarily on genetic analyses that have the most direct bearing on the proposed linkage of groups in America (Athapaskans and Tlingits) and Asia (Kets).

### 1.1. Methods

We employ two primary methods to address the issue of biological relationships between Kets and Na-Dene-speaking populations in the New World. The first method is biodistance. That is, researchers compile data on multiple variables across a range of populations and then employ distance statistics to determine relative pairwise similarity among groups. Say, for example, you have three samples: A, B, and C. Assume further that the pairwise distance values are A-B (0.50), A-C (0.50), and B-C (0.25). In this instance, B and C are most similar to one another and both are equally distant from A. Given a number of assumptions about methods of observation, evolutionary mechanisms, number of variables, etc. (cf. Scott 1992), the inference is that B and C share a common ancestor more recently than either group shares with A. This could be illustrated in a dendrogram (tree) or two dimensional diagram. Of course, no analysis is this simple but the general principle remains the same. Relatively small distance values between groups suggest a recent common ancestry, while large distances indicate a common ancestor at a more remote point in the past. The second method revolves around the presence or absence of shared and unique alleles or haplogroups. For example, do Kets and Athapaskans share an unusual gene/haplogroup that is never, or rarely, observed in other groups? When focus is on a single genetic marker, no distances are calculated nor are trees plotted. If Kets and Athapaskans share a unique allele, this would support the proposition of direct biological affiliation.

Given the literature at our disposal, it would be difficult to summarize and reanalyze data from earlier studies. However, we can extract the essence of the issues we are addressing. For example, from a biodistance standpoint, where do Kets fall in relation to Siberian and Native American population? Do they cluster most closely with Siberian or New World populations? Are there any overall linkages to Na-Dene in any particular genetic system? Are there any unique or rare genetic markers that indicate shared ancestry between Kets and Athapaskans in the early Holocene?

## 2. BIODISTANCE

Ruhlen (1998:13,994) proposed a distant linguistic relationship between speakers of Yeniseian and Na-Dene based on “36 sets of cognate words that appear to be shared by Yeniseian and Na-Dene, but not (for the most part) by other language families.” Given the distance involved between surviving members of these families, notably Kets in central Siberia and Athapaskans/Tlingits in the Americas, he ruled out borrowing as a possible explanation for the shared similarities. He concluded that many millennia ago, Na-Dene and Yenisei speakers formed a single population in Eurasia. “Part of this population migrated to the New World, giving rise to the Na-Dené languages, while the portion of the population that remained in Asia gave rise to the Yeniseian languages” (Ruhlen 1998:12,995).

Around the time Ruhlen (1998) was proposing a genetic relationship between Yeniseian and Na-Dene on linguistic grounds, Michael Crawford and his students and colleagues were pursuing genetic studies among Siberian populations. As Crawford had conducted field research in two Ket villages, he and his co-workers were in a position to test Ruhlen’s hypothesis using genetic data. A genetic test of the proposed linguistic hypothesis was published in an article entitled “Genetic Evidence for the Phylogenetic Relationship between Na-Dene and Yeniseian Speakers” (Rubicz et al. 2002).

The genetic data used by Rubicz et al. (2002) included eight alleles at four blood group loci, three alleles

at two immunoglobulin loci, and four mitochondrial haplogroups. The authors focused on the four mtDNA haplogroups that characterize ca. 97% of all Native Americans (i.e., A, B, C, D), but they did not consider subtypes or other common Asian and Eurasian haplogroups. In their analysis, they employed the method of Harpending and Jenkins (1973) to calculate a matrix of pairwise population distances. The distance matrix was subjected to principal components analysis, the final product of which was two eigenvectors representing the first and second principal components (PC) that were plotted on a two-dimensional map. When samples are plotted by PC I and PC II, proximity on the map indicates relative genetic similarity. The method also allows researchers to plot the location of alleles/haplogroups on the map to show how each gene (or haplogroup) contributes to the pattern of relationships.

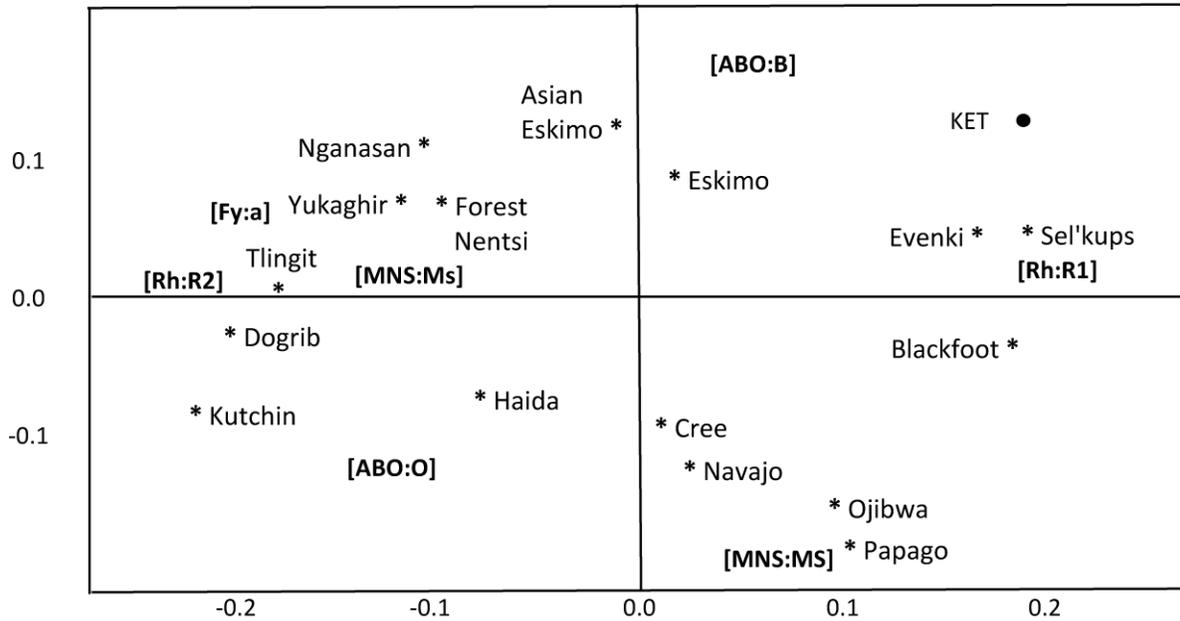
Two of the eigenvector plots provided by Rubicz et al. (2002) are redrawn as Figures 1 and 2. Figure 1, based on the analysis of seven alleles, includes seven Asian and ten New World samples. The first principal component (PC I) separates groups horizontally while PC II separates groups vertically. Kets are found in the upper right quadrant in close proximity to their Siberian neighbors, the Evenki and Selkups. Northern Athapaskans (Dogrib, Kutchin) and the Tlingit are distantly removed from the Kets on PC I and also show some separation on PC II. The Navajo are in the lower right quadrant, between two Algonquian groups (Cree, Ojibwa) and the Papago, a placement largely attributable to admixture with non-Athapaskan groups in the American Southwest (Cavalli-Sforza et al. 1994; Malhi et al. 2007; Scott and Turner 2008).

The key phenotypes or alleles that separate northern Athapaskans from Kets are  $RH^*R1$  and  $RH^*R2$  in the Rh system and  $ABO^*B$  in the ABO system. Genetically, Athapaskans show a number of distinct differences from North and South American Indians, although Algonquians and Northwest groups are exceptional to some extent (Szathmary 1979, 1981, 1984, 1993; Szathmary and Ossenberg 1978). For example, Athapaskans typically have a moderately high frequency of blood type A, an allele lacking in most Indian groups outside northern North America. In the complex Rh system, the  $RH^*R1$  and  $RH^*R2$  phenotypes dominate as they do with all American Indians but the ratio is reversed. In Athapaskans,  $RH^*R1$  is less frequent than  $RH^*R2$  while most other Indian populations consistently have much higher frequencies of  $RH^*R1$  (O'Rourke 2006). North Asian populations, like the Chinese, Japanese and Koreans have an  $RH^*R1/RH^*R2$  ratio similar to that of most American Indians (ca. 65%  $RH^*R1$ , 30%  $RH^*R2$ ). In central Siberia (e.g., Nganasan, Forest Nenets, Selkups), groups have a reversed  $RH^*R1/RH^*R2$  (ca. 40%  $RH^*R1$ , 55%  $RH^*R2$ ) ratio, comparable to that of Athapaskans. The  $ABO^*B$  allele, extremely common throughout much of Asia, is rare or absent in Athapaskan and American Indian populations (Mourant 1954; Mourant et al. 1976; Roychoudhury and Nei 1988).

Figure 2 is an eigenvector map based on frequencies of the mtDNA haplogroups A, B, C, and D. In this instance, the Kets cluster closely with Siberian populations who have relatively high frequencies of haplogroups C and D. The separation from Athapaskans is also pronounced because of their high frequency of haplogroup A. Although the Apache and Navajo line up with other Native American on PC I, admixture with non-Athapaskan groups in the American Southwest has increased their frequency of haplogroup B. Northern Athapaskans either lack or have a very low frequency of haplogroup B. Most Athapaskans are characterized by a high (or fixed) frequency of haplogroup A and a low frequency of haplogroup D. In southern Athapaskans, this profile includes haplogroups C and D obtained through gene flow with surrounding non-Athapaskan groups.

Given the relative distances between Athapaskans and Kets, Rubicz et al. (2002) conclude that genetic data do not support Ruhlen's Dené-Yeniseian hypothesis. They note that genes are more highly correlated with geography than with language (Hunley and Long 2005, Novembre et al. 2008, but cf. Belle and Barbujani 2007) and conclude "Contrary to Ruhlen's interpretation of the linguistic data, analysis of the genetic data shows that the Na-Dene cluster with other Native American populations, while the Kets genetically resemble the surrounding Siberian groups" (Rubicz et al. 2002:743).

Insofar as their data go, the interpretation of Rubicz et al. (2002) of no Dené-Yenisei linkage is accurate. However, there are limitations to their analysis. First, they rely on a small set of nuclear loci and alleles. Although this is dictated in part by the tests they conducted and available data in the literature, it is a modest sampling of a genetic profile. In their worldwide analysis of nuclear genetic markers, Cavalli-



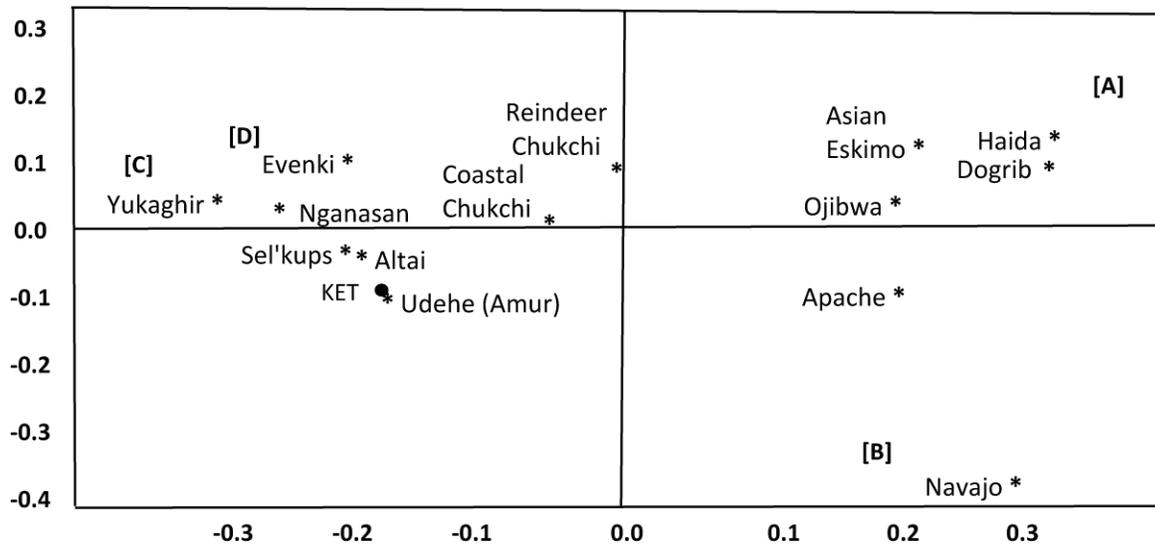
**FIGURE 1.** Relationships among Native American and Siberian populations based on six blood group alleles (adapted from Rubicz et al. 2002).

Sforza et al. (1994) evaluate patterns of variation based on over 120 alleles. As Livingstone (1991) noted, the precision of a distance study is strongly influenced by the number of variables used. Second, the power of mtDNA haplogroups to detect subtle relationships would be enhanced by a consideration of mutations in the control and coding regions that help define the subtypes of A, B, C, and D.

While most recent research on human population history has focused on nuclear genetic markers and mtDNA or Y chromosome haplogroups, the human leukocyte antigen (HLA) system also provides useful insights into origins and affinities. Uinuk-ool et al. (2002, 2004) analyzed the frequencies of 33 HLA class II alleles at the system's three most polymorphic loci (*HLADR\*B1*, *HLADQ\*A1*, *HLADQ\*B1*) in a wide range of world populations. We focus on the variation of Kets and Athapaskans in a broader Siberian-Native American milieu.

A dendrogram redrawn from Uinuk-ool et al. (2004) is shown as Figure 3. In the original and highly detailed dendrogram, there is a nested hierarchy of populations beginning with Africans, Europeans, and non-Siberian Asians. The only portion redrawn in detail shows the Siberian Asian and Native American branches. Beyond minor nuances, there are three major divisions in this section of the dendrogram. First, two Ket samples, along with the Evenki, Nganasan, Tofalar, and Tuva, separate from other Siberians at the first division. The second division separates North, South, and Central American Indians from a multi-branched grouping that includes Athapaskans and Eskimos on the one hand and six Siberian populations (Negidal, Nivkh, Udegey, Koryak, Chukchi, and Siberian Eskimo) on the other. In some respects, this finding corresponds to the position of Rubicz et al. (1998) that Kets cluster with Siberian populations and Athapaskans cluster with Native American populations. However, the placement of Athapaskan within a group of Siberians adds another dimension to this study. American Indian groups south of the subarctic are the most highly differentiated from Asian populations while Athapaskans and Eskimos exhibit more genetic similarities to Old World groups for alleles of the HLA system.

Bortolini et al. (2003) analyzed eight biallelic and six microsatellite polymorphisms on the non-recombining portion of the Y chromosome in several dozen Asian and New World populations. They found that the most common haplogroup in American Indians was Q-M3 (77%), with much lower frequencies of Q-M242 (9%), Q-M19 (6%), P-M45 (4%), Y\* (2%), and YAP (<1%). This contrasts markedly with their Na-Dene

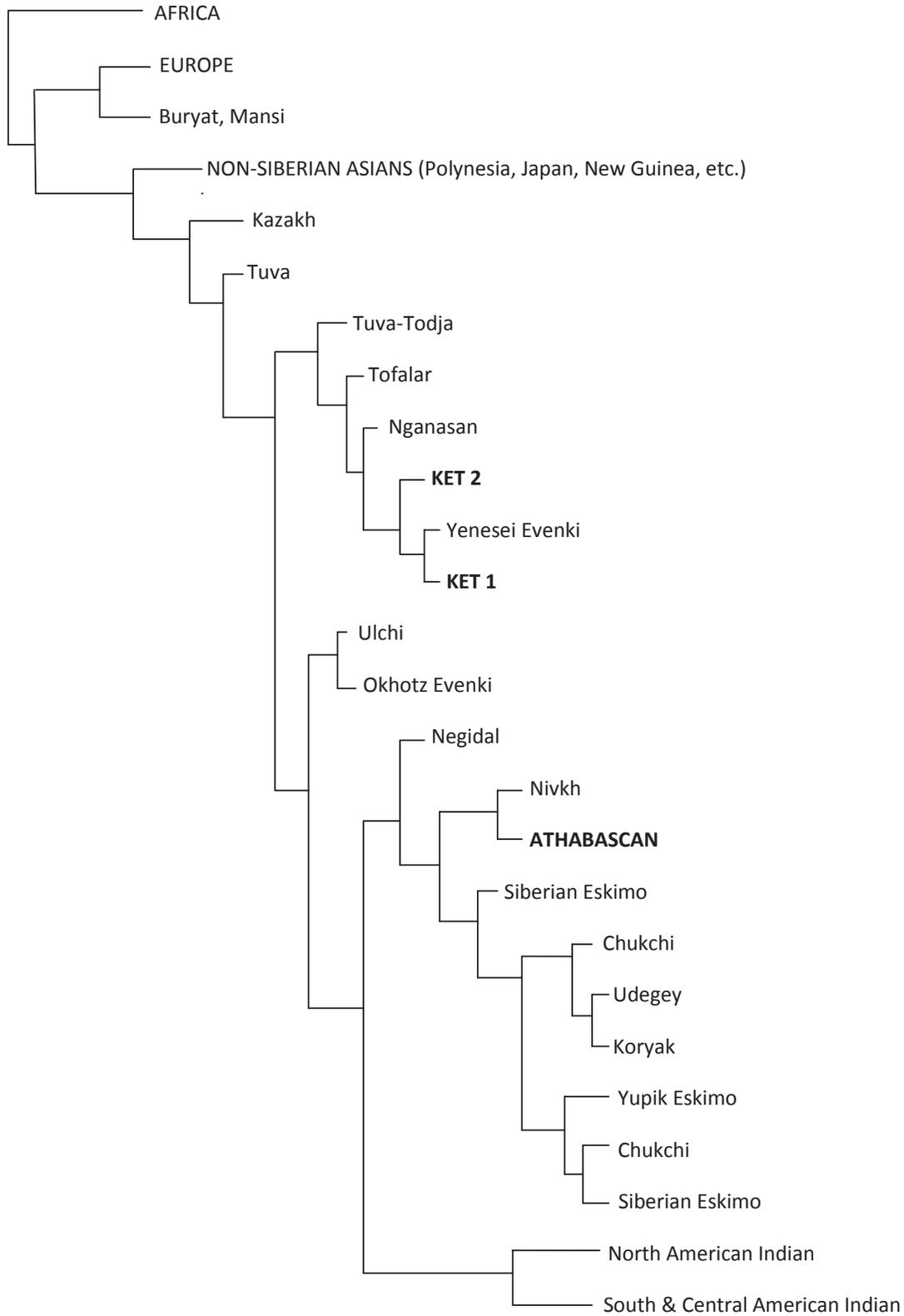


**FIGURE 2.** Relationships among Native American and Siberian populations based on four mtDNA haplogroups (adapted from Rubicz et al. 2002).

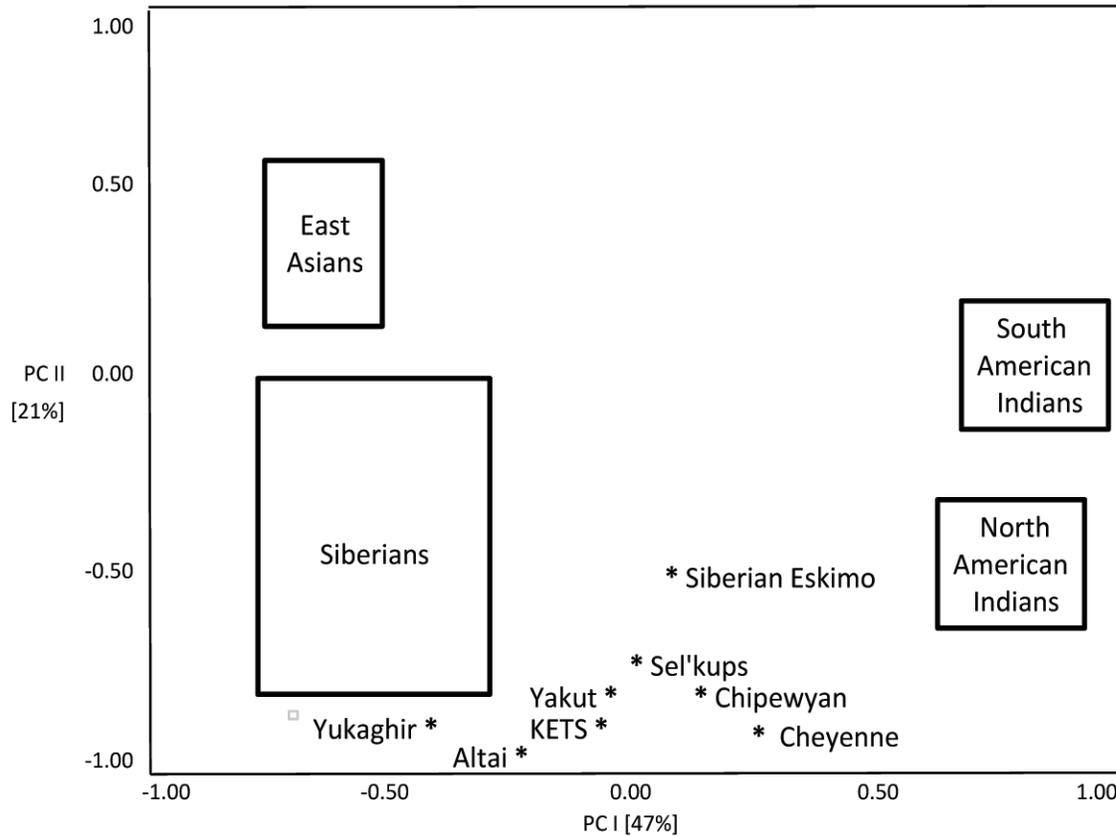
sample where the most common haplogroup is P-M45 (63%), followed by Q-M242 (25%), Q-M3 (6%), and C-RPS4y (6%). The latter haplogroup is lacking in American Indians, Africans, and Europeans but is very common in Mongolian populations (56%).

Bortolini et al. (2003) analyzed Y chromosome polymorphisms by principal components analysis and derived a two dimensional map (redrawn as Figure 4). For ease of viewing, when many groups were clustered together in a two-dimensional diagram, they were drawn as a rectangle that encompasses most of the variation in a particular region. East Asians, Siberians, and North-South American Indians are represented in this fashion. The only groups plotted individually were the Kets and the groups most similar to them. Kets fall between several Siberian groups (Yukaghir, Altai, Yakut, Selkups) and two American Indian groups (Chipewyan = Canadian Athapaskan and Cheyenne = Plains Algonquian). Based on these results, Bortolini et al. (2003:535) conclude that “The principal component analysis . . . suggests a close genetic relatedness between some Native Americans (the Chipewyan and the Cheyenne) and certain populations of central/southern Siberia (particularly the Kets, Yakut, Selkups, and Altai), at the resolution of major Y-chromosome haplogroups.”

Starikovskaya et al. (2004) tried to link New World and Asian populations through an analysis of 31 mtDNA subhaplogroups in 16 Siberian populations. They found that haplogroup A is relatively uncommon in Siberian groups but is nonetheless widespread in distribution. However, this haplogroup (defined by the 663 *HaeIII* site and HVS-I motif 16223-16290-16319-16362) is classified as A1. It lacks the mutation at np 16111 shown by A2 which distinguishes American Indians, Siberian Eskimos and the Chukchi. Haplogroup B, distinguished by a nine base pair deletion (8281-8289 del) and a control region motif of 16189-16519 was defined by five subtypes (B1-B5) in Siberian and Native American populations. Amerinds share five mutations (499, 827, 4820, 13590, 15535) with the Tubalar who are placed in the B1 subhaplogroup. The Native American subhaplogroup, designated B2, has additional mutations at nps 3547, 4977, 6473, and 11177 that have not been observed in Siberian populations. Haplogroup C, defined by the 13262 *AluI* site and HVS-I motif of 16223-16298-16327, was in high frequency throughout Siberia. The three subtypes of C (C1, C2, C3) all included mutations at nps 3552-9545-11914-13263-14318-16327. Of the three C subhaplogroups, Native Americans were most similar to the Ulchi, a Tungusic-speaking group from the lower Amur River region, sharing a mutation at 16325 and a 290-291 del. Additional mutational differences resulted in the placement of the Ulchi in C1a and American Indians in C1b. Starikovskaya and her colleagues (2004) found



**FIGURE 3.** Dendrogram based on HLA class II genes (adapted from Uinuk-ool et al. 2004).

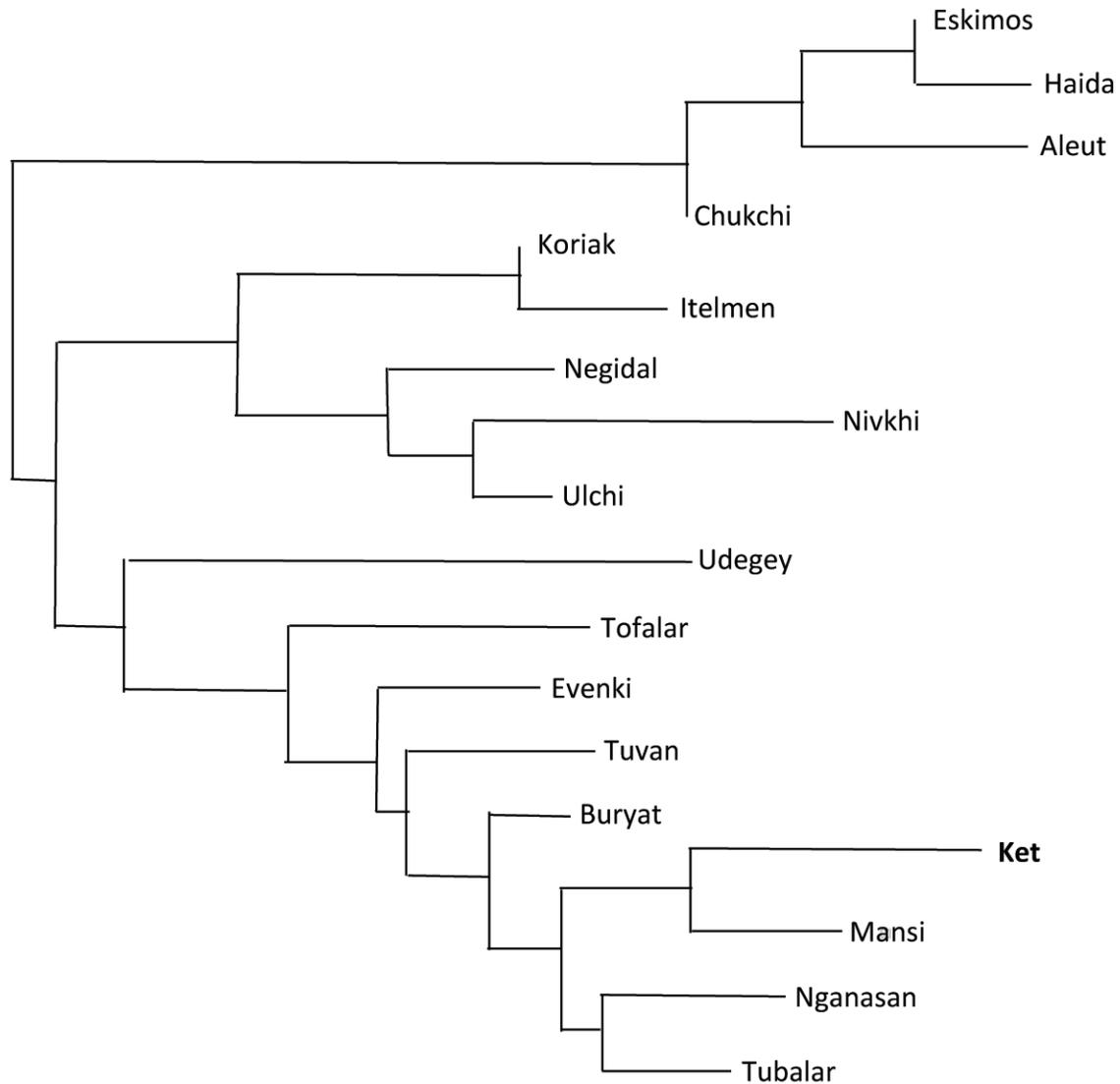


**FIGURE 4.** First and second principal components derived from analysis of Y chromosome polymorphisms (adapted from Bortolini et al. 2003).

that haplogroup D, defined by the lack of an Alu site (*-AluI* 5176) and an HVS-I motif of 16223-16362, typically lacked subhaplogroup mutations in Siberia. However, they found five subtypes of D that are pertinent to the issue of Asian-New World relationships. D1, defined by a mutation at np 16325, is typical of Native Americans who have haplogroup D. This subhaplogroup was also observed in four Ulchi but no other Siberian or east Asian population. The authors suggest a link between lower Amur River populations and Native Americans. Another D subhaplogroup, D2, is defined by the absence of the 3315 *HaeIII* site, the presence of the 8700 *AluI* site, defining substitutions at 16129 and 16271, and a motif of 3316-7493-8703-9536-11215-11959 (Tamm et al. 2007). Of interest here is that D2 is found only in Na-Dene (D2a), Aleut (D2b), and Eskimo (D2c) samples.

Using frequencies for 31 subhaplogroups of A, B, C, and D, Starikovskaya et al. (2004) derive a dendrogram for 16 Siberian and two Native American samples using a neighbor-joining method (Figure 5). Athapaskans are not represented in this tree, but Kets are included. In this milieu, heavily weighted by Siberians, the Kets cluster most closely with the Mansi, followed by the Nganasan and Tubalar. Their next closest ties are to other central Siberian groups. Groups from the Amur River basin and Kamchatka fall on another cluster. Not surprisingly, the two Native American groups (Haida, Aleut) are on the same branch of the tree, along with Siberian Eskimos.

From the standpoint of mtDNA, there are few subhaplogroups that directly link Siberian and Native American populations. Since Asian groups started making the trek across far eastern Asia and Beringia, enough time has passed to allow a number of unique mutations to appear in Native American groups. Despite this, Starikovskaya et al. (2004) feel they can make inferences about how Native American progenitors may go back to different regions of central and east Asia. For haplogroup A, the authors suggest that “the A1 mtDNAs observed in the Mansi and Kets are part of an A1 northward dispersal that presumably originated



**FIGURE 5.** Dendrogram based on analysis of 31 mtDNA subhaplogroups (adapted from Starikovskaya et al. 2004).

in the Altai-Sayan region, and gave rise to A2 after expanding into eastern Beringia” (Starikovskaya et al. 2004:85). For haplogroup B, the B1 variant is the only one that shares a coding region motif of 827-4280-13590-15535 with the Native American subhaplogroup B2. As this was observed only in one Tuvan and three Tubalar, this also points to the Altai-Sayan upland as the likely source of the Native American B2 subtype. For haplogroup C, the C2 and C3 subtypes are common in central Siberia but these differ notably from the C variant in Native Americans. Amerinds, who exhibit the C1b subhaplogroup, are most similar to the Ulchi who have the C1a subhaplogroup. This suggests that some Native American populations emerged from the Amur River region. Haplogroup D also seems to point to the Amur region. Subhaplogroup D1a, observed in four Ulchi, is the only variant related to the D1b variant that characterizes American Indians. While some subhaplogroups of C and D point to the Amur River region as a possible point of origins for American Indians, Native Americans also have C1c and C1d with specific coding region mutations that seem to be independent founding lineages not known in Asia (Tamm et al. 2007). In addition, D2 developed in

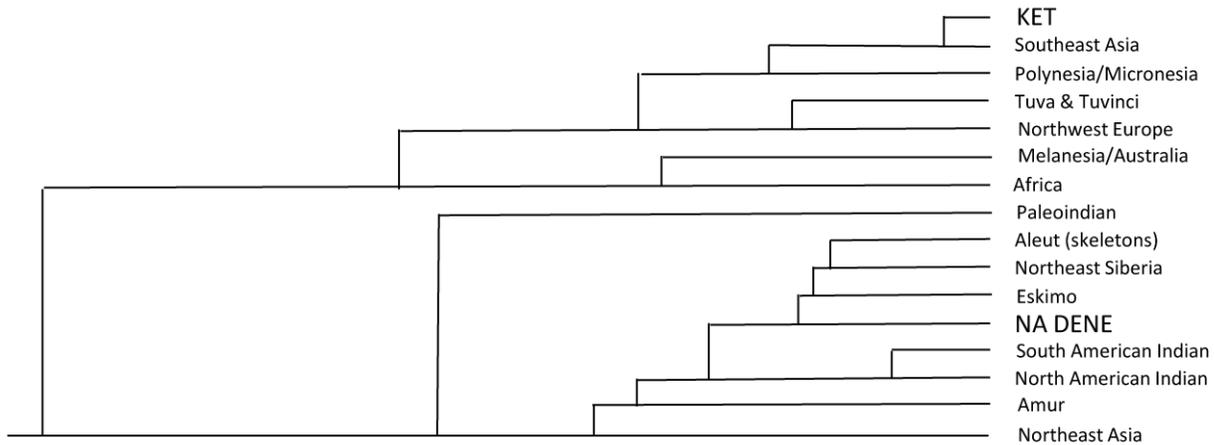


FIGURE 6. Dendrogram of world populations based on analysis of tooth crown and root morphology (adapted from Turner 1984).

Beringia, where Alaskan (Na-Dene, Aleut, Eskimo) and Chukotkan (Eskimos, Chukchi) populations express the variant.

From a dental standpoint, Athapaskans exhibit characteristics that are shared with other populations in the New World. That is, high frequencies of shovel-shaped incisors, incisor winging, cusp 6 and the protostylid of the lower molars, and low frequencies of lower premolar multiple lingual cusps and lower molar cusp 7. Carabelli's trait is common but is rarely expressed in cusp form. Two rooted lower canines, found almost exclusively in European populations, are absent in Athapaskans. Three-rooted lower first molars, the trait that gave rise to the three wave model of Greenberg et al. (1986), are in a frequency of about 20%, intermediate to Eskimo-Aleuts (>30%) and American Indians (6–8%) (Turner 1971).

While there are abundant dental morphological data on Athapaskans, comparable information is far more limited for the Kets. Turner (1984) observed a small sample of Kets for 29 tooth crown and root traits and calculated distance values between this sample and many Asian and New World populations. The dendrogram shown as Figure 6 is based on mean measure of divergence (MMD) distances between these populations. The Kets are the only small sample in the dendrogram. All others are composites based on hundreds or thousands of individuals.

Dentally, Kets do not exhibit the highly specialized dentition associated with Sinodonty (Turner 1987, 1990) that typifies populations in north and east Asia and all of the Americas. Instead, they show the more muted morphological profile that characterizes southeast Asian populations. In a worldwide analysis of dental morphological data, Scott and Turner (1997) found a similar grouping. East Asians (Japan and Taiwan) clustered with Native Americans while Southeast Asians and the Ainu clustered with central Siberians (Ugrian, Samoyedic, Altaian). Basically, the Kets dental profile is intermediate to the more distinctive European and Asian dental patterns, where the former is distinguished by morphological simplification and the latter is characterized by intensification of trait expression (e.g. shoveling, winging). For many other traits, Kets are intermediate to Europeans and north/east Asians (e.g. shovel-shaped incisors, double shoveling, cusp 6, hypocone, 2-rooted upper first premolars, etc.). For the hallmark trait Turner (1971) used to define three colonizing groups to the Americas (Eskimo-Aleut, Na Dene, Amerind), 1 of 20 Kets exhibited a three-rooted lower first molar. Although sample size is small, a frequency of 5% is closest to that of Amerinds.

Distance analyses that involve Kets, Athapaskans, and other Siberian, Asian, and New World populations show consistently the shared ancestry of all these groups. For the most part, however, Kets seem to be more closely aligned biologically with their Siberian neighbors than with any Native American population, including Athapaskans. However, Athapaskans, like Eskimo-Aleuts, have closer ties to Siberian populations

than do most other American Indians.

## **2.1. Rare variants and unique genetic markers**

Biodistance studies, by their very nature, may not be sensitive enough to pick up hints of deep common ancestry between two specific groups. Rare markers provide another avenue to evaluate a potential ancient genetic linkage between Kets and Athapaskans.

### **2.1.1 *mtDNA: haplogroup X***

Mitochondrial DNA haplogroups are denoted by letters (with subtypes noted by numbers and small case letters) running the alphabet from A to Z. For historical reasons, the first four letters of the alphabet, A, B, C, and D, were the haplogroups associated with all Native American populations (Wallace and Torroni 1992). Later, it was discovered that these four haplogroups accounted for 97% of the variation but there was another haplogroup, X, that was present in about 3% of Native Americans. To date, haplogroup X is most common in Algonquians (Ojibwa) where it occurs in a frequency of about 25%. It is about half that common in Siouan and Northwest Coast samples (Bianchi and Bailliet 1997; Ward et al. 1993). It has not been reported for American or Siberian Eskimos (Shields et al. 1993; Torroni et al. 1993). Although Torroni et al. (1993) and Brown et al. (1998) found haplogroup X in six out of 92 Navajo (6.5%), it was not evident in small samples of Apache ( $n=25$ ) and Dogrib ( $n=30$ ).

Initially, the discovery of haplogroup X led some workers to argue that Europeans had brought the variant across the Atlantic because, at the time, haplogroup X had not been found in any Asian populations. This position has now been modified on two grounds (Reidla et al. 2003). First, there are two primary types of haplogroup X, X1 and X2. X1 is known almost exclusively from Africa. While X2 is the haplogroup found in both Europeans and Native Americans, the 225A variant of X2 (X2b) characterizes most Europeans (25 of 27; Brown et al. 1998). The X2 haplotypes without the 225A mutation (X2a) characterizes most but not all American Indians. Moreover, most American Indians have coding and control region mutations that are not found in Europeans. While the X2 haplogroup does suggest a common ancestral population for Europeans and American Indians, the mutational differences that set the two groups apart indicate great time depth for this shared ancestry.

When Siberian populations, including Buryats, Tuvinians, Koryaks, Evens, Yakuts, Khakassians, Shors, Soyots, Altaians, and Evenks, were tested for haplogroup X, it was found only in seven Altaians (2 North, 5 South) (Derenko et al. 2001). None of the seven possessed the 225A variant common in European populations. However, they also lacked the 200G and 16213A mutations that characterize most American Indian X haplogroups. Reidla et al. (2003) report that two Evenks from central Siberia also have haplogroup X but neither showed the mutations characteristic of the Native American X2a subtype (one was X2b and the other X2\*). A reduced median network shows that Altaians are intermediate to European and American Indians for haplogroup X and may represent the stem ancestor for both groups (Derenko et al. 2001). Although central Siberian and New World populations share a low frequency of haplogroup X, the X2a subtype in Native Americans, defined by five mutations in the mtDNA coding (8913, 12397, 14502) and control regions (200 and 16213), has not been found in Asia. For the Kets, Derbeneva et al. (2002) did not report a single haplogroup X of any type, although the sample size was small.

### **2.1.2. *mtDNA: RsaI np 16,329 site loss***

For mitochondrial haplotype A, Native Americans have both subtypes A1 and A2, although the latter is more common. Significantly, there is a site loss associated with some A2 subtypes that has been found only in Na-Dene populations. Torroni et al. (1992:157) note that "This mutation occurs in all Nadene populations examined (50.0% of Tlingits, 26.7% of the Dogrib, and 27.1% of the Navajo), but not in Amerinds. Therefore, the RsaI np 16,329 site loss appears to be a specific genetic marker for the Nadene." Torroni et al. (1993) use this unique marker to argue that there was an independent origin of Na-Dené and American Indian populations in the New World. Interestingly, it is not present in the Haida (Merriwether 2006), a group that

some linguists put in the Na-Dene language family while others do not. A genetic variant unique to Na-Dene would be the ideal genetic bridge to central Siberia. Unfortunately, the RsaI np 16,329 site loss has not been reported in Kets or any surrounding central Siberian group.

### 2.1.3. *mtDNA: A2a subtype*

The five major mtDNA haplogroup lineages that entered the New World (A, B, C, D, and X) are now specified more precisely in terms of subtypes defined by mutations in the hypervariable (HV I and HV II) and coding regions. For Native Americans, Tamm et al. (2007) distinguish four major founding subtypes (A2, B2, C1, D1) and three minor subtypes (X2a, D2, D3). Of particular interest is subtype A2a which differs from A2 in having a coding region mutation at np 3330. Tamm et al. (2007) show a phylogeny of human mtDNA with special emphasis on New World and Asian populations. The branch of A2 is dominated by North and South American groups, but the marker A2a was observed in a North American Indian, a Siberian Eskimo/Chukchi, and, importantly, one Selkup. How this rare variant ended up in a central Siberian group can only be conjectured. While the Selkups are not Kets and they speak a different language (Uralic), the Kets and Selkups are closely aligned in many dendrograms, perhaps reflecting the role of geographic propinquity on historical patterns of gene flow. Another possibility is that this marker was reintroduced from the east during the Holocene as proposed under one dispersion model by Fortescue (this volume).

### 2.1.4. *Autosomal locus D9S1120*

Zhivotovsky et al. (2003) analyzed 377 autosomal short tandem repeat loci in 52 populations to assess the broad pattern of differentiation and dispersal of modern human populations on a world scale. The authors found one private allele that was limited to Native American populations. In fact, this was the only private allele they found that was exclusive to one geographic area. The 275 bp allele at the autosomal microsatellite locus D9S1120 was found in frequencies ranging from 0.20 to 0.30 in four American Indian populations (Maya, Pima, Colombians, Karitiana). A fifth Indian group, the Surui, had an exceptionally high frequency of 0.97, probably attributable to founder effect and genetic drift.

The discovery of a unique allele at the D9S1120 locus stimulated Shroeder et al. (2007) to survey this polymorphism in additional Native American and Asian populations. Specifically, they assessed the frequency variation of the D9S1120 275 bp allele in one Aleut, one Eskimo, two Na-Dene, nine North American Indian, and seven Siberian populations. Their findings corroborated and extended those of Zhivotovsky et al. (2003). That is, the allele was found in moderately high frequencies in all the newly sampled Native American groups, including Aleuts (0.229), Greenlandic Inuit (.387), and North American Indians (0.100–0.529, mean = 0.301). Two Na-Dene samples (Dogrib, 0.309; Apache, 0.313) had frequencies similar to those of Eskimo-Aleuts and American Indians.

The D9S1120 allele is not unique to Native Americans as it was found in the Chukchi (0.238) and Koryak (0.174) who are reckoned as far eastern Siberian or western Beringian groups. This is not altogether surprising as these Siberian groups often show genetic similarities to Native American populations (cf. Cavalli-Sforza et al. 1994). What is more interesting is that central and south Siberian groups, often thought to be the most likely source populations for Native Americans, lack this allele entirely. Samples lacking the allele include the Even, Mongolians, Altai Kazakhs, and Yakuts, along with many additional groups from the Altai (southern and northern) and north, east, and southeast Asia. Unfortunately, the Kets were not one of the Siberian groups sampled for this 'private' Native American allele. Despite this, even if found among the Kets, it would still not provide evidence for a direct Dene-Yenisei biological linkage because the allele is about equally common in Eskimo-Aleuts, the Na-Dene, and North and South American Indians.

### 2.1.5. *Albumin Naskapi (AL\*Naskapi)*

A rare albumin variant, referred to as albumin Naskapi, was first noted in a sample of Naskapi Indians from eastern Canada (Melartin and Blumberg 1966). Although originally found and named for an Algonquian population, a survey of this polymorphism in dozens of tribes and thousands of individuals in

North and Middle America, has shown this variant to be as common in Athapaskans as it is in Algonquians (O'Rourke 2006). In fact, the overall frequency in Athapaskans (3.4%) is slightly higher than the frequency in Algonquians (3.1%) (Scott and Turner 2008). The most remarkable aspect of this allele is that it is found only rarely outside of Athapaskan and Algonquian groups and in every such instance, groups that did have one or a few individuals with *AL\*Naskapi* were adjacent to either an Athapaskan or Algonquian group (e.g., three Ungava Bay Eskimos, three Sioux Indians, one Maricopa Indians, one Mohave Indians) (Schell and Blumberg 1988). Gene flow is the likely explanation for those rare instances where it is found outside the realm of Athapaskan-Algonquian speaking populations. More recently, it was found in 11 Bella Coola Indians (Salishan) and one Nootka. For these Northwest Coast groups, shared common ancestry is a more likely explanation than gene flow (Smith et al. 2000).

Beyond its presence in Athapaskans and Algonquians, the pattern of absence of *AL\*Naskapi* is interesting as well. Except for the three Ungava Bay Eskimos who were heterozygous for this allele, no additional cases surfaced in surveys encompassing over 1600 Eskimos, 100 Aleuts, and 450 Tlingit. In 20,218 Native North Americans (including some mestizos), over 95% of the *AL\*Naskapi* phenotypes are exhibited by either Athapaskans or Algonquians. *AL\*Naskapi* is almost totally absent in the Old World as well. In Eti Turks, an albumin variant referred to as Albumin Mersin exhibited a migration pattern on starch gel electrophoresis identical to that of *AL\*Naskapi* (Franklin et al. 1980). In two samples of Eti Turks, the frequency of this variant was around 9%, but not all surveyed Eti samples had the allele. Kaur et al. (1982) also report an albumin variant with properties similar to *AL\*Naskapi* in north India. Beyond these groups, this rare albumin variant has not been reported in any of the Asian populations that typically show genetic affinities to Native American populations. As deriving Athapaskans and/or Algonquians from Eti Turks or North Indians seems unlikely, the possibility exists that the gene arose independently in the New World and Old World.

Although using *AL\*Naskapi* to link Na-Dene populations and the Kets is not possible at this time, this is the kind of allele that would be useful in demonstrating an ancient genetic link between two groups. If the gene arose through mutation in the New World, it would not help corroborate Ruhlen's (1998) view that Na-Dene and Yenisei groups were derived from a common Eurasian stem population. However, finding *AL\*Naskapi* in the Kets could support one Fortescue model that holds there was an east to west movement of Dené-Yeniseian-speaking populations in the Holocene.

#### **2.1.6. Y chromosome markers**

Underhill et al. (1996) report a mutation on the non-recombining portion of the human Y chromosome that is unique to Native Americans. The locus, referred to as DYS199, is 201 bp and contains a C → T point mutation. In 173 individuals from Africa, Asia, Oceania, Europe, and the Americas, 45 exhibit the C→T point mutation and all 45 are Native Americans. The mutation is more common in American Indians (38/42, or 0.904) than Eskimos (4/6, or 0.667) and the Navajo (3/6, or 0.500), but the samples are too small to reach a conclusion on Native American heterogeneity. Suffice it to say that the allele is common to all Native Americans and seems to be in relatively high frequency. Unfortunately, the only Asian groups sampled were from China, Japan, and Cambodia.

Santos et al. (1999) evaluated Y chromosome polymorphisms in Native American and Siberian populations, including the Kets, and observed several interesting points. For example, most Native Americans fall in haplotype 31 which includes the DYS199 T SNP. Haplotypes 1 and 10 were the next most common in Native Americans; neither included the DYS199 T mutation but did include the 92R7 variant. For Kets, haplotype 20 was the most common and this was shared with one Native American, one Mongolian, and four Altaians. Two Kets also exhibited haplotype 32 which includes the DYS199 T mutation. However, we still face the problem that this seemingly unique American marker is not just in Na-Dene groups but is also found in many Eskimo-Aleuts and American Indians.

Karafet et al. (1999) evaluated additional Y chromosome markers in 2,168 males in 60 world populations, including Kets and Athapaskans, along with many European, African, Asian, Siberian, and Native American samples. They focused on 14 unique haplotypes, including what they refer to as 1G (i.e., DYS199 T). Among

Native Americans, the 1G haplotype was the most common (53.5%), followed by haplotype 1C (35.8%). Additional haplotypes in a frequency above 1% include 1B (4.3%) and 1F (4.0). With but five exceptions (3 Siberian Eskimos, 1 Chukchi, 1 Even), haplotype 1G was limited to Native Americans. Two very interesting points are evident in this article. First, the authors propose that the 1G haplotype was derived from the 1C haplotype. The 1C haplotype is relatively common in Europe (37.7%; range 14-69%) but is rare in North (28/438, or 6.4%), Central (11/202, or 5.4%), and East Asia (4/307, or 1.3%). What is intriguing is that 1C is in high frequency among the Kets (10/12, or 83.3%) and Selkups (93/122, or 76.2%) which sets them markedly apart from all other Asian populations. Finally, the only other haplotype exhibited in the Ket sample was 1F (2/12, or 16.6%). In the Americas, 15 individuals were 1F, and, excluding two Wayus from South America, all others were either Athapaskans (Tanana, Navajo) or Algonquians (Cheyenne). Of course, 1F is very common in North and Central Asia so this does not link Athapaskans and Kets.

Articles on Y chromosome polymorphisms written before 2002 used a variety of terminological systems (Y chromosome consortium 2002). In that year, workers standardized the names applied to the various single nucleotide polymorphisms (SNPs), simple tandem repeats (STRs), and indels (insertions and deletions). It now appears that only two major Y chromosome haplogroups entered the New World, Q and C. Karafet et al. (2006) note that the three major SNP haplogroups in the Americas are Q-P36, Q-M3, and C. The two Q haplogroups are found in virtually all Native American populations. From our vantage, it is of note that the C (P39) haplogroup is restricted largely to Athapaskans, although it also appears in the Cheyenne and Sioux. While Zegura et al. (2004:172) argue that Y chromosome variation is best interpreted as indicating a single migration from Asia to the Americas, they add that “both of these lineages seem to have originated in the Altai Mountain region.” The model that all Native Americans derive from a single common ancestral population that arrived in western Beringia during the latter stages of the Pleistocene is becoming increasingly popular (Mulligan et al. 2008; Tamm et al. 2007; Wang et al. 2007) and the geographic homeland of this ancestral population is often placed in central Siberia.

### 3.0. DISCUSSION

Speculation on the number of migrations to the New World has been a cottage industry in Anthropology and ancillary fields for the past two centuries (cf. Count 1950; Powell 2005). Splitters developed models that involved numerous migratory waves while lumpers favored two migrations, American Indians first and Eskimo-Aleuts second. More recently, single migration models are in vogue. Most theorists, but by no means all, have Native Americans emerging from somewhere in north, east, and/or central Asia.

In the mid-1980s, a three-wave model developed by linguist Joseph Greenberg, dental anthropologist Christy G. Turner, and geneticist Steven Zegura, proposed the Americas were settled by three separate migratory pulses out of Asia (Greenberg et al. 1986). The result of the first migration was all North and South American Indian populations, referred to collectively as Amerind or Macro-Indian. The progenitors of Na-Dene speaking populations of the interior western Subarctic and greater Northwest Coast arrived in the New World in a subsequent migration. Another colonizing population from Asia included the ancestors of Eskimo-Aleut populations who dispersed along subarctic and Arctic coasts from the Aleutian Islands to Greenland. By 1990, the three wave model was universally acknowledged if not invariably accepted.

Williams et al. (1985) concluded the pattern of variation in immunoglobulin markers (Gm system) among American Indians, Eskimo-Aleuts, and Na-Dene speakers was consistent with the three-wave model outlined by Greenberg and his co-workers (1986). In a massive worldwide analysis of nuclear markers, Cavalli-Sforza et al. (1994) found that genetic distances based on over 120 alleles were consistent with a model showing separation between American Indians, Na-Dene groups, and Eskimo-Aleuts, with the latter two more similar to one another than either was to American Indians. Some of the early research on mtDNA haplogroups also concluded that New World populations were derived through several migrations from Asia although the specifics were not in total accord with the three-wave model.

Today, most researchers agree that (1) all Native Americans share a common ancestor, and (2) this

common ancestor(s) resided in Asia during the late stages of the Pleistocene. Turner (1986) is explicit in his model where he proposed that three separate colonizing populations, derived from a common base in Asia, crossed into Beringia during the late Pleistocene. He envisioned Paleo-Indians trending north and east from north China, eventually reaching the Arctic continental shelf before moving across Beringia into Alaska. A few thousand years later, a second group moving in a more easterly direction reached the Amur River and Pacific coast where they developed an early maritime adaptation. These populations would represent the ancestors of Eskimo-Aleuts who settled initially along the southern coastline of Beringia. The Na-Dene were thought to have been derived from the wedge-shaped core, microblade producing populations represented archaeologically by the late Upper Paleolithic Diuktai culture. Turner proposed that the ancestors of the Dené entered Alaska after Paleo-Indians had migrated south through the ice-free corridor. Some recent research on mtDNA and Y chromosome haplogroups also indicates different Asian points of origins for New World populations, although this is usually given as two locations rather than three. Favored regions for deriving the ancestral populations of Native Americans are south central Siberia and the Amur River basin (Volodko et al. 2008; Schurr 2004).

As Mulligan et al. (2004:298) note, “The three-migration theory provided a provocative hook to frame a flood of molecular genetic studies that began in the 1990s.” Shortly after mtDNA studies focused their sights on Native American origins, researchers started taking issue with the three-migration model (Bonatto and Salzano 1994; Merriwether et al. 1997). Geneticists did not feel the distribution of the mtDNA haplogroups A, B, C, and D exhibited the trichotomy of frequencies that might be expected had there been three distinct migrations to the Americas. Despite this conclusion, there is a patterned difference between American Indians, Na-Dene/Northwest Coast groups, and Eskimo-Aleuts. Based on data provided by Merriwether et al. (1997:417), the proportions of A:B:C:D in Amerinds are 27:34:19:18, in Na-Dene/Northwest Coast they are 72:9:7:8, and for Eskimo-Aleuts 63:1:4:29. The relatively uniform distribution of the four haplogroups in Amerinds stands in contrast to the dominance of haplogroup A in Na-Dene/Northwest Coast groups and the high frequency of A and D in Eskimo-Aleuts. It should be noted, however, that the high A-D pattern in Eskimo-Aleuts results from the near fixation of A in Eskimos and very high frequency of D in Aleuts. Lumping them into the linguistic category of Eskaleut obscures dramatic genetic differences and corresponding divergent histories. Also, the sublineage of D in Aleuts and the rare D in Inupiat Eskimos are different. As in teeth and blood groups, Na-Dene and Eskimo-Aleut groups are closer to one another than either is to North and South American Indian populations.

Recently, several lines of evidence suggest the ancestors of all Native Americans arrived as a single founding population in Beringia between 15,000 and 30,000 years ago (Goebel et al. 2008; Tamm et al. 2007; Kitchen et al. 2008; Wang et al. 2007). To generate the diversity observed among Native Americans, some models envision an original founding group stalled on Beringia for many millennia before colonizing populations could eventually follow one of two routes (coastal and ice free corridor) to gain access to the vast remaining areas of North and South America. Appealing on genetic grounds, there is no archaeological evidence for a protracted occupation of central Beringia prior to southward dispersal. Other workers feel the single origin model does not account for the genetic complexities of New World colonization and differentiation. Volodko et al. (2008) feel there were at least two founding populations in Asia, the first from the Altai-Sayan upland or mid-lower Amur region (ca. 25,000–30,000 years ago) and the second from the general area of Amur-Mongolia-Manchuria around the end of the Pleistocene (11,800 years ago) (see also Perego, et al. 2009, O’Rourke 2009). Additional recent work on mtDNA whole genome sequences by Perego et al. (2009), also indicates two separate migrations to the Americas. One of these would have been through the traditional Beringian interior, introducing mtDNA haplogroup X2a to northeastern North America, while a second Pacific coastal migration is required to account for the coastal range of haplogroup D4h3.

If all Native Americans were derived from a single founding population that arrived in Beringia 15,000–30,000 years ago, what ramifications would this have for an ancient linkage between the Yeniseian and Na-Dene language families? This ‘single origins’ (SO) model contends that American Indians, Na-Dene speakers, and Eskimo-Aleuts all branched off of a single ancestral population in Beringia at different points

in time. If this model accurately portrays this situation, Kets would be equally related to all Native American populations, lacking no specific genetic affinity to Athapaskans and Tlingits. Such a model is consistent with the distribution of the private allele D9S1120 275 that is, at the same time, almost uniquely American (the neighboring Chucki and Koryaks being the only exceptions) with similar frequencies in American Indians, Eskimo-Aleuts, and Na-Dene populations. Other researchers feel that mtDNA and Y haplogroups point in the same direction. If the SO model ultimately proves to be the most parsimonious explanation for patterns of genetic variation in the New World, it is unlikely that any direct linkage between Kets and Na-Dene groups will be found. This runs counter to the position set forth by Ruhlen of a shared common ancestor of Yenisei-Na-Dene in Eurasia followed by a migration to the New World. However, if the Dené-Yeniseian hypothesis is substantiated, an alternative explanation is that the Yeniseian family was derived from an east to west movement into Siberia of proto-Dené-Yenisei speakers during the Holocene (Fortescue, this volume). Although many recent studies point to eastern and central Siberia as the 'starting gate' for the colonization of the Americas, the time depth involved would likely obscure deep linguistic ties. If the colonization was in a reverse direction and occurred at a later date, this might help resolve the conundrum. Unfortunately, at this time, there are very few 'genes across Beringia' that support this scenario.

Based on the mtDNA profile of the Kets, some workers suggest they have admixed with Russians to a significant extent. Naumova et al. (2008) estimate that Asians and Europeans have contributed about equally to the mtDNA variation in Kets. Derbeneva et al. (2002) analyzed 38 Kets for mtDNA and found Native American haplogroups represented 26.3% of the total assemblage (A—7.9%; C—15.8%, and D—2.6%) with no B or X haplogroups. Other common haplogroups among the Kets were U4 (28.9%), F (23.7%), and H (10.5%). U4 is also relatively common in the Mansi (16.3%), Nganasans (20.8%), and Northern Altaians (18.5%) but is rare in Northern Europe and most Uralic populations (Derbeneva et al. 2002). Given the intermediacy of central Siberian populations, they could represent a mix of European and Asian genetic elements. The alternative position is that the unusual combination of European (H, U, J, W, and subtypes) and Asian (A, C, D, and Z) mtDNA haplogroups may have arisen from an early L3 lineage that arrived in Siberia from the Middle East during the early Upper Paleolithic (Derbeneva et al. 2002). It is difficult to sort out to what extent the similarities with neighboring populations for either the Kets in Siberia or Athapaskans in North America might have been modified by gene flow. In the western subarctic, there are indications of gene flow between Athapaskans and Algonquians (Malhi et al 2007; Scott and Turner 2008). In central Siberia, the Kets exhibit genetic ties to the Selkups, Nganasan, and Mansi. At this point in time, far removed from the original divergence dates, it is difficult to determine the degree to which the ancestral gene pool has been diluted by admixture with adjoining groups. Basically, greater gene flow with neighboring groups would tend to obscure ancient genetic ties.

Wang et al. (2007:2059) feel the pattern of variation exhibited by mtDNA and Y chromosome haplogroups in Siberia, along with the restricted distribution of the D9S1120 allele 275 in Asia, could be explained in several ways: "the ancestral population that migrated to the Americas may have already acquired a degree of genetic differentiation from other Asian populations . . . descendants of the original Native American founders are no longer present elsewhere in Asia, or these descendants have not yet been genotyped at loci that carry apparently private Native American variants." In our case, we can add the proviso that Athapaskans are numerous, widespread and well studied. Kets, on the other hand, are so few in number that even if they were more thoroughly sampled, this small remnant group would not necessarily represent a random sample of the original Yeniseian gene pool. This is one possible explanation for the absence of clear cut genetic ties between Kets and Athapaskans.

While linguists have developed a solid case linking the North American language family Na-Dene with Yeniseian, we have not found comparable parallels in the biology of these 'groups'. There are several lines of evidence that point to central Siberia as the ancestral homeland for some portion or even all of the Native American gene pool. However, there is no specific gene, haplogroup, or dental trait that provides a direct link between the Kets and any Na-Dene speaking population. Part of the problem may relate to the fact that the Kets, who now number only a few hundred individuals, are not as well known biologically as they are

linguistically. The study of additional genetic markers could bring the Dené-Yeniseian linkage into clearer focus. At this time, we can infer that the ancestral populations of Na-Dene are linked to central Siberian and east Asian groups but can make no claim about their specific genetic affiliation with Kets.

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