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Beringia and the Global Dispersal of Modern Humans

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Abstract. Until recently, the settlement of the Americas seemed largely divorced from the out-of-Africa dispersal of anatomically modern humans, which began at least 50,000 years ago. Native Americans were thought to represent a small subset of the Eurasian population that migrated to the Western Hemisphere less than 15,000 years ago. Archaeological discoveries since 2000 reveal, however, that *Homo sapiens* occupied the high-latitude region between Northeast Asia and northwest North America (i.e., *Beringia*) before 30,000 years ago and the Last Glacial Maximum (LGM). The settlement of Beringia now appears to have been part of modern human dispersal in northern Eurasia. A 2007 model based on the analysis of mitochondrial DNA (mtDNA) in living people derives Native Americans from a population that occupied Beringia during the LGM ('Beringian Standstill Hypothesis'). The model suggests a parallel between ancestral Native Americans and modern human populations that retreated to refugia in other parts of the world during the arid LGM and is supported by evidence for comparatively mild climates and rich biota in south-central Beringia at this time (i.e., 30,000–15,000 years ago). These and other developments suggest that the settlement of the Americas may be integrated with the global dispersal of modern humans.

Key words: Northeast Asia, Alaska-Yukon, *Homo sapiens*, genetics, paleoecology

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INTRODUCTION

The absence of any compelling evidence for pre-modern forms of *Homo* in the Western Hemisphere has long supported the notion that all living Native Americans are descended from one or more populations derived from the other hemisphere. As early as 1590, a Spanish missionary suggested that ancestral Native Americans walked over a land connection between Asia and North America, rather than travelling across an ocean.¹ By the end of the 19th century, remains of Late Pleistocene mammals on islands in the Bering Sea and the Aleutians helped convince many that the land connection or “bridge” probably lay submerged in the shallow waters between Chukotka and Alaska. And although initial speculation focused on tectonics, by the 1930s, global sea level fluctuations (driven by changes in terrestrial ice-mass balance) were identified as the mechanism underlying creation of the *Bering Land Bridge*.² This conclusion tied the presence of the land connection between Asia and North America to periods when climates were significantly colder than those of the present day.

In 1937, Swedish botanist Eric Hultén (1894–1981) proposed that the modern tundra plants distributed around the Bering Strait region (including the Aleutians) had dispersed from a central place, which he identified as the now submerged plain between Chukotka and Alaska and named *Beringia* (after the European explorer who sailed into the strait in August 1728).³ The presence of the hypothesized mesic tundra refugium also was tied to periods when climates were colder than those of the present day.

American geologist David Hopkins (1921–2001) expanded Hultén’s geographic definition of Beringia to include portions of Northeast Asia and Alaska, and, by the final decades of the 20th century, Beringia was widely viewed as extending from the Verkhoyansk Mountains in the west to the Mackenzie River in the east.⁴ Defined more broadly, cold-climate Beringia contained a more diverse array of habitats than originally conceived: Hultén’s mesic tundra zone in the central lowland (i.e., Bering Land Bridge), surrounded by drier and more steppic areas in the uplands to the west and east. In fact, the central tundra zone is thought to have acted as an ecological barrier to some steppic species in Northeast Asia and Alaska/Yukon (see Figure 1).⁵⁻⁷

Regardless of its apparent suitability as a bridge between Asia and North America, Beringia’s role as a migratory route for the colonization of the Western Hemisphere can be confirmed only by the analysis of paleoanthropological data. These data comprise human genetics (as well as the genetics of several satellite or symbiotic species [e.g., domesticated dogs, body lice]), human anatomical remains, artifacts and features made by humans, and linguistic data. With the exception of the genetics and languages of living peoples of the region, relatively few of these data have been obtained from Beringia itself. Most of the central lowland lies below current sea level and is inaccessible to all but the smallest sampling (i.e., coring). The areas of Beringia that remain above water (i.e., Northeast Asia and Alaska/Yukon) are remote and largely undeveloped. To date they have yielded only a handful of archaeological sites and isolated fragments of human bone that antedate inundation of the land bridge (roughly 12,500 cal BP).

During the 1930s, two sets of archaeological remains with potential significance for the peopling of the Americas were discovered in central Alaska. The first were wedge-shaped microblade

cores and microblades thought to have been derived from Northeast Asia.⁸ In the 1960s and 1970s, it became clear that this microblade industry was indeed derived from Asia (central Siberia) and arrived in Beringia after the end of the Last Glacial Maximum (LGM) during the final millennia of the Pleistocene. It currently is dated in central Alaska to ~14,000 cal BP (but does not become widespread in Beringia until the Younger Dryas cold interval, which began about 12,800 cal BP).⁴ Frederick Hadleigh West (1928–2015) argued that it was an archaeological proxy for the people who dispersed throughout North (and South) America, despite the fact that the artifacts made by the latter are highly dissimilar (at least outside northwestern North America).⁹



Figure. 1. Map of Beringia, showing the boundaries of the Bering Land Bridge when sea level was 120 meters below that of the present day (LGM). The locations of archaeological sites and finds mentioned in the text also are shown.

The second set of remains encountered in the 1930s were lanceolate points, recovered from frozen muck deposits in central Alaska and exhibiting unmistakable parallels with Paleoindian artifacts on the North American Plains (but without apparent connection to Northeast Asia).¹⁰ More of these points, including some fluted forms, were recovered after the Second World War and at least some of them were found in datable contexts. Most are concentrated in northern Alaska, although they also are present in southwestern and south-central Alaska.¹¹ As early as the 1950s, the lanceolate points were thought to represent a northward movement of Plains hunters during late Paleoindian times. It now appears to have occurred during the Younger Dryas interval—driven by an expansion of steppe bison habitat in the north.¹² The points are unknown on the Asian side of the Bering Strait and their arrival in Alaska presumably postdates inundation of the land bridge.

During the 1960s and 1970s, evidence of other industries dating to the final millennia of the Pleistocene emerged in both western and eastern Beringia. In central Kamchatka, N. N. Dikov found an industry characterized by production of stemmed points buried beneath microblade assemblages of Younger Dryas age.¹³ More recent research at the sites indicates that the points are about 13,000 cal BP.¹⁴ This industry has never been found in dated context in eastern Beringia, but stemmed points now are dated as early as 13,500–13,000 cal BP in northwestern North America (i.e., contemporaneous to the oldest known fluted points).¹⁵ They are found in dated context (~13,000 cal BP) on the Channel Islands off the coast of southern California, associated with human skeletal remains and a coastal economy,¹⁶ and represent the only credible archaeological evidence of a population movement from Beringia to mid-latitude North America.

Another Beringian industry that came to light during the 1960s and 1970s was characterized by small teardrop-shaped points (“Chindadn points”). These initially were found in the Upper Tanana Valley in east-central Alaska in association with microblades,¹⁷ but later were found in assemblages without microblades in the northern foothills of the Alaska Range.¹⁸ The dating of the oldest site in the Alaska Range is ~13,500–13,000 cal BP, but a teardrop-shaped point recently was recovered from northwestern Beringia dating to ~14,900–13,500 cal BP.^{19,20} The status of the teardrop-shaped points and their relationship to the microblade industry always has been controversial, with some archaeologists suggesting that they actually are part of the latter (i.e., were made by the same people).⁹ In any case, these assemblages do not exhibit any clear parallels with known industries in either Northeast Asia or mid-latitude North America.

The 2002 discovery of artifacts near the mouth of the Yana River antedating the LGM profoundly altered the overall picture of Beringian archaeology. Three of the six discovered localities date to ~32,000 cal BP. Although the stone artifacts are rather generic, frozen sediments ensured preservation of many organics, which included bone awls, eyed needles, possible needle cases, decorated ivory vessels, and personal ornaments.²¹ The profusion of household goods suggests an extended occupation, and the array of faunal remains indicates a broad-based northern interior diet. Along with a 40,000-year-old site on the Arctic Circle in Russia²² and a 45,000-year-old human bone from western Siberia (57° North latitude),²³ the Yana River sites show that modern humans colonized the subarctic and arctic as part of their broader dispersal in northern Eurasia 45,000–30,000 cal BP. During this interval, fluctuating climates in the Northern Hemisphere were generally—if not consistently—cooler than those of the present day (see Figure 2).²⁴

The Yana River sites also reveal that Beringia was occupied before the beginning of the LGM. Although it is possible that settlement extended no farther east than the Yana River at this time, the location and contents of the sites indicate their occupants were adapted to a habitat (shrub tundra) that was widespread in Beringia. The low archaeological visibility of Pleistocene sites in this part of the world mentioned earlier probably explains the current lack of known pre-LGM sites in other areas of Beringia. The Yana River sites present us with a problem in human paleoecology: did humans abandon Beringia during the LGM, returning after 16,000 cal BP, or did they remain in all or part of Beringia throughout the LGM?

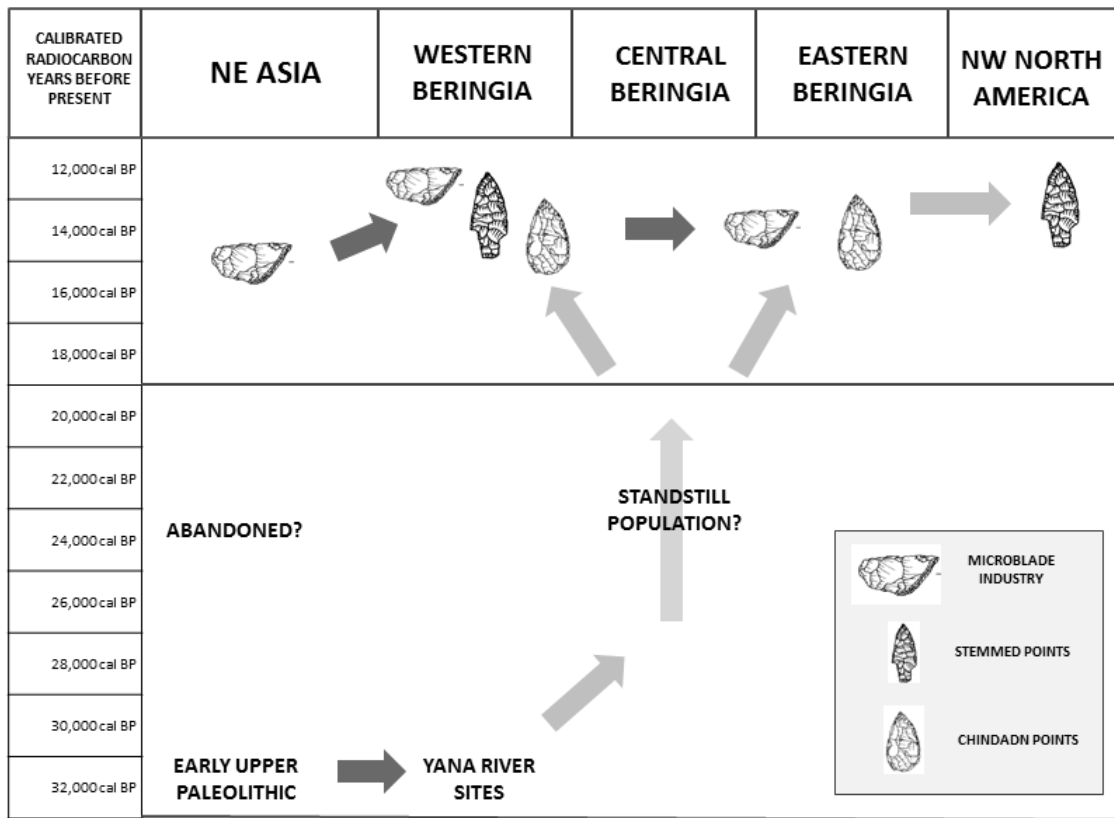


Figure 2. Archaeology of Northeast Asia, Beringia, and mid-latitude North America. The light gray arrows represent the Beringian Standstill Hypothesis (see text).

THE BERINGIAN ‘STANDSTILL’ HYPOTHESIS

The idea that humans were present in Beringia throughout the LGM was explicitly formulated by Tamm et al. in 2007 on the basis of mtDNA analyses.²⁵ According to the “Beringian Standstill Hypothesis” (also known as the “Beringian Incubation Model”), the Beringian population was genetically isolated from its source population in Northeast Asia at the beginning of the LGM (~30,000 cal BP). The Beringian LGM population included the following mtDNA sub-clades: A2, B2, C1b, C1c, C1d, C4c, D1, D4h3, and X2a. After the LGM (~14,000 cal BP), descendants of the isolated population spread into mid-latitude North America and South America, although some of the ‘standstill’ population (mtDNA sub-clade C1a) spread back into Northeast Asia. And, according to the hypothesis, there also was a post-LGM movement of people from Northeast Asia (mtDNA sub-clade D2) into Beringia (and northern North America) (Figure 3).

The empirical core of the model rests on the observation that the mtDNA of the ‘standstill’ sub-clades contains a significant number of substitutions that took place *after* the divergence from the Asian parent groups, but *before* the Beringian population dispersed throughout North and South America (i.e., the substitutions are widespread among living Native Americans in mid-latitude North America and South America). Using an estimated mutation rate of 3.5×10^{-8} /year/position,

Tamm et al. calculated that the period of isolation preceding the dispersal in the Western Hemisphere was approximately 10,000 years.

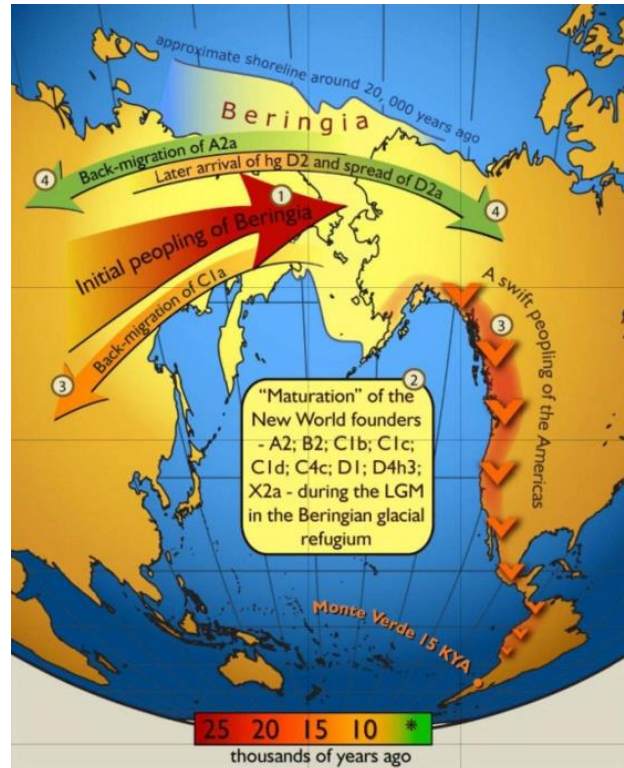


Figure 3. The *Beringian Standstill Hypothesis*, based on the analysis of mtDNA in living peoples, presented by Tamm et al. in 2007 (their Fig. 2).²⁵

The roots of the Beringian Standstill Hypothesis may be traced back to a controversial 1986 paper by Greenberg, Turner, and Zegura that introduced what is usually referred to as the ‘three-wave model.’²⁶ The model, based on a synthesis of linguistics, dental anthropology, and genetics, sub-divided all Native Americans into three major groups: (1) Amerind; (2) Na-Dené; and (3) Aleut-Inuit (termed ‘Aleut-Eskimo’ in the paper). It explained the linguistic, anatomical, and genetic differences among the groups as the product of separate migrations from Asia to the Americas. Because the Aleut-Inuit population had long been perceived as a late arrival in northern North America with close ties to modern Northeast Asian groups, the primary contribution of the ‘three-wave model’ was the separation of the Na-Dené (speakers of Athapaskan-Eyak, Tlingit, and Haida) from other Native American groups (but with closer ties to the Aleut-Inuit than other groups) and the inclusion of all remaining Native American groups into a single linguistic and biological entity (i.e., ‘Amerind’).

The three-wave model triggered an extended debate over both the relationships among and within Native American groups (cultural and biological) and the reasons underlying their differentiation. Some linguists were especially critical of the Amerind concept (as well as the Na-Dené category), arguing that Native American languages were highly diverse.²⁶ On the other hand, Szathmary—in a series of papers published before and after the three-wave model paper—

argued that the biological differences between the major groups had been overstated.^{27,28} Szathmary suggested the differences were better explained, not as separate migrations from Asia to the Americas, but as the result of the isolation of groups by coalescing glaciers (Laurentide and Cordilleran) after the initial migration to the western hemisphere.

By the early 1990s, estimates of the divergence time between Asian and Native American populations were published on the basis of mtDNA analyses, and these included estimates of 30,000 years or more.^{29,30} In 1997, Bonatto and Salzano published the results of an mtDNA study and—following Szathmary—concluded that coalescing glaciers had genetically isolated the Amerind south of the ice sheets from the ancestral Na-Dené and Aleut-Inuit in Beringia. They emphasized the role of Beringia not as ‘bridge’ or ‘corridor,’ but as a place where the Native American population had “settled and diversified before further colonization of the rest of the American continent.” Bonatto and Salzano labeled their model “out of Beringia” (as opposed to “out of Asia”).³¹ The Beringian Standstill Hypothesis, proposed ten years later, is a revised version of “out of Beringia” that postulates isolation of most of the ancestral Native American population in Beringia (not south of the ice).²⁵ The following year, Kitchen et al. estimated an effective population size (N_{ef}) of ~2,700 females for the ‘standstill’ population.³²

Tamm and colleagues never cited the original three-wave model in their 2007 Beringian Standstill paper (although they referenced Szathmary’s earlier work) and there are significant differences between the two models. Whereas Greenberg et al. 1986 postulated three separate migrations (or ‘waves’) from Asia to the Americas, the standstill hypothesis places the source of most Native Americans, including the Na-Dené and Aleut-Inuit, in Beringia. Tamm et al. envisioned Beringia as a post-LGM center of human population dispersal, analogous to Hultén’s 1937 thesis that tundra plants had dispersed from the central lowlands after each glacial period. As already noted, the postulated flow of people and/or genes out of Beringia included movements into Northeast Asia, as well as North America.

The pattern observed in the mtDNA data by Tamm and colleagues has yet to emerge with equal clarity in either Y-DNA or autosomal DNA. The lack of a similar pattern in the Y-DNA data conceivably reflects different histories of the paternal and maternal lineages—a pattern found in other parts of the world (e.g., southern Asia).³³ Some support for the standstill hypothesis in autosomal DNA may be found in the distribution of an allele at a microsatellite locus on chromosome 9 (D9S1120) which exhibits a pattern similar to that seen in the mtDNA data.³⁴ Also potentially significant is the evidence for a relatively minor *genetic bottleneck* in the Native American genome. In a 2007 analysis of single nucleotide polymorphism (SNP) data in 24 Native American populations, Wang et al. found only a 6–7% reduction in heterozygosity relative to the global average, which is consistent with the hypothesis (i.e., large and diverse source population in Beringia).³⁵ The results of a more recent whole-genome analysis by Reich et al. however are generally consistent with the original three-wave model.³⁶

Some support for the Beringian Standstill Hypothesis also may be found in a new analysis of Asian, Australian, and Native American teeth (which was a major component of the three-wave model), as presented in Box 1. Contrary to the Reich et al. whole-genome study, multivariate

analysis of the teeth suggests the Na-Dené and Aleut-Inuit are more closely related to other Native American groups than to the modern Asian population (see Figure 4).

Box 1: Dental Anthropology and the Beringian Standstill Hypothesis

G. RICHARD SCOTT

Although Aleš Hrdlička (1869–1943) noted in the early 20th century that shovel-shaped incisors were common in Asian and New World populations,¹⁰³ tooth morphology played a minor role in issues surrounding the peopling of the Americas until the 1970s. Christy G. Turner II (1933–2013) was the first to use dental morphology to develop a specific peopling model when he compared the frequencies of 3-rooted lower first molars (3RM1) among Native American groups, observing that Eskimo-Aleuts had an exceptionally high frequency of this accessory root (~30%), while it was relatively uncommon (~5%) in American Indian populations. Although data were limited at the time, the Navajo, an Athapaskan group, exhibited a 3RM1 frequency that fell between these extremes.¹⁰⁴ The observed pattern of dental morphology in New World populations became one of three supporting components of the “three-wave model” (along with linguistics and genetics) published in 1986 (see main text).²⁶

In addition to the tripartite subdivision of Native American dental traits, Turner noted a fundamental dichotomy in Asia that distinguished Northeast Asians, or *Sinodonts*, from Southeast Asians, or *Sundadonts*. Ancillary to this observation, he postulated that Sinodonts were ancestral to all New World populations, while Sundadonts were ancestral to Polynesians.¹⁰⁵ Australia and New Guinea did not fall clearly in either group, although he proposed the Australian dentition was proto-Sundadont.¹⁰⁶ The Sinodont/Sundadont dichotomy may reflect the initial dispersal pattern of modern humans in East Asia (i.e., bifurcation of northern and southern routes by the Himalayan Plateau).

Turner did not comment on the Beringian Standstill Hypothesis, but his large data set on tooth crown and root morphology may be used to address the issue, and to re-examine the related “three-wave model.” The following observations are based on the analysis of 24 crown and root traits in 135 samples (numbering several thousand individuals) analyzed as 12 broad regional and temporal groupings (Southeast Asia early, Southeast Asia late, East Asia, North America early, South America early, Eskimo-Aleut, Na-Dené/Northwest Coast, North American Indian, Mesoamerican, South American Indian, Australian, New Guinea).

To evaluate how dental morphology comports with the Beringian Standstill model, the pattern of variation shown by 24 individual traits is considered along with a multivariate analysis of all traits and groups. For individual traits, seven potential patterns are: (1) Sinodont only (East Asia = all New World groups, distinct from Southeast Asia); (2) Beringian Standstill (all New World groups similar, equally distinct from East and Southeast Asia); (3) Sinodont only plus Beringian Standstill (all New World groups similar and more similar to East Asia than Southeast Asia); (4) Sundadont early, Sinodont late (early New World groups more similar to Southeast Asia, later New World groups more similar to East Asia); (5) Sundadont only (Southeast Asia = all New World groups, distinct from East Asia); (6) Sundadont only plus Beringian Standstill (all New World groups similar and more similar to Southeast Asia than East Asia); and (7) undetermined (all groups similar). Model 4 is the one favored by many craniometricians, but it has no Beringian Standstill elements. The key point regarding Beringian Standstill models is that they involve relatively uniform frequencies among all New World groups and clear distinctions from all Old World groups (see Figure 4).

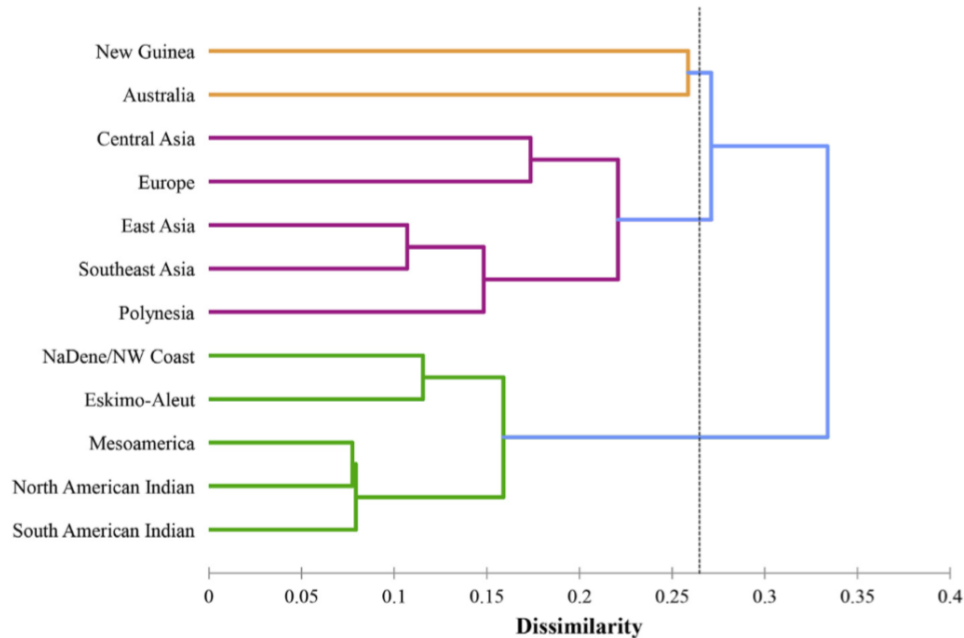


Figure 4. Dendrogram generated from a multivariate analysis of 24 dental traits in samples ($n = 135$) numbering several thousand individuals drawn from New Guinea, Australia, Southeast and East Asia, and North and South America.

Of 24 traits, only two show a pattern consistent with model 1 (enamel extensions, odontomes). Seven traits conform to the Beringian Standstill model 2 (4-cusped LM2, deflecting wrinkle, UI1 winging, Carabelli's trait, LP2 lingual cusp number, cusp 6, 2-rooted LM2). An additional five traits align with model 3 (shoveling, double-shoveling, 2-rooted UP1, UI2 interruption grooves, 3-rooted UM2). Three traits align with model 4 (pegged-reduced-missing UM3, 3-rooted LM1, 3-cusped UM2) but not a single trait conforms to either model 5 or 6. Seven of the 24 traits exhibited uniform frequencies with no distinct pattern. Overall, seven traits support the notion that Sinodonts gave rise to all New World populations while 12 of 24 traits support a Beringian Standstill. Only three traits support a Sundadont presence in the New World, including, paradoxically, the trait that provided the foundation of the three-wave model (3RM1).

Because biodistance methods for this sample set yield similar results, the focus is on one set of measures. A Euclidean distance matrix for 12 samples includes 11 pairwise comparisons between each sample and all other samples. If comparisons are limited to the average distances to the seven New World samples, the most distant groups are, not surprisingly, New Guinea (1.669) and Australia (1.491). Southeast Asia early (1.078) and late (1.038) are the next most divergent from the Americas. Of the Asian groups, East Asia (0.897) is the closest to New World groups, consistent with the Sinodont model. However, the significant point insofar as the Beringian Standstill model goes is that the average distances among the seven New World groups are remarkably uniform, i.e. North American early (0.719), South America early (0.524), Eskimo-Aleut (0.654), Na-Dené/Northwest Coast (0.538), North American Indian (0.501), Mesoamerica (0.544), and South American Indian (0.494). Five of the pairwise averages are essentially identical. The only exceptions are North American early (where sample size is an issue) and Eskimo-Aleut (who are closer to Siberia and East Asia than Amerind groups for all biological variables). The significance of the similar averages is that the Native American groups are distinctly separated from East Asia, suggesting they diverged from an

ancestor that had been removed from Northeast Asians for a period of time. Essentially, the New World was not peopled directly from Northeast Asia as there had to be a time lag for the ancestors to diverge from East Asians. Although Turner is still technically correct that New World populations are derived from Sinodonts, there was a period of time, presumably in Beringia, where populations became super Sinodonts, or Sinodonts on steroids. Although there are a number of traits that set East Asian Sinodonts apart from Southeast Asian Sundadonts, these traits become even more exaggerated in the ancestors of Native Americans. The dendrogram based on Bray Curtis dissimilarity measures provides a representation of divergence patterns indicated by tooth crown and root morphology.

Another recent development pertinent to the Beringian Standstill Hypothesis is computer modeling of the Laurentide-Cordilleran ice sheets, which suggests that access to mid-latitude North America from Beringia was completely blocked throughout most of MIS 3 and MIS 2 (~55,000–15,000 cal BP).³⁷ In other words, it appears unlikely that there was a human population in mid-latitude North America (and South America) before 15,000 cal BP, because modern humans probably were not present in Northern Asia before 50,000 years ago (and other forms of *Homo*, including Neandertals and Denisovans, do not appear to have occupied any places above latitude 60° N). Most of the estimated divergence times for the Native American sub-clades also indicate a post-15,000-cal-BP dispersal, consistent with the glacial chronology.³⁸

The ‘standstill’ hypothesis cannot be confirmed until there is not only human fossil and/or archaeological evidence of a population in Beringia during the LGM, but evidence that links this population to one or more of the Native American lineages that dispersed throughout the Western Hemisphere after 15,000 cal BP. The most conclusive evidence would be aDNA, but an archaeological proxy in the form of stemmed points, which represent the only diagnostic artifact dated to >13,000 cal BP in Beringia and mid-latitude North America, would also help confirm the model.

At present, however, the ‘standstill’ hypothesis provides a plausible explanation of the genetic and archaeological data, accounting for a number of otherwise puzzling aspects of those data. The hypothesis is accommodated by the paleo-ecological data, which—as described earlier—have long indicated an LGM tundra refugium in south-central Beringia, where winter temperatures and biological productivity were comparatively high.⁷ It may have been the only substantial source of wood above latitude 50° N during the LGM. Beringia supported a credible refugium for a large human population throughout the LGM, when most of northern Eurasia was abandoned by humans (see below).

The Beringian Standstill Hypothesis provides an explanation of why Native American population history lacks evidence for a significant genetic bottleneck associated with one or more migrations from Asia to the Americas.^{35,39} Genetic models of effective population size (based on mutation rates and overall diversity) predict a relatively large and stable—or slowly growing—population in Beringia during the LGM.⁴⁰ The prediction is consistent with accumulating evidence for the proliferation of many lineages during 25,000–15,000 cal BP. At present, a total of 16 maternal lineages have been identified in the ‘standstill’ population (on the basis of analysis of living people).⁴¹

From the archaeologist's perspective, the 'standstill' hypothesis provides an explanation for the single most confounding aspect of the relevant archaeological record—the absence of evidence for a group of people migrating from Northeast Asia to mid-latitude North America after the LGM. As described earlier, the archaeological record yields proxies in the form of diagnostic artifact types for movements from: (1) Northeast Asia into Beringia (wedge-shaped microblade cores) at ~14,000 cal BP; (2) Beringia into mid-latitude North America (stemmed points) at ~13,000 cal BP; and (3) mid-latitude North America into eastern Beringia (late Paleoindian points) at ~12,000 cal BP (i.e., during the Younger Dryas cold interval). The earliest reliably dated sites in mid-latitude North America and South America (~14,500 cal BP) antedate the arrival of the microblade technology in Beringia, which is—as currently dated—too young to represent a credible source for this technology.⁴²

Matching the archaeological record with genetic data is a challenge, however. To begin with, large-scale movements of people and/or genes take several forms.⁴³ In addition to the 'colonization' of a previously unoccupied region, migrating humans may filter into an area inhabited by another population and gradually intermarry with the latter. Alternatively, the incoming population may physically replace the existing inhabitants, or incoming groups of males may largely replace the existing male population. The various forms of 'migration' yield different genetic and archaeological signals. For example, replacement of an existing male population by in-migrating males might be represented by significant changes in stone artifacts but leave few traces in the mtDNA data. In the past, models of Native American settlement typically have assumed discrete population 'waves,' but the emerging picture—especially after the LGM—is more complex and probably involved more than one form of migration.

MODERN HUMANS COLONIZE NORTHERN EURASIA AND BERINGIA

It now is apparent that the initial colonization of Beringia occurred not in conjunction with the peopling of the Americas, but with the early settlement of northern Eurasia by modern humans. Multiple lines of evidence (genetics, dated fossil remains, and archaeology) indicate that *Homo sapiens* colonized northern Eurasia between 50,000 and 40,000 cal BP. Many areas may have been occupied during one or two major warm periods during this interval (Greenland Interstadials 12 and 11 [GI 12 & GI 11] in the Greenland ice core record).⁴⁴ While the oldest known sites in Beringia date to no more than ~32,000 cal BP (and correlate with a cold phase in the ice core record), a dated modern human bone from latitude 57°N in western Siberia indicates that similar habitat had been occupied by ~45,000 cal BP.^{21,23} New discoveries reported in early 2016 may document people in the Siberian Arctic and northwestern Beringia before 45,000 cal BP.⁴⁵

Although mtDNA has been superseded by whole-genome analyses for the reconstruction of human population histories, the maternal lineages and haplogroups provide useful markers (in concert with the paternal lineages or haplogroups, determined from the analysis of the non-recombining portions of the Y-chromosome). The identification of maternal lineages from aDNA extracted from dated human remains in Italy and Siberia reveals that the same mtDNA haplogroup (**R**) spread widely across northern Eurasia before 40,000 cal BP.^{23,46} This lineage is

closely linked, through **N**, with African lineage **L3** (the estimated coalescence time of mtDNA hg **M** and hg **L3** is ~70,000 years).⁴⁷ The presence of maternal lineage **R** in Northern Asia at least 45,000 years ago, combined with the absence of any evidence of genic exchange with the Denisovans (who interbred with modern human groups in Southeast Asia) indicates that modern humans colonized Siberia via a “northern route” from western Eurasia, and not via South and East Asia.^{23,48}

The four major Native American mtDNA haplogroups (**A**, **B**, **C**, and **D**) were established in Asia before the beginning of the LGM (~30,000 cal BP) according to estimates of their coalescence dates, and analysis of aDNA from *Tianyuan Cave* (northern China) confirms divergence of mtDNA **B** by 40,000 cal BP.^{49,50} The sub-clade of a less common mtDNA haplogroup (X2a [also X2g]) is unique to North America and unknown in Asia, while its parent group X2 is found in western Eurasia, leading to speculation about movements across the Atlantic. However, there is little if any genetic evidence for a direct connection between west Eurasians and Native Americans, and the most basal X2a lineage now is known from an early Holocene context in the Pacific Northwest (Kennewick).^{51,52} Recent analyses of the major Y-DNA haplogroups, which include **Q-M3** (Y-DNA at Kennewick) and **C-3b**, also suggest an origin in Asia, and at least some of them appear to have diverged before or during the LGM (new aDNA data indicates relatively rapid substitution rates in Y-DNA, suggesting that coalescence ages for paternal lineages have been under-estimated).^{23,53}

Significant portions of northern Eurasia, including Beringia, probably had not been occupied by humans before the arrival of *Homo sapiens*. This is suggested not only by an absence of fossils and archaeological remains that may be firmly assigned to other forms of *Homo* in places such as central Siberia, but also by the pattern of low biological productivity and extreme winter temperatures in these places. The most widespread non-modern human settlement of northern Eurasia is represented by the Neandertals (and their Denisovan cousins), whose remains are found in areas that today enjoy relatively high *net primary production* (NPP) and rich herbivore resources, including the Altai region of southwest Siberia.⁵⁴ And yet, analysis of their genetics indicates that populations were small (or “thin on the ground”) and subject to periodic stress and local extinction.⁵⁵ The absence of their remains in the colder and drier parts of northern Eurasia presumably reflects a lack of adequate local resources, perhaps exacerbated by high caloric demands.

Ethnographic data on recent hunter-gatherer ecology provides insight to how modern humans adapted to cold and dry habitats, which, in turn, helps identify their differences with other forms of *Homo*.⁵⁶ Recent hunter-gatherers developed a variety of technological and organizational adaptations to scarce resources and low temperatures. The former included mechanical instruments and facilities (including untended facilities or *automata* such as snares, traps, and weirs) for efficient harvesting of small mammals, fish, and birds.⁵⁷ Heavy consumption of smaller vertebrates often was essential in cold places where daily energy requirements could be more than 40% higher than for hunter-gatherers in tropical settings,⁵⁸ while available plant foods were few and large-mammal resources widely dispersed (in space and time). Complex clothing and shelter technology also was essential for coping with extreme winter temperatures,⁵⁹ and food storage technologies often were developed to adapt to seasonal variations in resource

availability. Organizational adaptations (also found in low-latitude regions where NPP was reduced) included maintenance of widespread alliance networks, high mobility, and strategic scheduling of seasonally available foods.⁵⁶

The human fossil and archaeological record of modern human settlement in Northern Asia (and Eastern Europe) 45,000–30,000 cal BP yields evidence of dietary, technological, and organizational adaptations found among recent hunter-gatherers in settings where NPP is below 250 g C/m²/yr and the January mean below -20°C. Stable isotope values on human bones from subarctic Siberia and the central East European Plain may indicate high consumption of fresh-water foods, which may have included water-birds as well as fish.^{23,60} Concentrations of hare remains on the East European Plain and the Yana River sites suggest harvesting of small mammals, possibly with snares and traps.^{21,61} Eyed needles from both Eastern Europe and southwest Siberia (also Yana River sites) confirm production of tailored, insulated clothing, and sites in southern Siberia may contain evidence of both spear-throwers (mechanical instrument) and food storage.^{62–64} The movement of raw materials over hundreds of kilometers indicates high mobility (and/or widespread social networks).^{61,65} By contrast, there is little or no evidence for these technological and organizational adaptations among other forms of *Homo* in northern Eurasia.

Between 45,000 and 30,000 cal BP, Beringia was an extension of Northern Asia. Global sea levels were generally 65–85 meters below those of the present day (see Figure 5), creating a broad land connection between Chukotka and western Alaska.⁶⁶ Pollen data from western Beringia suggest an environment that varied with space and time, including larch forest in some areas (e.g., Upper Kolyma River) during warmer intervals and shrub tundra or a mosaic of both habitats in other times and places.⁶⁷ The Yana River sites were occupied during a slightly cooler interval (~32,000 cal BP), when this part of Beringia supported a tundra-steppe. The faunal remains from the sites include steppe bison, reindeer, horse, and some mammoth; the small mammal remains are dominated by hare.²¹ Environments in eastern Beringia appear to have been drier than those of western Beringia, although they also have been described as tundra-steppe.^{4,68}

Traces of pre-LGM settlement in Beringia currently are confined to the Yana River sites, which are located in northwestern Beringia, more than 2,000 km from the Bering Strait. Although a worked mammoth tusk fragment dating to ~40,000 cal BP was found in gravel deposits along the Inmachuk River in northwest Alaska, it is problematic as evidence of a pre-LGM human presence in eastern Beringia, because it could have been picked up fresh from a permafrost context and worked by more recent inhabitants of the area.⁶⁹ As environments similar to that of the Yana River area ~32,000 cal BP appear to have existed in eastern Beringia—and a broad land connection between the two was present—the current lack of pre-LGM sites in Alaska/Yukon is more likely due to low archaeological visibility than the absence of human settlement. It now appears that the coalesced Laurentide and Cordilleran glaciers, not Beringian environments (or the Bering Strait), was the barrier to modern human colonization of the Western Hemisphere before the end of the LGM (Figure 6).³⁷

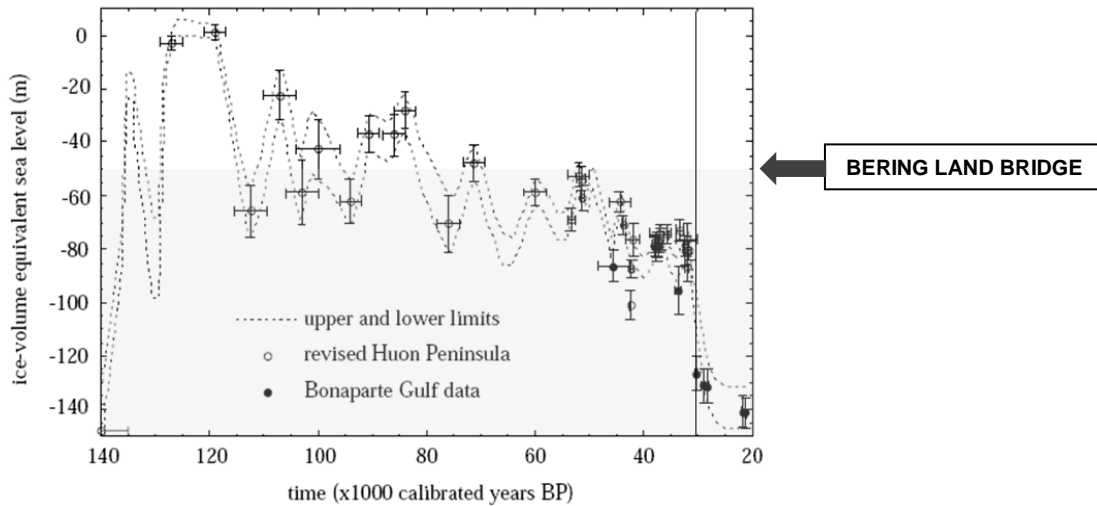


Figure 5. Global sea level for the interval between 140,000 and 20,000 cal BP. (from Lambeck et al. 2002 their Fig. 6).⁶³ The Bering Land Bridge emerges at 50 meters below present-day sea level. Between ~32,000 and 28,000 cal BP, sea level fell from roughly -75 meters to below -120 meters, exposing a larger portion of the Bering Platform (or land bridge) between latitudes 56° and 58° North.

CLIMATE-CHANGE APOCALYPSE: THE IMPACT OF THE LGM

The extreme cold and aridity of the LGM had a global impact on plant and animal life, forcing human populations to retreat to various terrestrial refugia in both northern and southern hemispheres. According to the Beringian Standstill Hypothesis, one of these LGM refugia was in Beringia. Although the presence of any humans in Beringia between 30,000 and 15,000 cal BP remains to be confirmed with dated fossils or artifacts (currently confined to problematic flaked mammoth bone dating to ~25,000 cal BP from Bluefish Caves in the northern Yukon),⁷⁰ paleo-environmental data indicate that conditions there probably were sufficient to sustain a population during the LGM.

Global ice volume during the LGM is estimated to be ~50 million km³ greater than that of the present day.⁷¹ Northwest Europe was largely covered by an expanded Scandinavian ice sheet, while the Laurentide/Cordilleran ice mass also experienced substantial growth.³⁷ At the peak of the LGM (~21,000 cal BP) mean global temperature is estimated at 5.1°C lower, and precipitation roughly 10% lower, than those of today.⁷² Computer modeling of LGM vegetation suggests a major expansion of desert areas (36% greater than those of the present interglacial) and contraction of grasslands (40% less than the same). Tropical forest was an estimated 20% less extensive, and extra-tropical forest an estimated 45% less, than that of the recent past. Only shrubs expanded relative to their post-glacial distribution. *Global NPP is estimated to have been slightly more than half of what it was during the post-glacial epoch* (before the industrial era).⁷²

The impact on the human population is illustrated by the genetics of living peoples, with some supporting aDNA. The living peoples of Africa, Europe, and Asia exhibit evidence of population

bottlenecks related to the effects of LGM climate on environments. Areas in the temperate zone and lower latitudes that are arid today, such as North Africa, the Arabian Peninsula, and upland zones in Southern Asia, apparently were abandoned. Much of Western and Eastern Europe was evacuated, as populations retreated south into multiple isolated refugia, and parts of Northern Asia also seem to have been abandoned.⁷³⁻⁷⁵

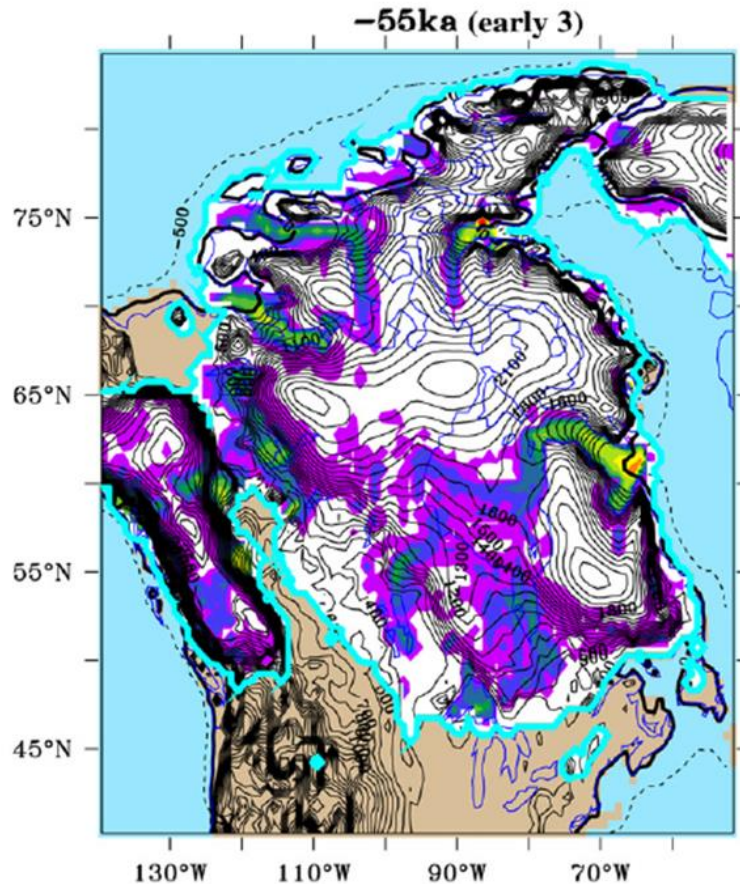


Figure 6. Laurentide / Cordilleran ice sheets at ~55,000 cal BP (from Stokes et al. 2012, their fig. 4),³⁶ based on the Glacial Systems Model (GSM). According to the GSM, the ice sheets had coalesced by the time that modern humans arrived in Northeast Asia (~45,000 cal BP), and probably blocked coastal and interior access to mid-latitude North America and South America until after the LGM (i.e., until after 16,000–15,000 cal BP).

The evidence of population bottlenecks in the genetic data are supported by patterns in the archaeological and human fossil record. At stratified sites in some of the areas listed above, a significant hiatus in occupation may be observed in deposits dating to the LGM. On a regional basis, a gap or depression in the radiocarbon chronology corresponding to the LGM (or the coldest phase of the LGM) may be recognized, while credible evidence for occupations of LGM age are confined to places where climates were warmer and/or wetter at the time (i.e., the refugia).⁷⁶⁻⁷⁸

What factor or combination of factors forced humans to abandon so much territory during the LGM (~30,000–16,000 cal BP)? Despite extreme cold and/or aridity in places such as central Siberia and interior Australia, it appears likely that it was the effect of these variables on plant and animal life that drove humans into the various refugia. If groups already were foraging across wide areas—tens of thousands of square kilometers—each year in these places, the sharp decline in NPP probably pushed them over the edge of sustainability. In low-latitude deserts, the scarcity of water alone may have been sufficient to preclude human settlement. In the higher latitudes, other factors may have come into play. Despite the development of insulated winter clothing, the extreme low temperatures may have been too much for people who retained the warm-climate anatomy of their recent ancestors.⁷⁶ The absence of wood in some areas also might have been an obstacle to year-round settlement—experimental research reveals that a modest quantity of wood is necessary to render bone practical as a fuel.⁷⁹

The impact of the LGM on Beringia was unique for several reasons. The global sea level record reveals that between 32,000 and 28,000 cal BP, sea level fell sharply—from a depth of roughly 75 meters to more than 120 meters below that of the present day (see Figure 5). As the bathymetry of the Bering Sea indicates, the LGM effect on sea level exposed a significantly larger area of the Bering Platform. Much of the expansion occurred in the southeastern margin of the land bridge (i.e., Bristol Bay area) at comparatively low latitude (roughly 56–58° N).

Modeling of NPP during the LGM suggests a relatively high level of plant productivity in this region due to the effects of moisture from the North Pacific (see Box 2; Figure 7)⁸⁰ while models of ocean temperature suggest minimal LGM reduction for the Bering Sea and Gulf of Alaska.⁸¹ The topography of what Hopkins described as a “monotonously flat plain” may have played a role in retaining moisture (i.e., rivers meandering across poorly-drained lowlands).⁸² In sum, the LGM actually created new habitat for interior hunter-gatherers in southern Beringia.

As described earlier, a tundra refugium on the land bridge exposed during the LGM was postulated by Hultén in the 1930s. In recent decades, a substantial amount of supporting data on LGM environments have been collected, including information from sediment cores drilled into the former surface of the land bridge.^{4,83} These data (pollen, plant macro-fossils, insect fauna) confirm the presence of a mesic tundra environment, not only on the exposed Bering Platform, but also extending into adjoining lowlands of Chukotka and Alaska.⁸⁴ Even the more steppic areas outside central Beringia supported a higher tundra component than previously believed.⁸⁵ Arboreal taxa—unlikely to have been present anywhere else at this latitude during the LGM—included spruce, birch, and alder.⁸⁶ The insect fauna from central Beringia indicate a smaller decline in temperature (3–5°C) than that estimated for other parts of the northern hemisphere.⁸⁷

A recent estimate of ‘standstill’ population size (based on genetic diversity and substitution rates, and using nuclear genomic as well as mtDNA data) is roughly 5,000 census individuals (generated from an estimated effective population size [N_e] of ~1,000), although a total population of 8,000–10,000 is considered possible.⁸⁸ The modeling of NPP for LGM Beringia described in Box 2, complemented with the paleo-environmental data mentioned above, provide a means for addressing the question of whether or not the mesic tundra zone in southern Beringia could have supported a population of this size. The model output suggests that—in addition to

the high NPP zone of roughly 200–250 g C/m²/yr in the southeastern land bridge—the southern half of central Beringia probably produced at least ~150 g C/m²/yr at the peak of the LGM (see Figure 7). Data on recent hunter-gatherers indicate that this level of NPP would have supported an interior Alaskan group (such as the *Ingalik*) at a density of at least 2.5 individuals per 100 km².⁵⁶ At this level, a ‘standstill’ population of 5,000–10,000 individuals would require a territory of between roughly 125,000 and 250,000 km², which appears to have been available in central Beringia.

Box 2: Modeling NPP for LGM Beringia

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NPP (*Net Primary Production* or *Net Primary Productivity*) is the rate of carbon flux from the atmosphere into plants, minus the carbon used in respiration. Pollen data indicate that above-ground plant productivity was markedly reduced in Beringia during the LGM.^{107,108} However, because of the low number of pollen sample sites, we do not know how NPP varied across the large sub-continent.

NPP for LGM Beringia was modeled by importing climate data into a vegetation model (*Biome4*). *Biome4*, which is driven by climatic and edaphic parameters, reconstructs steady state vegetation (biomes) using a coupled carbon and water flux model. An intermediary step entails calculation of leaf area index and potential net primary production (g C/m²/yr).^{109,110} To calculate NPP during the last ice age, LGM climatic parameters from the *Community Climate System Model 4.0* (CCSM4), a general circulation model with coupled land, atmosphere, ocean, and sea ice components,¹¹¹ were loaded into *Biome4* and CO₂ was set to 185 ppm.¹¹²

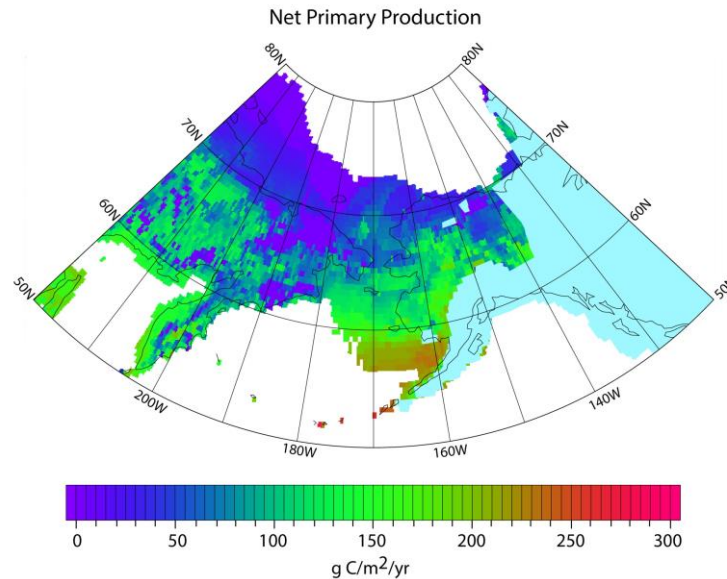


Figure 7. Net Primary Production or NPP (measured as g C/m²/yr, which is approximately 45% of total organic matter) for Beringia during the LGM (~21,000 cal BP), as predicted by the *Biome4* model. According to the model, the most productive areas would have been found on the southeastern margin of the Bering Land Bridge, much of which was not exposed until the LGM.

As shown in Figure 7, the resulting NPP estimates indicate that the southeastern margins of the Bering Land Bridge were more productive than regions to the north and farther from the coast. This suggests that the sparse herbaceous tundra typical of interior LGM sites may have included greater numbers of woody plants along the southern coast. This is consistent with a pollen analysis of a marine sediment core extracted from a location immediately offshore of the southeastern Bering Land Bridge, where (if the pollen is not reworked) woody plants, such as birch, alder, and willow, along with the occasional spruce, may have been present.⁸⁶

Wherever it was located, the genetic diversity of the standstill population suggests that it may have been distributed across a large area—perhaps even subdivided among several regions. Diversification (geographic structure) among multiple ‘refugia’ populations in southern Beringia during the LGM would be expected to yield substantial geographic structure to colonizing populations moving south of the receding ice sheets after the LGM, as each of these ‘refugia’ populations contributed independent streams of migrating colonists. Such geographic structure is indeed observed in both mitochondrial and nuclear genetic data from both modern and ancient DNA studies.^{25,36,38,89,90} The pattern also would help explain the linguistic diversity of the groups that dispersed in the Americas after 15,000 cal BP.^{91,92}

Moreover, groups are likely to have foraged over wide areas during the course of the year. Seasonal movements into the more steppic areas, such as central Alaska, to exploit large grazers (e.g., horse, bison) may have been critical to augmenting the plant and animal resources of the mesic tundra zone. The same groups could have wintered in the latter, where the January mean was relatively mild and wood was available for fuel. The presence of wood as a supplement to bone fuel (which burns at a very high rate in the absence of wood) may have been an important factor.⁷⁹

POST-LGM BERINGIA AND HUMAN SETTLEMENT OF THE AMERICAS

The LGM ended 17,000–16,000 cal BP, when glaciers began to retreat, opening access to coastal areas in northwest North America and, somewhat later (15,000–14,000 cal BP), an interior corridor in western Canada. Mesic tundra vegetation spread out of central Beringia, as Hultén hypothesized, following higher temperature and moisture into upland areas. Shrub tundra appeared in the northern foothills of the Alaska Range at about 13,000 cal BP.⁹³ Sea level rise lagged behind the other post-LGM events and central Beringia was not flooded until after 13,000 cal BP and the arrival of people in southern South America.

Following the LGM, populations expanded out of refugia in Africa, Europe, Asia, and Australia, and both genetic and archaeological data (as well as linguistics) suggest movements into and out of Beringia in the millennia after 16,000 cal BP. Central Siberia (Lena Basin) was occupied 16,000–15,000 cal BP by people who manufactured wedge-shaped microblade cores with a distinctive technique (“Yubetsu”).⁹⁴ They probably were derived from people in southern Siberia, who made similar artifacts during the later LGM.⁹⁵ Wedge-shaped microblade cores produced with the Yubetsu technique are dated to 14,150–13,870 cal BP in south-central Alaska

(*Swan Point*), and apparently represent the movement of these people into eastern Beringia ~14,000 cal BP.⁹⁶

Who made the wedge-shaped microblade cores? In the original ‘three-wave model’ paper, Greenberg et al. suggested that this industry was produced by the Na-Dené.²⁶ According to the standstill hypothesis, however, the Na-Dené are derived primarily from Beringia, although this potentially applies only to the maternal lineages.²⁵ Recently, two mtDNA sub-clades (C1b and B2) were identified in human remains recovered from an archaeological site in central Alaska (*Upward Sun River*) assigned to a younger version of the microblade industry (*Denali complex*) that is widespread in Beringia during the Younger Dryas cold interval (~12,800–11,300 cal BP).^{97,98} Both sub-clades are assigned to the Beringian ‘standstill’ population by Tamm et al.,²⁶ which is not consistent with the view that the microblade industry was brought to Beringia by people from Central Siberia after the LGM. Alternatively, the maternal lineages at Upward Sun River might be related to the movement of people into parts of Alaska from the northern Plains during the Younger Dryas (for which there is supporting archaeological evidence, as noted above).¹¹ An even younger version of the microblade industry is known from *Saqqaq* in Greenland (~4,000 cal BP), where it is associated with mtDNA sub-clade D2a1 (and Y-DNA Q1a) derived—according to Tamm et al.—from Northeast Asia after the LGM.^{26,99}

The archaeological record yields evidence of another industry in Beringia 15,000–14,000 cal BP that conceivably represents the descendants of the ‘standstill’ population, spreading out of their postulated refugium in the central lowland after the LGM. New dates from a site near the mouth of the Indigirka River in northwestern Beringia (*Berelekh*) indicate the presence of people making teardrop-shaped bifacial points (‘Chindadn points’) and stemmed points at 14,900–13,500 cal BP.²⁰ As described earlier, stemmed points are found in younger occupations at *Ushki* in central Kamchatka (~13,000 cal BP), while Chindadn points are known from sites of comparable age (~14,000–13,300 cal BP) in south-central Alaska and southwest Yukon.¹⁷⁻¹⁹

Although the Chindadn points have never been found outside Beringia, stemmed points are known from early dated assemblages in northwest North America and on the Pacific coast. They are associated with the lineages that dispersed throughout mid-latitude North America and South America after 15,000 cal BP,^{15,90} suggesting that at least one of these lineages was present in Beringia at this time. By contrast, the microblade technology never expanded out of northern North America.

On the other hand, stemmed (or ‘tanged’) points also are known from Japan and parts of the Northeast Asian mainland as early as ~15,500 cal BP and represent a possible source for the artifacts in Kamchatka and, ultimately, mid-latitude North America.¹⁰⁰ The design of, and flaking techniques (diagonal parallel flaking) applied to, the stemmed points in Japan are not similar to those found at Ushki, however, and the former are part of a local industry (*Incipient Jomon*). At present, their relationship is problematic.

The economy of the people who made the Beringian industry reflected a mesic tundra setting with some echoes of the arctic steppe.⁴ The hunting of large mammals was focused on sheep and wapiti, while bison were hunted with increasing emphasis as their habitat expanded during the

Younger Dryas interval (after 13,000 cal BP).^{11,96} The broad-based diet was typical for northern interior foragers of the postglacial epoch and included a significant proportion of small mammals and birds, as well as fish (especially in the younger sites). It reflects intricate seasonal scheduling of resource use and a heavy investment in complex technology, including automata.

The dispersal out of eastern Beringia into mid-latitude North America probably was accelerated by the loss of habitat as the central lowland flooded during the final millennia of the Pleistocene, as well as the influx of people from Northeast Asia (represented by the microblade assemblages). As retreating glaciers opened up new habitat on the northwest Pacific coast and the western interior of Canada (i.e., “ice-free corridor”), both factors may have pushed the fast growing Beringian population into mid-latitude North America and farther south.

Although there is genetic evidence for coastal and interior movements from Beringia,⁸⁹ the former may have been the primary route—a rich marine resource base would have promoted rapid population growth and movement along the narrow coastal zone. The stemmed points at sites such as *Arlington Springs* on the southern California coast (~13,000 cal BP)¹⁶ are a credible proxy for coastal movements from southern Beringia. The mtDNA sub-clade D4h3a exhibits a strong association with Pacific coastal areas (both North and South America) in living Native American populations,⁸⁹ and has been identified in aDNA from Southeast Alaska dating to ~10,500 cal BP.⁹⁰ Recent identification of the same mtDNA sub-clade from an infant burial at *Anzick* (Montana) dating to ~12,600 cal BP may indicate that the well-known *Clovis complex* also was produced by people derived from the Pacific coast.¹⁰¹

The genetics of Native American dispersal, including a growing number of dated aDNA samples, indicate both rapid population growth and dispersal throughout the Americas between ~14,500 and 13,000 cal BP and dated archaeological sites confirm the spread of people to the southern tip of South America by 13,000 cal BP.⁴² The pattern is most easily accounted for by postulating a large and diverse population in Beringia at 15,000–14,000 cal BP (i.e., the hypothesized ‘standstill’ population).

Several lines of evidence indicate movements of people from Beringia back into Northeast Asia after the LGM. Two mtDNA sub-clades in Northeast Asia that appear to have originated in Beringia are C1a and A2a; the movement of the latter into western and southern Siberia is thought to have taken place a few thousand years ago.²⁵ A recent analysis of the Na-Dené and Yeniseian languages indicates a back-migration from Beringia into Siberia and central Asia (rather than the reverse).¹⁰² These events may not have any archaeological correlates, underscoring the earlier observation that ‘migrations’ take many forms, and the later movements into and out of Beringia may represent phenomena of a very different order from the earlier movements of people into and out of Beringia.

CONCLUDING OBSERVATIONS

The central theme of this review is that Native American origins probably can be integrated with the out-of-Africa dispersal of anatomically modern humans. If most anthropologists once be-

lieved that the Western Hemisphere was initially settled by a small subset of the Northeast Asian population at the end of the Pleistocene, recent discoveries now confirm that modern humans occupied the high-latitude region that once joined Asia and North America more than 30,000 cal BP. Genetic data, which now are available in very large quantities, indicate that Native Americans are derived from a relatively large and diverse subset of the modern humans who colonized northern Eurasia before the LGM. At least some linguists believe that the diversity of Native American languages reflects a similar time depth.^{91,92}

It remains to be seen if the Beringian Standstill Hypothesis, as formulated by Tamm and colleagues in 2007, will be confirmed with archaeological data and human remains (including aDNA) but it offers an explanation of several aspects of the paleoanthropological record that have long perplexed researchers. One of these is the seeming disconnect between Northeast Asian and North American archaeology at the time that Native Americans dispersed throughout the Western Hemisphere (~15,000–12,000 cal BP). The standstill model suggests a parallel between the ancestral Native American population in Beringia and other populations of modern humans forced into African, Asian, and Australian refugia during the arid LGM. The presence of a viable refugium for thousands of people in Beringia between 30,000 and 15,000 cal BP is supported by paleoecological data and modeling. At the same time, new modeling of the North American ice sheets suggests that access to the rest of the Western Hemisphere was not an option for modern humans until after the LGM.³⁷

Of critical importance to researching the standstill hypothesis is confirmation of divergence between the Native American lineages and their Eurasian source populations before the LGM (i.e., >30,000 cal BP). The issue is likely to be resolved with the analysis of aDNA from dated human remains in northern Eurasia. It also remains to be confirmed that a human population was actually present in Beringia during the LGM (and that it was indeed the ancestral Native American population, as hypothesized by Tamm et al.). Finally, many questions remain unanswered regarding the complicated movements of people and/or genes into and out of Beringia after the LGM. Some of them have been documented with archaeological, linguistic, and/or genetic data, but others are problematic and/or disputed. The post-LGM population history of Beringia—as a postulated center of dispersal—also is an important part of the standstill hypothesis.

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