Beringia and the Global Dispersal of Modern Humans

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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. Archeological discoveries since 2000 reveal, however, that *Homo sapiens* occupied the high-latitude region between Northeast Asia and northwest North America (that is, 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, the Beringian Standstill Hypothesis, which is based on analysis of mitochondrial DNA (mtDNA) in living people, derives Native Americans from a population that occupied Beringia during the LGM. 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. It is supported by evidence of comparatively mild climates and rich biota in south-central Beringia at this time (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.

The absence of any compelling evidence of premodern 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 traveling across an ocean.[1] By the end of the nineteenth 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. 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[3] (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. He named this place *Beringia*, after the European explorer who sailed into the strait in August 1728. 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

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Figure 1. Map of Beringia showing the boundaries of the Bering Land Bridge when sea level was 120 meters below the present-day level (LGM). The locations of archeological sites and finds mentioned in the text also are shown. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

and Alaska and, by the final decades of the twentieth century, Beringia was widely viewed as extending from the Verkhoyansk Mountains in the west to the Mackenzie River in the east. Defined more broadly, cold-climate Beringia contained a more diverse array of habitats than had originally been conceived: Hultén's mesic tundra zone in the central lowland (that is, 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 (Fig. 1).[4–7]

Regardless of its apparent suitability as a bridge between Asia and North America, Beringia's role as a migratory route for the settlement of the Western Hemisphere can be confirmed only by the analysis of paleo-anthropological data. These data comprise human genetics (as well as the genetics of several satellite or symbiotic species, such as body lice or domesticated dogs); 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 (that is, coring). The areas of Beringia that remain above water (Northeast Asia and Alaska/Yukon) are remote and largely undeveloped. To date, they have yielded only a handful of archeological 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 archeological 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 LGM during the final millennia of the Pleistocene. This industry, currently dated in central Alaska to ~14,000 cal BP, does not become widespread in Beringia until the Younger Dryas cold interval, which

began about 12,800 cal BP.[4] Frederick Hadleigh West[9] argued that it was an archeological 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.

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; 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. That movement 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. 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[13] found an industry characterized by production of stemmed points buried beneath microblade assemblages of Younger Dryas age. More recent research at the sites indicates that the points are about 13,000 cal BP.[14] This industry has never been found in a dated context in eastern Beringia, but stemmed points now are dated as early as 13,500-13,000 cal BP in northwestern North America; that is, they are contemporaneous with 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
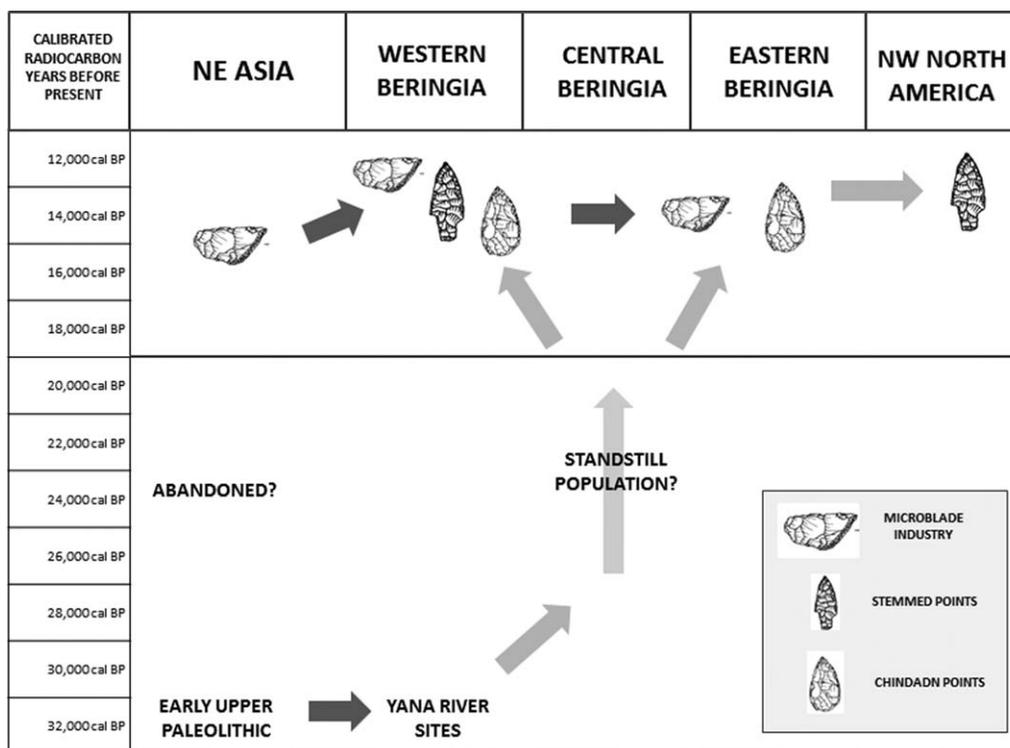
Figure 2. Archeology of Northeast Asia, Beringia, and mid-latitude North America (Diagnostic stone artifacts). The light gray arrows represent the Beringian standstill hypothesis. (The late Paleoindian lanceolate point types of eastern Beringia thought to be derived from the North American Plains are omitted from this figure.)

credible archeological 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 has always been controversial, with some archeologists suggesting that the points actually are part of the microblade industry; that is, that they 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 archeology. 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, including bone awls, eyed needles, possible needle cases, decorated ivory vessels, and personal ornaments.[21] The profusion of household goods suggests an extended occupation, while 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 Russia[22] 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 (Fig. 2).[24]

The Yana River sites also show that Beringia was occupied before the beginning of the LGM. Although it is possible that settlement at this time extended no farther east than the Yana River, the location and contents of the sites indicate that their occupants were adapted to a habitat (shrub tundra) that was widespread in Beringia. The low archeological 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?

THE BERINGIAN "STANDSTILL" HYPOTHESIS

The idea that humans were present in Beringia throughout the LGM

Figure 3. The Beringian standstill hypothesis, based on the analysis of mtDNA in living peoples, presented by Tamm and colleagues[25]. in 2007 (their Fig. 2). (Reproduced from PLoS One 2007: e829 under the terms of the Creative Commons Attribution (CCBY) license). (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

was explicitly formulated by Tamm and coworkers[25] in 2007 on the basis of mtDNA analyses. 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 ($\sim$30,000 cal BP). The Beringian LGM population included the following mtDNA subclades: A2, B2, C1b, C1c, C1d, C4c, D1, D4h3, and X2a. After the LGM ($\sim$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 subclade C1a) spread back into Northeast Asia. According to the hypothesis, there also was a post-LGM movement of people from Northeast Asia (mtDNA subclade D2) into Beringia and northern North America (Fig. 3).

The empirical core of the model rests on the observation that the mtDNA of the "standstill" subclades 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 (that is, the substitutions are widespread among living Native Americans in mid-latitude North America and South America). Using an estimated mutation rate of 3.5 x 10^{-8}/year/position, Tamm and colleagues calculated that the period of isolation preceding the dispersal in the Western Hemisphere was approximately 10,000 years.

The roots of the Beringian standstill hypothesis can be traced back to a controversial 1986 paper by Greenberg, Turner, and Zegura,[26] in which they introduced what is usually referred to as the "three-wave model." This model, based on a synthesis of linguistics, dental anthropology, and genetics, subdivided all Native Americans into three major groups: Amerind, Na-Dené, and 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 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, Amerind.

The three-wave model triggered an extended debate over the relationships both 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,[27,28] 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. Szathmary suggested that the differences were better explained not as separate migrations from Asia to the Americas, but as the result of the isolation of groups by the coalescing Laurentide and Cordilleran glaciers after the initial migration to the Western Hemisphere.

By the early 1990s, estimates of the divergence time between Asian and Native American populations based on mtDNA analyses were published. These included estimates of 30,000 years or more.[29,30] In 1997, Bonatto and Salzano[31] 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," which postulates isolation of most of the ancestral Native American population in

Box 1. Dental Anthropology and the Beringian Standstill Hypothesis

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Although Aleš Hrdlička (1869-1943) noted in the early twentieth century that shovel-shaped incisors were common in Asian and New World populations,[103] tooth morphology had 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 model of specific peopling 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%), but that 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.[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 that the Australian dentition was proto-Sundadont.[106] The Sinodont-Sundadont dichotomy may reflect the initial dispersal pattern of modern humans in East Asia (that is, 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 can be used to address the issue and to reexamine the related three-wave model. The following observations are based on the analysis of 24 crown and root traits in 135 samples from several thousand individuals. These were 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, and 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 (Fig. 4).

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; these include, 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
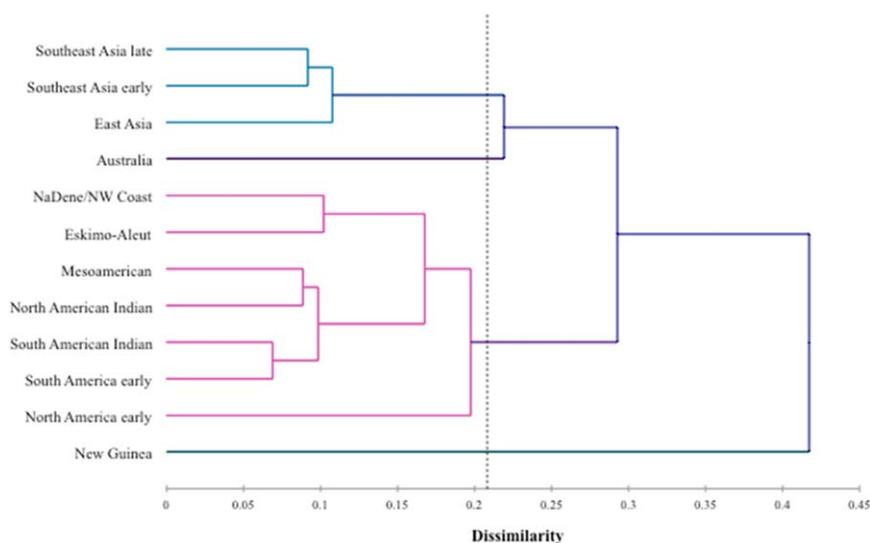

Figure 4. Dendrogram generated from a multivariate analysis of 24 dental traits in samples (n = 135) from several thousand individuals from New Guinea, Australia, Southeast and East Asia, and North and South America. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

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 with regard to the Beringian standstill model is that the average distances among the seven New World groups are remarkably uniform; that is, 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 for a time from Northeast Asians. Essentially, the New World was not peopled directly from Northeast Asia because 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 time period, presumably in Beringia, when populations became super Sinodonts, or Sinodonts on steroids. Although there are various 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.

Beringia (not south of the ice).[25] The following year, Kitchen, Miyamoto, and Mulligan[32] estimated an effective population size (N_{ef}) of ~2,700 females for the "standstill" population.

Tamm and colleagues never cited the original three-wave model in their 2007 Beringian standstill paper, although they referenced Szathmary's earlier work. There are significant differences between the two models. Whereas Greenberg and colleagues[26] 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 and coworkers envisioned Beringia as a post-LGM center of human population dispersal, analogous to Hultén's[3] 1937 thesis that tundra plants had dispersed from the central lowlands after each glacial period. As noted earlier, the postulated flow of people and/or genes out of Beringia included movements into Northeast Asia, as well as North America.

The pattern that Tamm and colleagues observed in the mtDNA data 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 that is found in other parts of the world, such as southern Asia.[33] Some support for the standstill hypothesis in autosomal DNA can be found in the distribution of an allele at a microsatellite locus on chromosome 9 (D9S1120), which exhibits a pattern similar to that in the mtDNA data.[34] Also potentially significant is the evidence of 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 and coworkers[35] found only a 6%-7% reduction in heterozygosity relative to the global average, This is consistent with the hypothesis of a large and diverse source population in Beringia. The results of a more recent whole-genome analysis by Reich, Patterson, and Campbell[36] are generally consistent with a Beringian standstill, but not with the original three-wave model.

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. As in the case of the whole-genome study by Reich, Patterson, and Campbell,[36] multivariate analysis of the teeth now suggests that the Na-Dené and Aleut-Inuit are more closely related to other Native American groups than to the modern Asian population (Fig. 4).

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] 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. 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. Most of the estimated divergence times for the Native American subclades also indicate a post-15,000-cal-BP dispersal, which is consistent with the glacial chronology.[38]

The standstill hypothesis cannot be confirmed until there is not only human fossil and/or archeological evidence of a population in Beringia during the LGM, but also evidence linking 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 archeological 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 archeological data, accounting for various 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.

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

From the archeologist's perspective, the standstill hypothesis provides an explanation for the single most confounding aspect of the relevant archeological record, which is the absence of evidence of a group of people migrating from Northeast Asia to mid-latitude North America after the LGM. As described earlier, the archeological record yields proxies in the form of diagnostic artifact types for movements from Northeast Asia into Beringia (wedge-shaped microblade cores) at ~14,000 cal BP; Beringia into mid-latitude North America (stemmed points) at ~13,000 cal BP; and mid-latitude North America into eastern Beringia (late Paleoindian points) at ~12,000 cal BP (that is, during the Younger Dryas cold interval). The earliest reliably dated sites in mid-latitude

North America and South America (~14,500 cal BP) precede 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 archeological 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 members of that population or, alternatively, physically replace the existing inhabitants. Incoming groups of males also may largely replace the existing male population. The various forms of migration yield different genetic and archeological 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 dis-

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crete 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, including genetics, dated fossil remains, and archeology, 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 the interval of 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 central Siberia indicates that a 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 nonrecombining 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
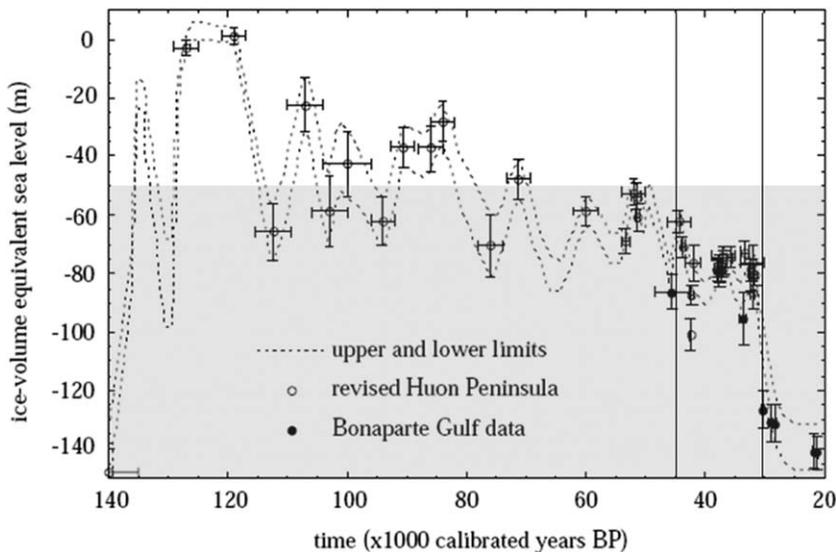
Figure 5. Global sea level for the interval between 140,000 and 20,000 cal BP (modified from Lambeck and coworkers 2002, their Fig. 6).[66] The Bering Land Bridge emerges at 50 meters below present-day sea level. Between ~32,000 and 28,000 cal BP, sea level fell from roughly -75 meters to below -120 meters, exposing a larger portion of the Bering Platform (or land bridge) between latitudes 56° and 58° North. Original figure reproduced from Lambeck K, Yokoyama Y, Purcell T. 2002. Into and out of the Last Glacial Maximum: sea-level change during Oxygen-Isotope Stages 3 and 2. Quat Sci Rev 21: 343–360 with permission from Elsevier.

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. Analysis of aDNA from Tianyuan Cave in northern China confirms divergence of mtDNA **B** by 40,000 cal BP.[49,50] The subclade 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 of a direct connection between west Eurasians and Native Americans. The most basal X2a lineage 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. 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 underestimated.[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 archeological 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 nonmodern 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"[55]) and subject to periodic stress and local extinction. 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 with regard to how modern humans adapted to cold and dry habitats, which, in turn, helps identify their differences from 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] 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 archeological record of modern human settlement in Northern Asia (and Eastern Europe) between 45,000 and 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/m^2/yr and the January mean is below -20°C. Stable isotope values on human bones from subarctic Siberia and the central East European Plain indicate high consumption of freshwater foods, which may have included waterbirds as well as fish.[23,60] Concentrations of hare remains on the East European Plain and at 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. Sites in southern Siberia may contain evidence of both spear-throwers (mechanical instrument) and food storage.[62–64] The movement of
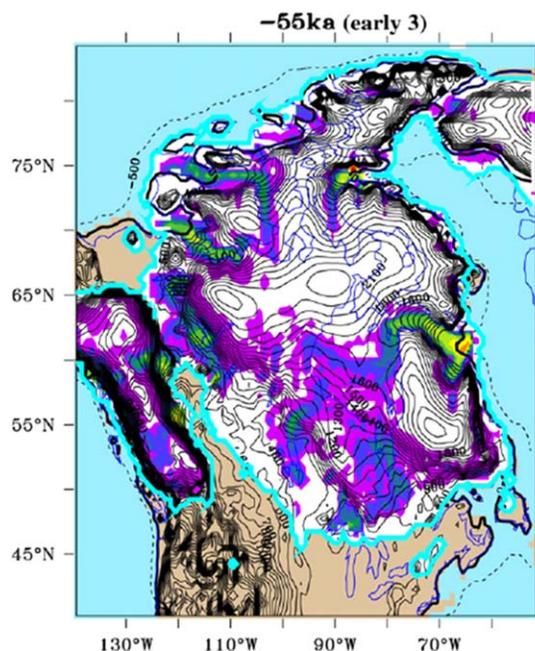
Figure 6. Laurentide/Cordilleran ice sheets at ~55,000 cal BP (from Stokes et al. 2012, their fig. 4),[37] based on the Glacial Systems Model (GSM). According to the GSM, the ice sheets had coalesced by the time modern humans arrived in Northeast Asia (~45,000 cal BP) and probably blocked coastal and interior access to mid-latitude North America and South America until after the LGM (that is, until after 16,000–15,000 cal BP). Reproduced from Stokes CR, Tarasov L, Dyke AS. 2012. Dynamics of the North American ice sheet complex during its inception and build-up to the Last Glacial Maximum. Quat Sci Rev 50: 86–104 with permission of Elsevier. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

raw materials over hundreds of kilometers indicates high mobility and/or widespread social networks.[61,65] In contrast, there is little or no evidence of 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 present-day levels (Fig. 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, such as the 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. Faunal remains from the sites include steppe bison, reindeer, horse, and some mammoth; the small mammal remains are dominated by hare.[21] Environ-

ments 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; it could have been picked up fresh from a permafrost context and worked by more recent inhabitants of the area.[69] Because 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 was present between the two, the current lack of pre-LGM sites in Alaska/Yukon is more likely a result of low archeological visibility than the absence of human settlement. It now appears that it was not Beringian environments

(or the Bering Strait) that was the barrier to modern human dispersal in the Western Hemisphere before the end of the LGM, but the coalesced Laurentide and Cordilleran glaciers (Fig. 6).[37]

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. Paleoenvironmental data indicate that conditions there probably were sufficient to sustain a population during the LGM, even though the presence of any humans in Beringia between 30,000 and 15,000 cal BP remains to be confirmed with dated fossils or artifacts. Such evidence currently is confined to problematic flaked mammoth bone dating to ~25,000 cal BP from Bluefish Caves in the northern Yukon.[70]

Global ice volume during the LGM is estimated to have been ~50 million km^3 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 grew substantially.[37] At the peak of the LGM (~21,000 cal BP), mean global temperature is estimated to have been 5.1°C lower, and precipitation roughly 10% lower, than their levels 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 is estimated to have been 20% less extensive, and extratropical forest 45% less than that of the recent past. Only shrubs expanded relative to their postglacial distribution. Global NPP is estimated to have been slightly more than half of what it was during the postglacial 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

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Box 2. Modeling NPP for LGM Beringia

NANCY H. BIGELOW

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 subcontinent.

NPP for LGM Beringia was modeled by importing climate data into a vegetation model (Biome4). This model, 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 $C/m^2/yr$).[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 CO_2 was set to 185 ppm.[112]

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 from 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]
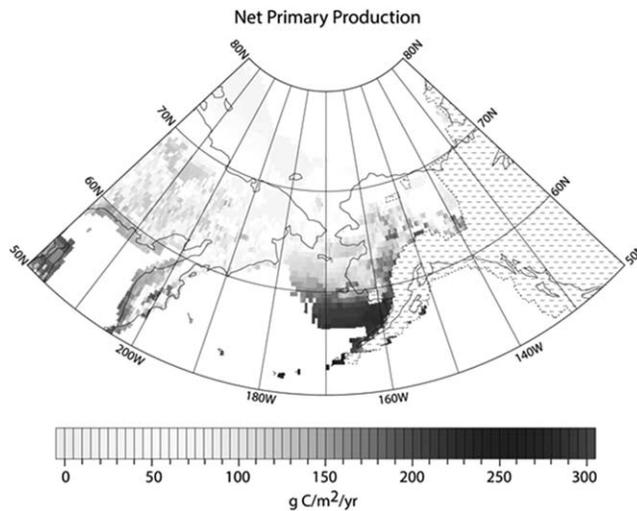

Figure 7. Net Primary Production or NPP (measured as g $C/m^2/yr$, which is approximately 45% of total organic matter) for Beringia during the LGM (~21,000 cal BP), as predicted by the Biome4 model. According to the model, the most productive areas would have been found on the southeastern margin of the Bering Land Bridge, much of which was not exposed until the LGM.

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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. Parts of Northern Asia also seem to have been abandoned.[73–75]

The evidence of population bottlenecks in the genetic data are supported by patterns in the archeological 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 of occupations of LGM age are confined to the refugia, where climates were warmer and/or wetter at the time.[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, each year, groups were already foraging

across areas of tens of thousands of square kilometers 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 has shown 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 shows 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 the present-day level (Fig. 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 (the 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 (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[82] described as a "monotonously flat plain" may have played a role in retaining moisture, with rivers meandering across poorly drained lowlands. In sum, the LGM actually created new habitat for interior hunter-gatherers in southern Beringia.

As described earlier, Hultén postulated a tundra refugium on the land bridge exposed during the LGM in the 1930s. In recent decades, a substantial amount of supporting data on LGM environments has been collected, including information from sediment cores drilled into the for-

mer surface of the land bridge.[4,83] These data, including pollen, plant macro-fossils, and 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 was thought.[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 indicates 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. However, a total population of 8,000-10,000 is considered possible.[88] The modeling of NPP for LGM Beringia described in Box 2, complemented by the previously noted paleo-environmental data, provide a means of 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/m^2/yr in the southeastern land bridge, the southern half of central Beringia probably produced at least ∼150 g C/m^2/yr at the peak of the LGM (Fig. 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 km^2.[56] At this level, a standstill population of 5,000-10,000 individuals would have required a territory of between roughly 125,000 and 250,000 km^2, which appears to have been available in central Beringia.

Wherever it was located, the genetic diversity of the standstill population suggests that it may have been distributed across a large area, and perhaps even subdivided among several regions. Diversification (geo-

graphic structure) among multiple refugia populations in southern Beringia during the LGM would be expected to have yielded substantial geographic structure to populations moving south of the receding ice sheets after the LGM, as each of these refugia populations contributed independent streams of migrating people. 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] This pattern also would help explain the linguistic diversity of the groups that dispersed in the Americas after 15,000 cal BP.[91,92]

Groups are also likely to have foraged over wide areas during the course of a year. Seasonal movements into the more steppic areas, such as central Alaska, to exploit large grazers such as horse or bison may have been critical to augmenting the plant and animal resources of the mesic tundra zone. The same groups could have wintered in that zone, where the January mean was relatively mild and wood was available for fuel. The presence of wood as a supplement to bone fuel, which, in the absence of wood, burns at a very high rate, 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; 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 archeological 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 at 16,000–15,000 cal BP by people who, using a distinctive technique (*Yubetsu*) manufactured wedge-shaped microblade cores.[94] They probably were derived from people in southern Siberia, who made similar artifacts during the later LGM.[95] Wedge-shaped microblade cores produced by 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 their original "three-wave model" paper, Greenberg, Turner, and Zegura[26] suggested that this industry was produced by the Na-Dené. 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 subclades, C1b and B2, were identified in human remains recovered from an archeological site in central Alaska (*Upward Sun River*). This site was assigned to a younger version of the microblade industry (Denali complex) that was widespread in Beringia during the Younger Dryas cold interval (~12,800-11,300 cal BP).[97,98] Tamm and colleagues[25] assigned both subclades to the Beringian standstill population, 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, as noted earlier, there is supporting archeological evidence.[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 subclade D2a1 (and Y-DNA Q1a), derived, according to Tamm and coworkers, from Northeast Asia after the LGM.[25,99]

The archeological record yields evidence of another industry in Beringia at 15,000-14,000 cal BP. This industry 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 noted 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 that time. In 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; they represent a possible source for the artifacts in Kamchatka and, ultimately, mid-latitude North America.[100] However, the design and flaking technique (diagonal parallel flaking) applied to stemmed points in Japan are not similar to those found at Ushki, but instead 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, which was typical for northern interior foragers of the postglacial epoch, included a significant proportion of small mammals and birds, as well as fish, especially in the younger sites. This diet 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 by 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 (that is, the 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 of 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 Spring*s* on the southern California coast (~13,000 cal BP)[16] are a credible proxy for coastal movements from southern Beringia. The mtDNA subclade 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 subclade 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.

Dated archeological 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; that is, the hypothesized standstill population.

Several lines of evidence indicate movements of people from Beringia back into Northeast Asia after the LGM. Two mtDNA subclades 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 archeological correlates, underscoring the earlier observation that migrations take many forms. 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 believed 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 joined Asia and North America more than 30,000 cal BP. Genetic data, which now are available in 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 whether the Beringian standstill hypothesis formulated by Tamm and colleagues[25] in 2007 will be confirmed by archeological data and human remains, including aDNA, but it offers an expla-

nation of several aspects of the paleo-anthropological record that have long perplexed researchers. One of these is the seeming disconnect between Northeast Asian and North American archeology 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]

In researching the standstill hypothesis, it will be critically important to confirm the divergence between the Native American lineages and their Eurasian source populations before the LGM (>30,000 cal BP). The issue is likely to be resolved by the analysis of aDNA from dated human remains in north-

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ern 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 and coworkers. Finally, many questions remain unanswered regarding the complicated movements of people and/or genes into and out of Beringia after the LGM. Some of the answers have been documented with archeological, linguistic, and genetic data, but others are problematic or disputed. The post-LGM population history of Beringia as a postulated center of dispersal also is an important part of the standstill hypothesis.

REFERENCES

1 de Acosta J. 2002. Historia natural y moral de las Indias. Durham: Duke University Press.

2 Hopkins DM. 1967. Introduction. In: Hopkins DM, editor. The Bering land bridge. Stanford: Stanford University Press. p 1–6.

3 Hultén E. 1937. Outline of the history of arctic and boreal biota during the Quaternary Period. New York: Lehre J. Cramer.

4 Hoffecker JF, Elias SA. 2007. Human ecology of Beringia. New York: Columbia University Press.

5 Guthrie RD. 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammoth tooth pits, buckles, and inside-out Beringia. Quaternary Sci Rev 20: 549–574.

6 Elias SA, Crocker B. 2008. The Bering land bridge: a moisture barrier to the dispersal of steppe-tundra biota? Quaternary Sci Rev 27: 2473–2483.

7 Meiri M, Lister AM, Collins MJ, et al. 2013. Faunal record identifies Bering isthmus conditions as constraint to end-Pleistocene migration to the New World. Proc R Soc Lond B Biol Sci 281:20132167.

8 Nelson N. 1935. Early migration of man to America. Nat Hist 35:356.

9 West FH. 1996. Beringia and New World origins. In: West FH, editor. American beginnings: the prehistory and paleoecology of Beringia. Chicago: University of Chicago Press. p 537–559.

10 Rainey F. 1940. Archaeological investigation in central Alaska. Amer Antiq 4: 299–308.

11 Hoffecker JF. 2011. Assemblage variability in Beringia: the Mesa factor. In: Goebel T, Buvit I, editors. From the Yenisei to the Yukon: interpreting lithic assemblage variability in late Pleistocene/early Holocene Beringia. College Station: Texas A&M University Press. p 165–178.

12 Shapiro B, Drummond AJ, Rambaut A, et al. 2004. Rise and fall of the Beringian steppe bison. Science 306:1561–1565.

13 Dikov NN. 1979. Drevnie Kul'tury Severo-Vostochnoi Azii. Moscow: Nauka.

14 Goebel T, Waters MR, Dikova M. 2003. The archaeology of Ushki Lake, Kamchatka, and the Pleistocene peopling of the Americas. Science 301:501–505.

15 Jenkins DL, Davis LG, Stafford TW, et al. 2013. Geochronology, archaeological context, and DNA at the Paisley Caves. In: Graf KE, Ketron CV, Waters MR, editors. Paleoamerican odyssey. College Station: Texas A&M University Press, p 485–510.

16 Erlandson JM, Rick TC, Braje TJ, et al. 2011. Paleoindian seafaring, maritime technologies, and coastal foraging on California's Channel Islands. Science 331:1181–1185.

17 Cook JP. 1996. Healy Lake. In: West FH, editor. American beginnings: the prehistory and paleoecology of Beringia. Chicago: University of Chicago Press. p 323–327.

18 Powers WR, Hoffecker JF. 1989. Late Pleistocene settlement in the Nenana Valley, central Alaska. Am Antiq 54: 263–287.

19 Graf KE, DiPietro LM, Krasinski KE, et al. 2015. Dry Creek revisited: new excavations, radiocarbon dates, and site formation inform on the peopling of eastern Beringia. Am Antiq 80: 671–694.

20 Pitulko VV, Basilyan AE, Pavlova EY. 2014. The Berelekh "graveyard": new chronological and stratigraphical data from the 2009 field season. Geoarchaeol 29:277–299.

21 Pitulko V, Nikolskiy P, Basilyan A, et al. 2013. Human habitation in arctic western Beringia prior to the LGM. In: Graf KE, Ketron CV, Waters MR, editors. Paleoamerican odyssey. College Station: Texas A&M University Press. p 13–44.

22 Pavlov P, Svendsen JI, Indrelid S. 2001. Human presence in the European Arctic nearly 40,000 years ago. Nature 413:64–67.

23 Fu Q, Li H, Moorjani P, et al. 2014. Genome sequence of a 45,000-year-old modern human from western Siberia. Nature 514:445–449.

24 Andersen KK, Bigler, M, Clausen HB, et al. 2007. A 60,000 year Greenland stratigraphic ice core chronology. Climate Past Discuss 3:1235–1260.

25 Tamm E, Kivisild T, Reidla M, et al. 2007. Beringian standstill and spread of Native American founders. PLOS One:e829.

26 Greenberg JH, Turner CG, Zegura SL. 1986. The settlement of the Americas: a comparison of the linguistic, dental, and genetic evidence. Curr Anthropol 27:477–497.

27 Szathmary EJE, Ossenberg, NS. 1978. Are the biological differences between North American Indians and Eskimos truly profound? Curr Anthropol 19:673–701.

28 Szathmary EJE. 1993. Genetics of aboriginal North Americans. Evol Anthropol 1:202–220.

29 Torroni A, Neel JV, Barrantes R, et al. 1994. Mitochondrial DNA "clock" for the Amerinds and its implications for timing their entry into North America. Proc Natl Acad Sci USA 91: 1158–1162.

30 Forster P, Harding R, Torroni A, et al. 1996. Origin and evolution of Native American mtDNA variation: a reappraisal. Am J Hum Genet 59:935–945.

31 Bonatto SL, Salzano FM. 1997. A single and early migration for the peopling of the Americas supported by mitochondrial DNA sequence data. Proc Natl Acad Sci USA 94:1866–1871

32 Kitchen A, Miyamoto MM, Mulligan CJ. 2008. A three-stage colonization model for the peopling of the Americas. PLOS One 3:e1596.

33 Majumder PP. 2010. The human genetic history of South Asia. Curr Biol 20:R184–187.

34 Schroeder KB, Schurr TG, Longet JC, et al. 2007. A private allele ubiquitous in the Americas. Biol Lett 3:218–223.

35 Wang S, Lewis CM, Jakobsson M, et al. 2007. Genetic variation and population structure in Native Americans. PLoS Genet 3:e185.

36 Reich D, Patterson N, Campbell D. 2012. Reconstructing Native American population history. Nature 488:370–374.

37 Stokes CR, Tarasov L, Dyke AS. 2012. Dynamics of the North American ice sheet complex during its inception and build-up to the Last Glacial Maximum. Quaternary Sci Rev 50:86–104.

38 O'Rourke DH, Raff JA. 2010. Human genetic history of the Americas. Curr Biol 20:R202–R207.

39 O'Rourke DH. 2011. Contradictions and concordances in American colonization. Evo Edu Outreach 4:244–253.

40 Mulligan CJ, Kitchen A. 2013. Three-stage colonization model for the peopling of the Americas. In: Graf KE, Ketron CV, Waters MR, editors. Paleoamerican odyssey. College Station: Texas A&M University Press. p 171–181.

41 Achilli A, Perego UA, Lancioni H, et al. 2013. Reconciling migration models to the Americas with the variation of North American Native mitogenomes. Paleoamerican Odyssey: Program and Abstracts. Sante Fe, New Mexico. p 34.

42 Waters MR, Stafford TW. 2013. The first Americans: a review of the evidence for the Late-Pleistocene peopling of the Americas. In: Graf KE, Ketron CV, Waters, MR, editors. Paleoamerican odyssey. College Station: Texas A&M University Press. p 541–560.

43 O'Rourke DH. 2012. Why do we migrate? A retrospective. In: Crawford MH, Campbell BC, editors. Causes and consequences of human migration. Cambridge: Cambridge University Press. p 527–536.

44 Hoffecker JF. 2009. The spread of modern humans in Europe. Proc Natl Acad Sci USA 106: 16040–16045.

45 Pitulko VV, Tikhonov AN, Pavlova EY, et al. 2016. Early human presence in the Arctic: evidence from 45,000-year-old mammoth remains. Science 351:260–263.

46 Benazzi S, Slon V, Talamo S. 2015. The makers of the Protoaurignacian and implications for Neandertal extinction. Science 348: 793–796.

47 Behar DM, van Oven M, Rosset S, et al. 2012. A "Copernican" reassessment of the human mitochondrial DNA tree from its root. Am J Hum Genet 90:675–684.

48 Goebel T. 2015. The overland dispersal of modern humans to eastern Asia. In: Kaifu Y, Izuho M, Goebel T, et al., editors. Emergence and diversity of modern human behavior in Paleolithic Asia. College Station: Texas A&M University Press. p 437–452.

49 Wells S. 2007. Deep ancestry: inside the Genographic Project. Washington: National Geographic.

50 Fu Q, Meyer M, Gao X, et al. 2013. DNA analysis of an early modern human from Tianyuan Cave, China. Proc Natl Acad Sci USA110:2223–2227.

51 Raff JA, Bolnick DA. 2015. Does mitochondrial haplogroup X indicate ancient trans-Atlantic migration to the Americas? A critical re-evaluation. PaleoAmerica 1:297–304.

52 Rasmussen M, Sikora M, Albrechtsen A, et al. 2015. The ancestry and affiliations of Kennewick man. Nature 523:455–458.

53 Dulik MC, Zhadanov SI, Osipova LP, et al. 2012. Mitochondrial DNA and Y chromosome variation provides evidence for a recent common ancestry between Native Americans and indigenous Altaians. Am J Hum Genet 90:229–246.

54 Eisfelder C, Klein I, Huth J, et al. 2014. Spatio-temporal patterns and dynamics of net primary productivity for Kazakhstan. Earth Environ Sci 17:012028.

55 Churchill SE. 2014. Thin on the ground: Neandertal biology, archeology and ecology. Hoboken:Wiley-Blackwell.

56 Kelly RL. 2013. The lifeways of hunter-gatherers: the foraging spectrum. Cambridge: Cambridge University Press.

57 Oswalt WH. 1976. An anthropological analysis of food-getting technology. New York: John Wiley & Sons.

58 Harrison GA, Weiner, JS, Tanner JM, et al. 1977. Human biology: an introduction to human evolution, variation, growth and ecology. Oxford: Oxford University Press.

59 Gilligan I. 2010. The prehistoric development of clothing: archaeological implications of a thermal model. J Archaeol Theor Meth 17:15–80.

60 Richards MP, Pettitt PB, Stiner MC, et al. 2001. Stable isotope evidence for increasing dietary breadth in the European mid-Upper Paleolithic. Proc Natl Acad Sci USA 98:6528–6532.

61 Hoffecker JF. 2005. Innovation and technological knowledge in the Upper Paleolithic of northern Eurasia. Evol Anthropol 14:186–198.

62 Golovanova LV, Doronichev VB, Cleghorn NE, et al. 2010. Significance of ecological factors in the Middle to Upper Paleolithic transition. Curr Anthropol 51:655–691.

63 Dereviako AP, Shunkov MV, Markin SV. 2014. Dinamika Paleoliticheskikh Industrii v Afrike i Evrazii v Pozdnem Pleistotsene i Problema Formirovaniya Homo sapiens. Novosibirsk: Institute of Archaeology and Ethnography SB RAS Press.

64 Buvit I, Terry K, Izuho M, et al. 2015. The emergence of modern behavior in the Trans-Baikal, Russia. In: Kaifu Y, Izuho M, Goebel T, et al., editors. Emergence and diversity of modern human behavior in Paleolithic Asia. College Station: Texas A&M University Press. p 490–505.

65 Rybin EP. 2015. Middle and Upper Paleolithic interactions and the emergence of "modern behavior" in southern Siberia and Mongolia. In: Kaifu Y, Izuho M, Goebel T, et al., editors. Emergence and diversity of modern human behavior in Paleolithic Asia. College Station: Texas A&M University Press. p 470–489.

66 Lambeck K, Yokoyama Y, Purcell T. 2002. Into and out of the Last Glacial Maximum: sea-level change during oxygen-isotope stages 3 and 2. Quaternary Sci Rev 21:343–360.

67 Brigham-Grette J, Lozhkin AV, Anderson PM, et al. 2004. Paleoenvironmental conditions in western Beringia before and during the Last Glacial Maximum. In: Madsen DB, editor. Entering America. Northeast Asia and Beringia before the Last Glacial Maximum. Salt Lake City: University of Utah Press. p 29–61.

68 Matheus P, Kunz M, Guthrie RD. 2003. Using frequency distributions of radiocarbon dates to detect relative changes in Pleistocene mammal populations — a test case from northern Alaska. Third International Mammoth Conference, Program and Abstracts.

69 Gelvin-Reymiller C, Reuther JD, Potter BA, et al. 2006. Technical aspects of a worked proboscidean tusk from Inmachuk River, Seward Peninsula, Alaska. J Archaeol Sci 33:1088–1094.

70 Cinq-Mars J. 1990. La place des Grottes du Poission-Bleu dans la prehistoire Beringienne. Revista Arquelog'a Am 1:9–32.

71 Lambeck K, Rouby H, Purcell A, et al. 2014. Sea level and global ice volumes from the Last Glacial Maximum to the Holocene. Proc Natl Acad Sci USA 111:15296–15303.

72 Claussen M, Selent K, Brovkin V, et al. 2013. Impact of CO_2 and climate on Last Glacial Maximum vegetation — a factor of separation. Biogeosciences 10:3593–3604.

73 Cherni L, Fernandes V, Pereira JB, et al. 2009. Post-Last Glacial Maximum expansion from Iberia to North Africa revealed by fine characterization of mtDNA H haplogroup in Tunisia. Am J Phys Anthropol 139:253–260.

74 Černý V, Mulligan CJ, Fernandes V, et al. 2010. Internal diversification of mitochondrial haplogroup R0a reveals post-Last Glacial Maximum demographic expansions in South Arabia. Mol Biol Evol 28:71–78.

75 Cai X, Qin Z, Wen B, et al. 2011. Human migration through bottlenecks from Southeast Asia into East Asia during Last Glacial Maximum revealed by Y chromosomes. PLoS One 6: e24282.

76 Hoffecker JF. 2005. A prehistory of the North. New Brunswick: Rutgers University Press.

77 Williams AN, Ulm S, Cook AR, et al. 2013. Human refugia in Australia during the Last Glacial Maximum and terminal Pleistocene: a geospatial analysis of the 25–12 ka Australian archaeological record. J Archaeol Sci 40:4612–4625.

78 Buvit I, Terry K, Izuho M, et al. 2015. Last Glacial Maximum human abandonment of the Transbaikal. PaleoAmerica 1:374–376.

79 Théry-Parisot I, Costamagno S, Brugal J-P, et al. 2005. The use of bone as fuel during the Palaeolithic, experimental study of bone combustible properties. In: Mulville J, Outram AK, editors. The zooarchaeology of milk and fats. Oxford: Oxbow Books. p 50–59.

80 Yurtsev BA. 2001. The Pleistocene tundra-steppe and the productivity paradox: the landscape approach. Quaternary Sci Rev 20:165–174.

81 Zhuang K, Giardino JR. 2012. Ocean cooling pattern at the Last Glacial Maximum. Adv Meteorol 2012:e213743.

82 Hopkins DM. 1959. Cenozoic history of the Bering Land Bridge. Science 129:1519–1528.

83 Elias SA, Short SK, Nelson CH, et al. 1996. Life and times of the Bering Land Bridge. Nature 382:60–63.

84 Anderson PM, Lozhkin AV. 2015. Late Quaternary vegetation of Chukotka (Northeast Russia), implications for Glacial and Holocene environments of Beringia. Quaternary Sci Rev 107:112–128.

85 Willerslev E, Davison J, Moora M, et al. 2014. Fifty thousand years of Arctic vegetation and megafaunal diet. Nature 506:47–51.

86 Westbrook R, Fowell S, Bigelow N, et al. 2012. Evidence for glacial refugium in central Beringia. GSA Annual Meeting, 180-10, Charlotte North Carolina, 4–7 November 2012.

87 Elias SA. 2001. Mutual climatic range reconstructions of seasonal temperatures based on Late Pleistocene fossil beetle assemblages in Eastern Beringia. Quaternary Sci Rev 20:77–91.

88 Mulligan CJ, Kitchen A. 2013. Three-stage colonization model for the peopling of the Americas. In: Graf KE, Ketron CV, Waters, MR, editors. Paleoamerican odyssey. College Station: Texas A&M University Press. p 171–181.

89 Perego UA, Achilli A, Angerhofer N, et al. 2009. Distinctive Paleo-Indian migration routes from Beringia marked by two rare mtDNA haplogroups. Curr Biol 19:1–8.

90 Raff JA, Bolnick DA, Tackney JC, et al. 2011. Ancient DNA perspectives on American colonization and population history. Am J Phys Anthropol 146:503–514.

91 Nichols J. 1990. Linguistic diversity and the first settlement of the New World. Language 66: 475–521.

92 Campbell L. 1997. American Indian languages: the historical linguistics of Native America. New York: Oxford University Press.

93 Bigelow NH, Powers WR. 2001. Climate, vegetation, and archaeology 14,000–9000 cal yr B.P. in central Alaska. Arctic Anthropol 38:171–195.

94 Mochanov YA, Fedoseeva SA. 1996. Dyuktai Cave. In: West FH, editor. American beginnings: the prehistory and paleoecology of Beringia. Chicago: University of Chicago Press. p 164–174.

95 Goebel T. 2002. The "microblade adaptation" and recolonization of Siberia during the late Upper Pleistocene. In: Elston RG, Kuhn SL, editors. Thinking small: global perspectives on microlithization. Archaeol Pap Am Anthropol Assoc 12:117–131.

96 Potter BA, Holmes CE, Yesner DR. 2013. Technology and economy among the earliest prehistoric foragers in interior eastern Beringia. In: Graf KE, Ketron CV, Waters MR, editors. Paleoamerican odyssey. College Station: Texas A&M University Press. p 81–103.

97 Potter BA, Irish JD, Reuther JD, et al. 2014. New insights into eastern Beringian mortuary behavior: a terminal Pleistocene double infant burial at Upward Sun River. Proc Natl Acad Sci USA 111:17060–17065.

98 Tackney JC, Potter BA, Raff J, et al. 2015. Two contemporaneous mitogenomes from terminal Pleistocene burials in eastern Beringia. Proc Natl Acad Sci USA 112:13833–13838.

99 Rasmussen M, Li Y, Lindgreen S, et al. 2010. Ancient human genome sequence of an extinct Palaeo-Eskimo. Nature 463:757–762.

100 Nagai K. 2007. Flake scar patterns of Japanese tanged points: toward an understanding of technological variability during the Incipient Jomon. Anthropol Sci 115:223–226.

101 Rasmussen M, Anzick SL, Waters MR, et al. 2014. The genome of a Late Pleistocene human from a Clovis burial site in western Montana. Nature 506:225–229.

102 Scioli MA, Holton G. 2014. Linguistic phylogenies support back-migration from Beringia to Asia. PLoS One 9:e91722.

103 Hrdlička A. 1920. Shovel-shaped teeth. Am J Phys Anthropol 3:429–465.

104 Turner CG. 1971. Three-rooted mandibular first permanent molars and the question of American Indian origins. Am J Phys Anthropol 34:229–241.

105 Turner CG. 1990. Major features of Sundadonty and Sinodonty, including suggestions about East Asian microevolution, population history, and late Pleistocene relationships with Australian aboriginals. Am J Phys Anthropol 82:295–317.

106 Turner CG. 1992. The dental bridge between Australia and Asia: following Macintosh into the East Asian hearth of humanity. Perspect Hum Biol 2/Archaeol Oceania 27:143–152.

107 Anderson PM, Edwards ME., Brubaker LB. 2004. Results and paleoclimate implications of 35 years of paleoecological research in Alaska. In: Gillespie AR, Porter SC, editors. The Quaternary Period in the United States. Elsevier: Amsterdam. p 427–440.

108 Bigelow NH. 2013. Pollen records, late Pleistocene/northern North America. In: Elias SA, Mock CJ, editors. Encyclopedia of Quaternary science, 2nd ed. Elsevier: Amsterdam. p 39–51.

109 Haxeltine A, Prentice IC. 1996. Biome3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. Global Biogeochem Cycles 10:693–709.

110 Kaplan JO, Bigelow NH, Prentice IC, et al. 2003. Climate change and Arctic ecosystems 2 modeling, paleodata-model comparisons, and future projections. J Geophys Res 108:12-1–12-17.

111 Gent PR, Danabasoglu G, Donner LJ, et al. 2011. The community climate system model version 4. J Climate 24:4973–4991, 10.1175/2011JCLI4083.1.

112 PMIP3. 2014. Paleoclimatic modelling intercomparison project phase III. https://pmip3.lsce.ipsl.fr/.