

THE PHYSICAL ANTHROPOLOGICAL INTERMEDIACY PROBLEM OF NA-DENÉ/GREATER NORTHWEST COAST INDIANS

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ABSTRACT

For more than thirty years, it has been recognized that the dentition of the Indians of the Alaskan Interior and Pacific Northwest has crown and root trait frequencies that are often intermediate between those of Eskimo-Aleuts and all North and South American Indians. When many dental morphological variables are assessed simultaneously, tooth-based distance values show that Na-Dené/Greater Northwest Coast (ND-GNWC) samples fall between Eskimo-Aleuts and American Indians. The largest analysis of nuclear genetic markers to date reveals a similar pattern (Cavalli-Sforza et al. 1994). The divergence of Eskimo-Aleuts, American Indians, and ND-GNWC populations from a common ancestor in Northeast Asia was initially driven by chance forces (founder effect/genetic drift), but ND-GNWC intermediacy found in recent populations is likely due to gene flow in the New World between American Indian (cf. Algonkian) and ND-GNWC groups.

KEYWORDS: colonization of New World, dental morphology, genetics

INTRODUCTION

In evaluating population relationships, an important concept is that of a common ancestral population. Assuming monophyletic origins of anatomically modern humans, all populations, whether they come from Africa, Europe, Asia, the Pacific, or the Americas can trace their ancestry back to a common ancestor. Our problem does not go that deep in time (>100,000 years) but instead centers on the relatively recent divergence of Native American populations (i.e., within the past twenty-five thousand years). The majority of researchers concur that Native American populations are most similar to and were ultimately derived from Northeast Asian groups. Additionally, numerous genetic and dental studies show that Native Americans are more closely related to one another than they are to Northeast Asians. These observations raise two interrelated questions: (1) What was the pattern of branching that

led to divisions within the New World, and (2) How did evolutionary processes lead to the patterns of relationships indicated by different biological systems?

First, of the four major evolutionary mechanisms that lead to population differentiation (natural selection, genetic drift, gene flow, mutation), mutation has not been a major contributor to Native American population history because mutation rates are very low for any given genetic locus. Despite this caveat, there are some interesting and unique alleles that may have arisen through mutation once populations reached the New World. These rare variants, while not particularly useful in genetic distance analyses, nonetheless provide insights into the broader issue of branching patterns among Native American groups (Lampl and Blumberg 1979). Another issue is whether or not the biological traits (alleles, phenotypes) under con-

sideration are subject to natural selection. For the most part, the alleles, haplogroups, and dental traits studied in Native Americans are assumed to be selectively neutral. Researchers have expended much energy trying to elucidate the selective significance of various genes and traits, but among the few successes are alleles that confer some protection from malaria (e.g., HbS, HbC, HbE, α and β thalassemia) or body form characteristics associated with latitude and extremes in ambient temperature (i.e., Bergmann and Allen rules). Malaria is not an issue in the New World. Given the high degree of latitudinal variation in the Americas, however, some body dimensions might be subject to natural selection and thus reflect ecogeographical rules (Newman 1953). Because some anthropometric variables may be subject to selection, we limit most of our attention to genetic markers and tooth crown and root traits, the majority of which have no demonstrated correlation with fitness (i.e., are selectively neutral).

Given the rarity of mutations and ubiquity of selectively neutral traits, genetic drift and gene flow are the primary forces that influence population differentiation. The effects of these two processes are opposite. Genetic drift and its spatial component, founder effect, are stochastic processes that lead to population divergence when groups split from a common ancestral population. The subsequent rate of change brought about by drift is determined by effective population size (with smaller populations diverging more rapidly than large ones), and time (with greater time depth, separation from a common ancestor results in greater divergence) (Falconer 1981). After a splitting event and concomitant geographic isolation, genetic drift invariably results in population differentiation. By contrast, gene flow always produces convergence—when members of two divergent populations exchange genes, the result is a hybrid population that falls somewhere between the two ancestral populations, with placement determined by the proportionate genetic contribution of each ancestral group.

Biological or genetic distance statistics, which estimate the degree of similarity or dissimilarity among three or more groups, provide values that measure relative population relationships (Buikstra et al. 1990; Constandse-Westermann 1972; Weiner and Huizinga 1972). Assuming that many (e.g., twenty or more) genes or traits are used to calculate population distances, and that chance processes (genetic drift and founder effect) are the primary differentiating mechanisms, the pairwise distance values between three or more diverging groups are dictated by their pat-

tern of splitting from a common ancestral population. For example, consider groups A, B, and C. If the conditions above hold (selectively neutral traits and geographic isolation of A, B, and C) and these three hypothetical groups bud off from a common ancestor at about the same point in time, the distance values between A-B, A-C, and B-C should be equal (Fig. 1). If A splits off from the common ancestor first, with B-C remaining a single lineage, when B and C ultimately do diverge, the relative distance values are A-B equals A-C, with both distance values greater than B-C. With these principles in mind, the basic question we pose is how Na-Dené/Greater Northwest Coast populations (ND-GNWC) came to assume an intermediate position relative to Eskimo-Aleuts on the one hand and North and South American Indians on the other.

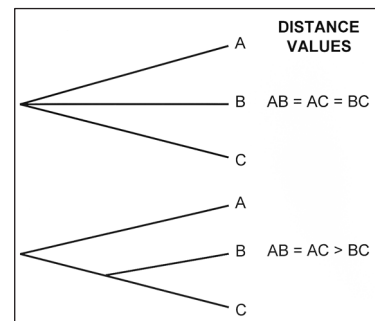


Figure 1. Hypothetical branching patterns and associated distance values, given the assumption that founder effect and genetic drift are the primary mechanisms underlying differentiation.

DENTAL VARIATION

Empirically, native Northwest Coast–Alaska interior populations (ND-GNWC) exhibit dental trait frequencies that suggest intermediacy between the populations of Eskimo-Aleuts and a territorially large group consisting of all North and South American Indian populations whose dental trait frequencies are remarkably similar throughout the Americas (Turner 1984, 1985a, 1986). Dental trait intermediacy associated with the Na-Dené language family was first noticed in a study of lower first molar root number in New World populations. Lower first molars exhibit either two or three roots. Turner (1971) found that the less common three-rooted phenotype, or 3RM1, was in low frequency (5–6 percent) in North and South American Indian populations but was exceptionally frequent in Eskimos and Aleuts (30–40 percent). A small Athapaskan sample (Navajo) had an intermediate

frequency of 27 percent. With the accumulation of additional data from all parts of the Americas, this pattern of 3RM1 variation was confirmed (cf. Turner 1983, 1984). Moreover, a high frequency of 3RM1 was also found in Northeast Asians, adding further support to the position that this region was the source for populations ultimately ancestral to New World peoples (Scott and Turner 1997, 2006; Turner and Scott 2007).

In a series of articles, Turner (1983, 1984, 1985a, 1985b, 1986) presented data on more than two dozen crown and root variables in Native American dental samples stretching from Point Barrow, Alaska, to the southern reaches of South America. Here we reduce that data set based on dozens of populations and thousands of individuals to three groupings that make up the essence of our problem: American Arctic (Eskimos and Aleuts), Northwest North America (Athapaskans, Greater Northwest Coast), and North-South Amerind (all groups from North and South America not included in the above two groupings).

In Table 1, which shows dental trait frequencies for the three Native American groupings, Northwest North

America shows intermediate frequencies for thirteen of twenty-three traits. By contrast, the American Arctic falls between the other two groupings for six dental traits, while American Indians show intermediacy in only one case. For Cusp 5 (UM1) and Cusp 7 (LM1), American Arctic and American Indians have the same mean trait frequency. Four-cusped lower first molars are absent in all three groupings, so there is no intermediacy for this variable. While intermediate dental trait frequencies are not invariant for Northwest North America, they are by far the most common for this group.

Another way to evaluate intermediacy is to tabulate the number of pairwise comparisons where two of the three samples show the most similarity. In this regard, American Arctic and Northwest North America are closest for ten dental traits while Northwest North America and American Indians are most similar for eight traits. By contrast, there are only four instances in which American Arctic and American Indian samples are the most similar. Mean differences in dental trait frequencies show the same

Table 1. Crown and root trait frequencies in composite samples from the American Arctic, Northwest North America, and North and South American Indians.

Trait (tooth)	American Arctic	Northwest North America	North & South Amerind	Most similar groups
Winging (UI1)	0.232	0.358	0.500	AA-NNA
Shoveling (UI1)	0.692	0.831	0.919	NNA-NSA
Double-shoveling (UI1)	0.349	0.567	0.705	NNA-NSA
Interruption grooves (UI2)	0.596	0.650	0.510	AA-NNA
Bushman canine (UC)	0.000	0.004	0.016	AA-NNA
Odontomes (UP and LP)	0.062	0.065	0.044	AA-NNA
3-cusped upper molar (UM2)	0.306	0.142	0.115	NNA-NSA
Carabelli's cusp (UM1)	0.019	0.055	0.056	NNA-NSA
Cusp 5 (UM1)	0.167	0.214	0.167	AA-NSA
Enamel extensions (UM1)	0.459	0.509	0.437	AA-NSA
4-cusped lower molar (LM1)	0.000	0.000	0.000	AA-NNA-NSA
4-cusped lower molar (LM2)	0.052	0.044	0.086	AA-NNA
Y pattern (L)M2	0.200	0.118	0.098	NNA-NSA
Cusp 6 (LM1)	0.504	0.503	0.551	AA-NNA
Cusp 7 (LM1)	0.085	0.068	0.085	AA-NSA
Deflecting wrinkle (LM1)	0.300	0.365	0.381	NNA-NSA
2-rooted upper premolar (UP1)	0.049	0.067	0.143	AA-NNA
3-rooted upper molar (UM2)	0.374	0.415	0.559	AA-NNA
2-rooted lower canine	0.003	0.000	0.007	AA-NNA
Tomes' root (LP1)	0.034	0.093	0.199	AA-NNA
3-rooted lower molar (LM1)	0.311	0.165	0.065	NNA-NSA
1-rooted lower molar (LM2)	0.312	0.387	0.328	AA-NSA
Distal trigonid crest (LM1)	0.187	0.078	0.042	NNA-NSA

Note: bold-faced reflects intermediate frequency of the three groups.

pattern. The mean pairwise frequency differences among the three groupings are: American Arctic–Northwest North America (6.67 percent), Northwest North America–American Indian (6.18 percent), and American Arctic–American Indian (10.65 percent). Again, there is a distinct separation between American Arctic and American Indian while Northwest North America is about equally similar to the other two groupings.

For qualitative variables such as nonmetric dental traits, a frequently used biological distance statistic is the Mean Measure of Divergence, or MMD (Berry and Berry 1967; Green and Suchey 1976). If dental trait frequencies exhibit a tendency for Northwest North American samples to be intermediate between Eskimo–Aleuts on the one hand and American Indians on the other, what do biological distance values show? The MMD values in Table 2, based on average pairwise distance among the groups (with North American and South American Indians treated individually), show that Northwest North American populations are most similar to North American Indians (0.058), with a slightly larger mean distance to Eskimo–Aleuts (0.078). However, the mean distance between North American Indians and Eskimo–Aleuts (0.169) is more than twice as great as either of these groups is from Northwest North America, providing additional support for intermediacy. In addition, both Northwest North America and Eskimo–Aleut show larger differences from South American Indians (0.123 and 0.260) than from North American Indians. Despite this, the pairwise distance between North American and South American Indians is quite small (0.072), supporting the position held by Turner (1984, 1985a) that American Indians from both continents show dental homogeneity.

GENETIC VARIATION

Native Americans have been intensively studied for genetic markers of the blood for more than fifty years. Initial focus was on the ABO, Rh, and MNSs systems but this short list of loci was ultimately augmented by dozens of additional loci and alleles (see summaries in Mourant 1954; Mourant et al. 1976; Roychoudhury and Nei 1988). Early workers, dealing with a limited number of genetic systems, reached widely disparate conclusions on the meaning of genetic variation. The quantity and quality of genetic data are now sufficient to yield relatively consistent results.

Szathmary (1979, 1981, 1993) focused on Native populations from the Subarctic and Arctic regions of the

New World and Siberia. Her position, exemplified by the title of her article “Are the Biological Differences Between North American Indians and Eskimos Truly Profound?” (Szathmary and Ossenberg 1978), runs counter to the long-held view of Laughlin (1963, 1966) that the major dichotomy in the New World was between Eskimo–Aleuts, on the one hand, and American Indians on the other. However, a closer examination of Szathmary’s analyses and conclusions shows that the groups she refers to broadly as North American Indians are primarily Algonkians of the Eastern Subarctic and Athapaskans of the Western Subarctic. North American Indians from the United States Southeast, United States Southwest, and Mexico are not included in her analyses.

While Szathmary did not actually analyze a complete representative sample of North American Indians, her findings are instructive. Prior to her work, most researchers assumed a fairly large “genetic gulf” between Eskimos and Indians, but she has rightly pointed out that this gulf is not invariably large, especially when comparisons are made to Indian populations of the Western (Athapaskan) and Eastern (Algonkian) Subarctic.

Because Szathmary focused on northern groups, we wanted to evaluate the issue of ND–GNWC intermediacy with a larger set of Native American populations using distance values from *The History and Geography of Human Genes* (Cavalli-Sforza et al. 1994). After extracting data from hundreds of sources, Cavalli-Sforza et al. (1994) provided a meta-analysis of human genetic variation based on 120 nuclear alleles. For New World groups, this involved the calculation of mean gene frequencies across many groups to characterize broader geographic or language-based groupings. The groups most pertinent to our question include: Na-Dené (Alaskan), Na-Dené (Canada), Na-Dené (Southern), Eskimo (Siberia), Eskimo (Alaskan Inupik), Eskimo (Yupik), Eskimo (Canada), and Eskimo (Greenland). These were analyzed along with data from

Table 2. Average distance values (MMDs) between Northwest North Americans, Eskimo–Aleuts, and North and South American Indians based on twenty-nine crown and root traits

	NNA	EA	NAI	SAI
Northwest North America	0			
Eskimo–Aleut	0.076	0		
North American Indian	0.058	0.169	0	
South American Indian	0.123	0.260	0.072	0

four North American Indian (Penutian, North Central Amerind, Keresiouan, Almosan), three Siberian (Chukchi, Reindeer Chukchi, Koryak), and six South American groups (Andean, Equatorial, Macro-Carib, Macro-Ge, Macro-Panoan, Macro-Tucanoan).

Cavalli-Sforza and his colleagues calculated genetic distance values among the twenty-three groups of Native Americans and Siberians. Rather than reproducing this large distance matrix with twenty-three rows and columns, we analyzed those elements of the matrix most relevant to the issue of ND-GNWC intermediacy. Specifically, we calculated the mean distance of all members of one meta-grouping (i.e., a combination of several linguistic or geographic groups, including Na Dené North, Na Dené South, Eskimo, Siberia, North American Indian, South American Indian) with all the distances of another such grouping. For example, there are two northern Na-Dené groups and five Eskimo groups, so the total number of pairwise distances between these two groupings is ten.

The mean distance values between the six meta-groupings are shown in Table 3, along with the number of values used to derive each mean distance. The key points evident in this table are: (1) the similar values between Alaskan Na-Dené and both Eskimo (0.72) and North American Indian (0.79) groups, with a larger distance between the latter two groups (0.95); (2) the generally small mean distance values for Na-Dené South, especially when compared to Alaskan Na-Dené (0.42) but even smaller for North American Indians (0.29), indicating that gene flow has significantly influenced the genetic make-up of southern Athapaskans; (3) the very small distance value between North and South American Indians (0.39), supporting Turner's dental analysis that shows that these two groups are homogeneous; and (4) the consistently large distances between Siberian and all Native American groups, a find-

ing that suggests that all Native Americans branched off a Siberian ancestor at about the same time.

The efficacy of gene flow as it impacts southern Athapaskans is shown in Fig. 2. Illustrating the distances of Cavalli-Sforza et al. (1994) using an unweighted pair groups clustering algorithm, the major subdivision in the

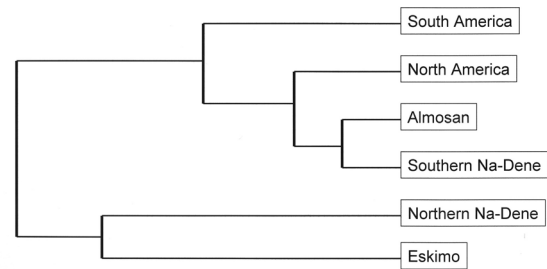


Figure 2. Dendrogram of Native American relationships based on analysis of genetic distance values using an unweighted pair groups clustering algorithm.

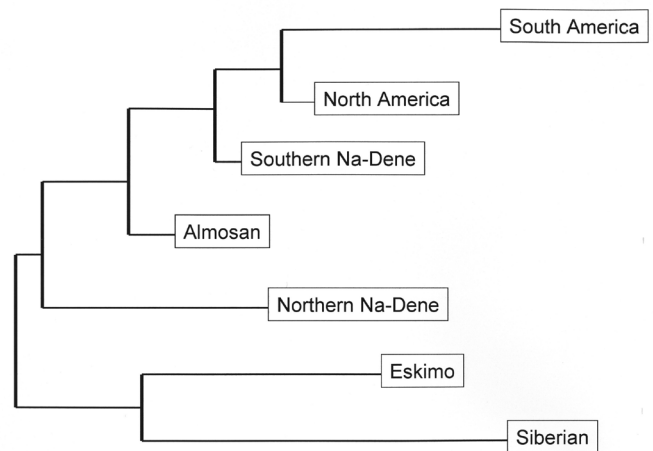


Figure 3. Dendrogram of Native American relationships based on analysis of genetic distance values using Nei's neighbor-joining method clustering algorithm.

Table 3. Mean genetic distance values among major New World groupings, with focus on Na Dene, Eskimo, and American Indian (calculated from distance values in Cavalli-Sforza et al., 1994)

	ND-N	ND-S	ESK	SIB	NAI	SAI
Na Dené—north	0					
Na Dené—south	0.42 (2)	0				
Eskimo	0.72 (10)	0.92 (5)	0			
Siberian	1.32 (10)	0.89 (5)	0.97 (15)	0		
North American Indian	0.79 (8)	0.29 (4)	0.95 (20)	1.07 (12)	0	
South American Indian	1.24 (12)	0.59 (6)	1.39 (30)	1.52 (18)	0.39 (24)	0

Numbers in parentheses refer to number of distance values used to calculate mean.

New World is between northern Na-Dené and Eskimo on the one hand, and American Indians on the other. Interestingly, southern Na-Dené clusters more closely with Almosan (Algonkian and Mosan speaking groups) than with their linguistic relatives in Canada and Alaska. Using Nei's neighbor-joining method (Fig. 3), a slightly different pattern emerges. In this instance, northern Na-Dené is in the uppermost cluster with American Indian groups, while Eskimo clusters with Siberian. Southern Na-Dené is once again pulled more tightly into the North American Indian sphere, a result that has no other ready explanation beyond gene flow bringing about convergence.

Genetic analysis follows much the same pattern as that revealed by dental morphology—Athapaskans and Greater Northwest Coast populations assume an intermediate position relative to Eskimo-Aleuts and American Indians. In fact, the parallel goes even further. In the Cavalli-Sforza et al. (1994) volume, one dendrogram of world variation has Northwest North Americans clustering with North and South American Indians, while Eskimos cluster with Siberians (Fig. 2.3.2.A; p. 78). In another dendrogram focusing on New World variation (Fig. 6.9.1; p. 323), Eskimos cluster with northern Athapaskans, with all other North and South American Indians on another cluster (which includes southern Athapaskans). For dental morphology, Powell (1993) arrived at a similar result in his analyses of Turner's (1985a, 1986) data set on Native American dental variation. Using an unweighted pair groups method, Powell derived a tree that linked North American Indians with South American Indians, while Northwest Coast Indians clustered with Aleuts, Eskimos, and Siberians. Evaluating the same data set using a maximum parsimony tree, he found that Northwest Coast Indians clustered with North and South American Indians, while Northeast Siberians, Aleuts, and Eskimos were on a separate cluster. In other words, two large data sets on different biological systems reveal similar and inconsistent conclusions regarding Na-Dené affinities. Similarities are shown to both Eskimo-Aleuts and to American Indians, with method of analysis and sample array impacting the final Na-Dené linkage with other Native American populations.

INSIGHTS FROM A RARE VARIANT: ALBUMIN NASKAPI

Although mutations do not often contribute to population affinity assessment, one rare variant in the albumin system is an exception. This allele, Albumin Naskapi, is

essentially a New World mutation that has attained polymorphic frequencies in populations from only two North American language groups: Athapaskan and Algonkian. It is completely absent in the overwhelming majority of other Native American groups, including Eskimo-Aleuts. The rarity of this selectively neutral trait and its curious geographic/linguistic distribution may contribute significantly to unraveling the question of ND-GNWC intermediacy.

Table 4 shows the distribution of Albumin Naskapi in more than twenty thousand native North Americans

Table 4. Distribution of the Albumin Naskapi allele in Eskimo-Aleut, Na-Dene, and American Indian populations.

Language family	<i>n</i>	Naskapi phenotype	AL Naskapi allele frequency
Eskimo (1)	1,529	3	0.001
Eskimo (2)	184	0	0.000
Aleut (1)	99	0	0.000
Na-Dené			
Tlingit-Haida (1)	456	0	0.000
Haida (2)	69	0	0.000
Athapaskan (1)	2,222	161 (5)*	0.039
Athapaskan (2)	881	39	0.022
Salishan (2)	111	11	0.050
Wakashan (2)	257	1	0.002
Algonkian (1)	2,596	162 (6)*	0.034
Algonkian (2)	382	9	0.012
Siouan (1)	887	3	0.002
Siouan (2)	105	3	0.014
Zunian (1)	655	0	0.000
Zunian (2)	202	0	0.000
Uto-Aztecan (1)	2,587	1	0.000
Uto-Aztecan (2)	414	0	0.000
Yuman (1)	310	2	0.003
Yuman (2)	796	0	0.000
Muskogean (1)	413	0	0.000
Muskogean (2)	119	0	0.000
Macro-Nahua (1)	880	0	0.000
Macro-Maya (1)	1,123	0	0.000
Macro-Mixteco (1)	468	0	0.000
Tarasco (1)	167	0	0.000
Mestizo (1)	2,306	0	0.000
Total	20,218	395 (11)*	0.010

(1) Schell and Blumberg, 1988; (2) Smith et al. 2000; *homozygotes in parentheses

(Schell and Blumberg 1988, Smith et al. 2000). Some key points in this table are:

Of 395 Native Americans that have the Albumin Naskapi phenotype, 371 (94 percent) come from Athapaskan or Algonkian speaking groups. If you add two more Northwest Coast groups to this total (Salishan, Wakashan), the number goes up to 383 (97 percent).

Only eleven individuals are homozygous for Albumin Naskapi, and in every instance they come from Athapaskan or Algonkian groups.

Although this albumin variant is named Albumin Naskapi, after a northeastern Algonkian group, it is in very similar frequencies in Athapaskans (3.4 percent) and Algonkians (3.1 percent) so the point of origin of the variant is unclear.

The few exceptions to the general Athapaskan-Algonkian rule come from groups that abut Athapaskan (Uto-Aztecan, Yuman) or Algonkian groups (Eskimo, Siouan), making gene flow the likely source of the allele.

With the exception of three Ungava Eskimos (who are adjacent to Algonkian groups), no other Eskimo or Aleut has tested positive for this allele.

More than five hundred Tlingit-Haida have been tested for this variant but none has the marker.

In samples that include more than five thousand Southeastern United States and Mesoamerican Indians, not a single case of Albumin Naskapi was found

Albumin Naskapi occurs in only two Old World groups—Eti Turks and North Indians (Franklin et al. 1980, Kaur et al. 1982); based on geography, history, and many other genetic variables, it seems likely that Albumin Naskapi arose as independent mutations in these populations.

The ramifications of these observations are presented in the next section.

BRANCHING PATTERNS AND THE QUESTION OF INTERMEDIACY

Fig. 4 shows five branching scenarios and three points of divergence for Native American populations, the assumption being that Eskimo-Aleut, ND-GNWC, and American Indian groups all shared a common ancestor at some point. For scenario A, all three groups diverged from a common ancestor at the same point in time. Scenario B has American Indians diverging first, with a subsequent splitting event for Eskimo-Aleut and ND-GNWC. With scenario C, Eskimo-Aleuts diverge first, with ND-GNWC

and American Indians diverging from a later common ancestor. The final two scenarios (D and E) are B and C with the added element of gene flow, between either ND-GNWC and American Indians or between ND-GNWC and Eskimo-Aleuts. The vertical lines extending from 1, 2, and 3 refer generally to where divergence occurred. For 1, in all instances, only one proto-Native American population entered the New World, with differentiation occurring after arrival. For 2, some (B, C, D, E) or all (A) of the divergence between the three groups took place in the Old World. Finally, with 3, all three groups diverged before entering the Americas. These models do not specifically suggest when the three groups last shared a common ancestor; it could be associated with an earlier (e.g., 20–30,000 BP) or later (12–20,000 BP) date.

Given dental variation and distances, genetic variation and distances, plus the distribution of Albumin Naskapi, what pattern of divergence shown in Fig. 4 is the most parsimonious? Taking each scenario in turn:

A. The possibility that the three groups diverged from a common ancestor at about the same point in time is not consistent with dental or genetic evidence. With this scenario, the three pairwise distances should all be about the same, but this is never the case. ND-GNWC

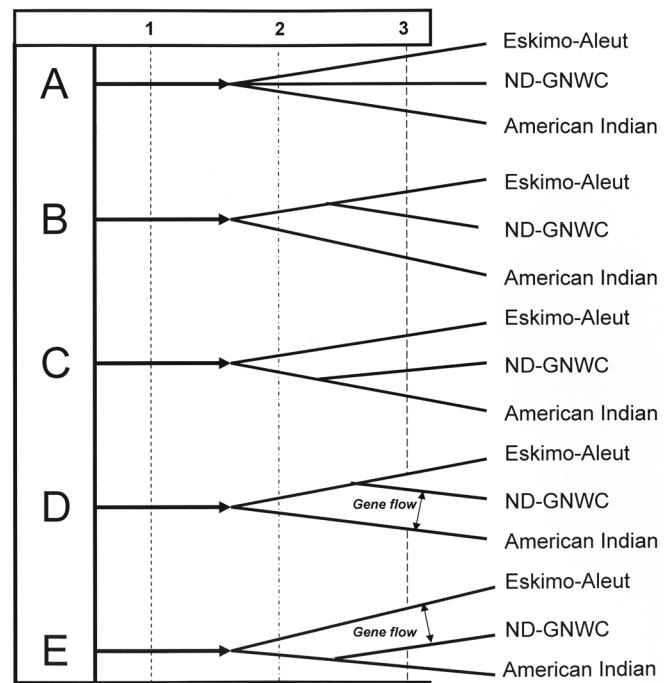


Figure 4. Five hypothetical branching scenarios for Eskimo-Aleut, Na-Dene/Greater Northwest Coast, and American Indian populations; scenarios D and E involve gene flow and convergence.

is usually about equidistant from Eskimo-Aleut and American Indian, while the latter two groups always show the largest pairwise distance.

- B. Here the notion is that Eskimo-Aleuts and ND-GNWC groups shared a common ancestry following an earlier split from groups ultimately ancestral to American Indians. This interpretation has been suggested by many workers, with Szathmary the leading proponent. The problem in this case is that Eskimo-Aleuts and ND-GNWC should always show the smallest pairwise distances, with both equidistant from American Indians. This holds for neither dental nor genetic distance analyses.
- C. In this instance, ND-GNWC and American Indians are thought to be more closely related, with Eskimo-Aleuts as the outlier. For anthropologists, this scenario was close to dogma, as many workers (cf. Laughlin 1963) never distinguished between the two groups, referring to them together as American Indians. It was this position that Szathmary and Ossenberg (1978) challenged when they posed the question of whether or not there was a major difference between Eskimos and (northern) North American Indians.
- D and E. These scenarios involve gene flow as an important contributor to ND-GNWC intermediacy and the direction of the gene flow is important. In D, Eskimo-Aleut and ND-GNWC share a more recent common ancestry (see B), but their distance values are pulled toward American Indians because of gene flow. For E, ND-GNWC and American Indians are thought to share a more recent common ancestor (see C) but admixture with Eskimo-Aleuts has pulled them toward those groups. The distance values based on tooth morphology and nuclear genetic markers cannot distinguish between either of these models. To help resolve this conundrum, another look at Albumin Naskapi is necessary.

There are several aspects to the distribution of Albumin Naskapi that favor scenario D. First, this allele is absent in Eskimos and Aleuts (given the likely assumption that the three Ungava Bay Eskimos who express this gene received it via gene flow from neighboring Algonkian groups). To argue scenario B, one would have to explain how the gene was maintained in a relatively high frequency in Athapaskans but somehow disappeared from the Eskimo-Aleut gene pool. Second, linguists see no ties whatsoever between Athapaskan and Algonkian, so simply attributing the allele's presence to a common ancestor does not

seem plausible. It is more likely that the allele is shared in common because of gene flow between Athapaskans and Algonkians, perhaps at a very early date (cf. Smith et al., 2000). If so, this would lend support to scenario D. As to timing, the absence of the Naskapi allele in Tlingit-Haida is also instructive. These groups are thought to have diverged from Athapaskans about forty-five hundred years ago (Michael Krauss, personal communication), with Tlingit-Haida adapting to the coast and Athapaskans settling the interior regions of Canada and Alaska, where they would have eventually come in direct contact with Algonkian groups. Although it is difficult to tie the spread of an archaeological tradition with specific ethnic/linguistic groups, the spread of the Northern Archaic tradition into Alaska may be a candidate that would explain how a broad range of contact developed between Athapaskans and Algonkians in the western Subarctic.

OTHER LINES OF EVIDENCE

MITOCHONDRIAL DNA

In one of the earliest studies of mtDNA variation in arctic populations, Shields et al. (1993) found a close similarity between Alaskan and Greenlandic Eskimos and Na-Dené groups (Athapaskans, Haida)—so close, in fact, that using a mutation rate of 1 percent sequence divergence per 8,950 years, the authors calculated an average divergence date between 5,100 and 7,100 years ago for these circumarctic populations. Three Northwest Coast groups, although more distantly related, also shared close genetic ties to Eskimos and Na-Dené speakers. The authors note “these Circumarctic populations originated from an Asiatic population whose own ancestors had previously contributed to a substantial fraction of the lineage ancestry of contemporary Pacific Northwest Amerind populations” (Shields et al. 1993:560). This observation adds credence to our methodological decision to include Greater Northwest Coast groups with Na-Dené.

Native Americans have four main mtDNA haplogroups referred to as A, B, C, and D, along with a relatively rare haplogroup X. Jobling et al. (2004) provide a figure on the distribution of these haplogroups, which supports many of the points made in this paper. First, Eskimos and Na-Dené speakers both have very high frequencies of haplogroup A with haplogroup B low or absent. Eskimos and Aleuts do differ from Na-Dené in having a much higher frequency of D. By contrast, North

Amerinds, Central Amerinds, and South Amerinds have moderate and variable frequencies of A (20–55 percent), uniform frequencies of B (30–40 percent), low to moderate frequencies of C (10–25 percent), and very low frequencies of D (0–10 percent). These data support the general notion of American Indian homogeneity and the greater similarity between Eskimo and Na-Dené than between other American Indians.

Brown et al. (1998) evaluated the rare haplogroup X to determine if there was some linkage between Native Americans and Europeans. They found that the geographic distribution of X in the New World was restricted largely to northern North American Indians, including Algonkians, Siouans, Northwest Coast groups, and Apacheans (Na-Dené). Although this observation lacks specificity, it does add another line of evidence suggesting affinity and/or gene flow among Native Americans of the Subarctic, Plains, and Northwest Coast.

Although mtDNA researchers working on variation among Native American populations have weighed in on issues regarding the timing of dispersal and the number and sequence of migrations, there is as yet no consensus. As Eschleman et al. (2003:15) conclude, “It is not surprising that mitochondrial DNA has largely confirmed the findings of classical genetic markers regarding genetic relationships among Native American tribal groups and yet has not conclusively resolved raging debates regarding number of migrations, source populations, and the timing of these migrations.” With more research in this area, especially on ancient DNA, perhaps these data will contribute in a more decisive way to evaluating the scenarios shown in Fig. 4.

ANTHROPOMETRY

Jantz et al. (1992) analyzed anthropometric data on fifteen thousand Native Americans collected under the direction of Franz Boas during the Jesup North Pacific Expedition (1897–1903). Two of their major conclusions relate directly to the subject of this paper. First, they did not find that either Eskimo-Aleuts or Na-Dené speakers were as strongly differentiated from other Native American groups as indicated by blood group markers and dental morphology. Second, they concur with Szathmary that Na-Dené groups show greater similarity to Eskimo-Aleut than to Algonkians, supporting “the position that Na-Dené and Eskimo-Aleut share a more recent common ancestry than either does with Algonkians” (Jantz et al. 1992:458).

Ousley (1995) focused on another subset of Boas’ anthropometric data, which involved six body and six face measurements. Using canonical discrimination analysis, he found that Eskimos of southwest Alaska were generally similar to Aleuts and some Northwest Coast Indian tribes. Although measurement data may be tied in part to climate, the observation that Na-Dené and Eskimo-Aleut are relatively similar is in agreement with divergence scenario C. These data cannot show, however, the gene flow indicated by Albumin Naskapi that supports scenario D.

CONCLUSIONS

All Native Americans share the same general Sinodont dental pattern that occurs in Northeast Asia. However, this pattern differs in some respects within the New World, and the most prominent characteristic of this difference is that it corresponds roughly with language families. Hence, these dental trait frequencies were used by Greenberg et al. (1986), along with linguistic, genetic, and archaeological evidence, to define three matching New World linguistic, dental, and genetic divisions. These corresponded approximately to the distribution of the Eskimo-Aleut, Na-Dené, and Amerind language families, a position also supported by genetic data (Cavalli-Sforza et al. 1994). Since 1983, Turner has added more data from the Northwest Coast region, and as a result it is likely that some other language family or families could be involved, not just Na-Dené (Turner 1985a, 1986), a suggestion first made by Paleoindian and Northwest Coast archaeologist Roy A. Carlson (1990) and supported by subsequent genetic analyses (cf. Shields et al. 1993).

Turner (1983) envisioned four possible migration scenarios to account for the pattern of dental variation in the New World:

1. Three migrations (Paleoindian, Na-Dené, Eskimo-Aleut, with Aleut and Eskimo diverging after arrival in New World);
2. Four migrations (Paleoindian, Na-Dené, Eskimo, Aleut, with the latter two groups diverging prior to arrival in New World);
3. Two migrations (Paleoindian, Eskimo-Aleut, with Na-Dené forming in America through admixture between Paleoindians and Aleuts); and
4. Three migrations (Paleoindian, Eskimo, Aleut, with Na-Dené forming through admixture between Paleoindian/Paleo-Indians and Aleuts).

In later papers, Turner (1985a, 1985b, 1986) proposed that the scenario of three separate migrations (scenario 1) was the most parsimonious model, since it integrated the largest amount of information from linguistics, physical anthropology, genetics, archaeology, and natural history. These three divisions were interpreted as the result of three separate, previously divergent migrations from Siberia. The first late Pleistocene colonists of Alaska and the New World are thought to have been ancestral Paleoindians or Epi-Clovis. They probably were proto-Amerind (Macro-Indian) speakers. Most likely next to arrive were Na-Dené speakers, who were equated with Alaskan Paleoarctic and Siberian Diuktai cultures. Last, or arriving at the same time as Na-Dené but by a Beringian coastal route rather than through the interior Beringian plain, were maritime Aleut-Eskimo folk with the Aleutian Anangula culture derived from the lower Amur-Hokkaido region. Given the considerable late Pleistocene environmental and archaeological variation in eastern Siberia (Derevyanko et al. 1998; Lbova et al. 2003; Ovodov and Martynovich 2000; Tseitlin 1974; West 1996), late Pleistocene pre-Beringian human diversity in Siberia was likely greater than that which was carried to Alaska.

Additional analysis supports the three migration scenario and adds new insights into the sequence of divergence events given ND-GNWC biological intermediacy. The three migration model of Turner is not couched in terms of most recent common ancestor—rather, he has three separate migrations coming out of Siberia in the sequence of American Indian, Na-Dené, and Eskimo-Aleut. When this is considered in light of the divergence patterns in Fig. 4, scenario D can be reconciled with Turner's model by adding that Paleoindians diverged first out of a Northeast Asian population base, while Eskimo-Aleuts and Na-Dené did not diverge until some later time (but in Siberia). Ultimately, the three groups did migrate separately into the New World but at that time, Eskimo-Aleut and Na-Dené were more closely related to one another than either was to American Indians. Subsequent gene flow between American Indians (notably Algonkians) and Na-Dené groups resulted in convergence between these groups, producing the pattern of intermediacy for ND-GNWC that would not have been generated if all three groups had been derived from a common ancestor at about the same time.

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