АРХЕОЛОГИЯ

Beringia and the Settlement of the Western Hemisphere

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Previously, we addressed the problem of what variable(s) limited widespread human settlement of the Americas before ~15 ka. We concluded that while non-modern human taxa (e. g., Neanderthals) probably did not inhabit high-latitude environments (due to cold climate and/or low plant and animal productivity) and thus could not disperse in the Western Hemisphere

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via Beringia, modern humans likely were denied access to mid-latitude North America >15 ka by coastal and interior ice sheets. Here we reexamine the problem with respect to modern humans in light of a revised chronology for glaciers and sea level, new research in paleo-genomics, and some new archaeological discoveries. During 35–30 ka, a lineage with west Eurasian roots occupied the Great Arctic Plain and may have expanded into eastern arctic Beringia and mid-latitude North America via an ice-free corridor. An East Asian lineage associated with microblade technology occupied the Lena Basin during the LGM and expanded onto the Great Arctic Plain >15 ka, possibly as early as the GI 2 interstadial (24–23 ka). Their immediate descendants probably occupied the southern Bering Land Bridge and Northwest Pacific coast >15 ka and dispersed widely in the Western Hemisphere during GI 1 (14.5–12.9 ka), primarily if not exclusively via a coastal route. The coalesced Laurentide and Cordilleran ice sheets blocked interior access to mid-latitude America until 13.8 ± 0.5 ka (and possibly later due to the length and narrow width of the ice-free corridor >13 ka).

Keywords: settlement of the Americas, Beringia, Northern Asia, modern humans, paleogenetics, sea level change, glacier pulse, paleoecology.

Берингия и заселение Западного полушария

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Ранее нами была рассмотрена проблема влияния естественных факторов на расселение человека в Америку ~15 тыс. лет назад. Древние представители людских популяций (например, неандертальцы), скорее всего, не были способны к освоению природной среды высоких широт из-за холодного климата и/или недостаточной продуктивности растений и животных и не могли заселить Западное полушарие через Берингию. Современный человек не мог попасть туда >15 тыс. лет назад, поскольку доступ в заледниковую область Северной Америки, вероятно, был перекрыт ледниковыми щитами. Здесь мы возвращаемся к вопросу о расселении современного человека в свете новых данных, в том числе обновленной хронологии изменения очертаний ледников и положения уровня моря, новых археологических открытий, а также результатов исследований в области палеогеномики. В интервале 35–30 тыс. лет назад население с западно-евразийскими корнями занимало Великую Арктическую равнину и, возможно, распространилось в восточную арктическую Берингию и средние широты Северной Америки через межледниковый коридор. Население, относящееся к восточноазиатской генетической линии, связанное с технологией микропластин, во время последнего ледникового максимума занимало бассейн реки Лены и распространилось на Великую Арктическую равнину >15 тыс. лет назад, возможно, уже в интерстадиале GI 2 (24–23 тыс. лет назад). Их непосредственные потомки, вероятно, занимали южную часть Берингийского моста и северо-западное побережье Тихого океана >15 тыс. лет назад. Они широко расселились в Западном полушарии в интерстадиале GI 1 (14,5–12,9 тыс. лет назад) в основном, если не исключительно, прибрежным путем (ранее 13,8 ± 0,5 тыс. лет назад внутриматериковый маршрут был перекрыт ледниками).

Ключевые слова: заселение Америки, Берингия, Северная Азия, анатомически современные люди, изменения уровня моря, пульсация ледников, палеоэкология.

What was the role of Beringia in the settlement of the Western Hemisphere?

In an earlier publication[1], we addressed the problem of what variable(s) limited widespread human settlement of the Americas before ~15,000 cal BP (15 ka). We concluded that high-latitude environments (specifically, cold climates and/or low biotic productivity) probably prevented Neanderthals, Denisovans, and other non-modern human taxa from occupying Beringia and settling the Western Hemisphere. For modern humans, we concluded that only the presence of large ice sheets blocked access from Beringia to most of the Western Hemisphere, while high-latitude environments were not an absolute barrier to human settlement (Fig. 1).

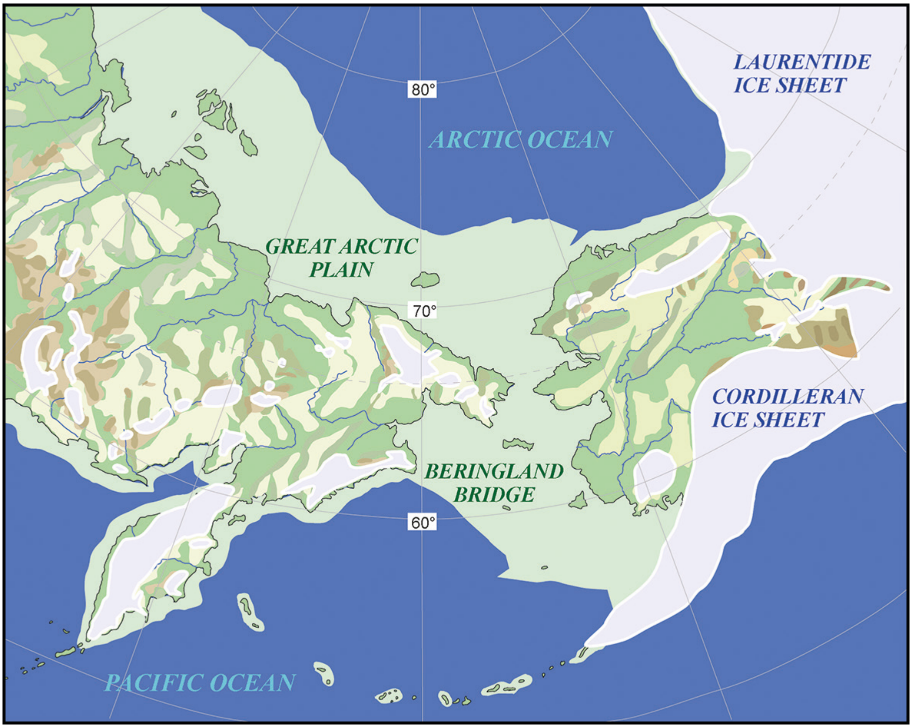

Fig. 1. Map of Beringia during the Last Glacial Maximum showing the two major areas of exposed continental shelf that were occupied by humans >15 ka. Illustration prepared by L. K. Takahashi and E. Y. Pavlova

A significant revision of the glacier and sea-level chronology for 45–15 ka reveals a more complex pattern for modern humans, however[2]. It now is apparent that the Bering Strait was flooded during an interval of a relatively high sea level during *Marine Isotope*

[1] *Hoffecker J. F., Pitulko V. V., Pavlova E. Y.* Climate, technology and glaciers: The settlement of the Western Hemisphere // Vestnik of Saint Petersburg University. History. 2019. Vol. 64, issue 2. P. 327–355.

[2] See, for example: *Batchelor C. L., Margold M., Krapp M. et al.* The configuration of Northern Hemisphere ice sheets through the Quaternary // Nature Communications. 2019. Vol. 10. P. 3713.

Stage 3 (MIS 3)[3] and potentially a barrier to human settlement >35 ka. On the other hand, both a land connection between western and eastern Beringia and a wide ice-free corridor in northwestern North America had been present for several thousand years before glacial readvances blocked interior access from Beringia to mid-latitude North America. Additionally, new research in paleo-genomics has provided an overall framework for modern human population history in Eurasia and the Americas[4]. In some regions, developments in paleo-genomics have been accompanied by or supplemented with new discoveries in archaeology, allowing at least partial integration of paleo-genomics and archaeology for Northeast Asia, Beringia, and North America[5].

Two major lineages are implicated in the settlement of Beringia during MIS 3 and MIS 2, and both may have occupied eastern Beringia and the Western Hemisphere. Both lineages inhabited the exposed East Siberian Arctic Shelf and adjoining lowlands of arctic Beringia (*Great Arctic Plain*) but only one lineage appears to have occupied the southern margin of the exposed Bering-Chukchi Platform (i. e., southern *Bering Land Bridge*). The Western Hemisphere was settled as result of a complex interplay between human adaptations to these exposed continental shelf areas and advance and retreat of glaciers in the coastal and interior regions of northwestern North America.

A revised chronology for sea level and glaciers

The discovery of ancient beach levels dating to ~40 ka at elevations comparable to those of the present day triggered a reassessment of sea-level history for MIS 3 (57–29 ka). This, in turn, encouraged a reexamination of terrestrial ice volumes and the size of continental ice sheets in North America during MIS 3. The glacial and sea-level chronology for MIS 3 accordingly has been revised with significant implications for human settlement of Beringia and the Western Hemisphere.

Dated beach levels along the Atlantic coast of North America, supported by sedimentary core records from East Asia, indicate relatively high global mean sea level (GMSL) during MIS 3. According to a revised curve for the Late Pleistocene, GMSL reached a peak of 40 meters below that of the present day at ~45 ka, and subsequently fell rapidly after 40 ka with a minimum of roughly –130 meters at the beginning of the Last Glacial Maximum (LGM) ~26.5 ka[6]. GMSL rose rapidly after 16 ka, reaching an essentially modern level during the early Holocene (~8 ka)[7].

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[3] *Pico T., Creveling J. R., Mitrovica J. X.* Sea-level records from the U. S. mid-Atlantic constrain Laurentide Ice Sheet extent during Marine Isotope Stage 3 // Nature Communications. 2017. Vol. 8. P. 15612.

[4] See, for example: *Sikora M., Pitulko V. V., Sousa V. C. et al.* The population history of northeastern Siberia since the Pleistocene // Nature. 2019. Vol. 570. P. 182–188.

[5] See, for example: *Yu H., Spyrou M. A., Karapetian M. et al.* Paleolithic to Bronze Age Siberians reveal connections with First Americans and across Eurasia // Cell. 2020. Vol. 181. P. 1–14; *Kılınç G. M., Kashuba N., Koptekin D. et al.* Human population dynamics and *Yersina pestis* in ancient northeast Asia // Science Advances. 2021. Vol. 7. P. eabc4587.

[6] *Pico T., Mirovica J. X., Ferrier K. L., Braun J.* Global ice volume during MIS 3 inferred from a sea-level analysis of sedimentary core records in the Yellow River Delta // Quaternary Science Reviews. 2016. Vol. 152. P. 72–79; *Pico T., Creveling J. R., Mitrovica J. X.* Sea-level records from the U. S. mid-Atlantic constrain Laurentide Ice Sheet extent during Marine Isotope Stage 3. P. 15612.

[7] *Lambeck K., Rouby H., Purcell A. et al.* Sea level and global ice volumes from the Last Glacial Maximum to the Holocene // Proceedings of the National Academy of Sciences. 2014. Vol. 111. P. 15296–15303.

The revised sea-level curve indicates that while a significant portion of the shallow East Siberian Arctic Shelf was exposed throughout MIS 3, most of the Bering-Chukchi Platform, including the Bering Strait was submerged ~45 ka[8]. Thus, at the time when modern humans initially dispersed in Northeast Asia, a land connection between Asia and North America was absent. According to the revised curve, the Bering Land Bridge (BLB) did not emerge until ~35 ka, when GMSL fell below -53 meters (i. e., depth of Bering Strait). The BLB experienced rapid expansion after 35 ka and was — due to the bathymetry of its southern margin — almost fully exposed at the beginning of MIS 2 (29 ka)[9]. The land connection between Asia and North America was severed 12–11 ka although a significant portion of the East Siberian Arctic Shelf remained exposed until the early Holocene (Fig. 2).

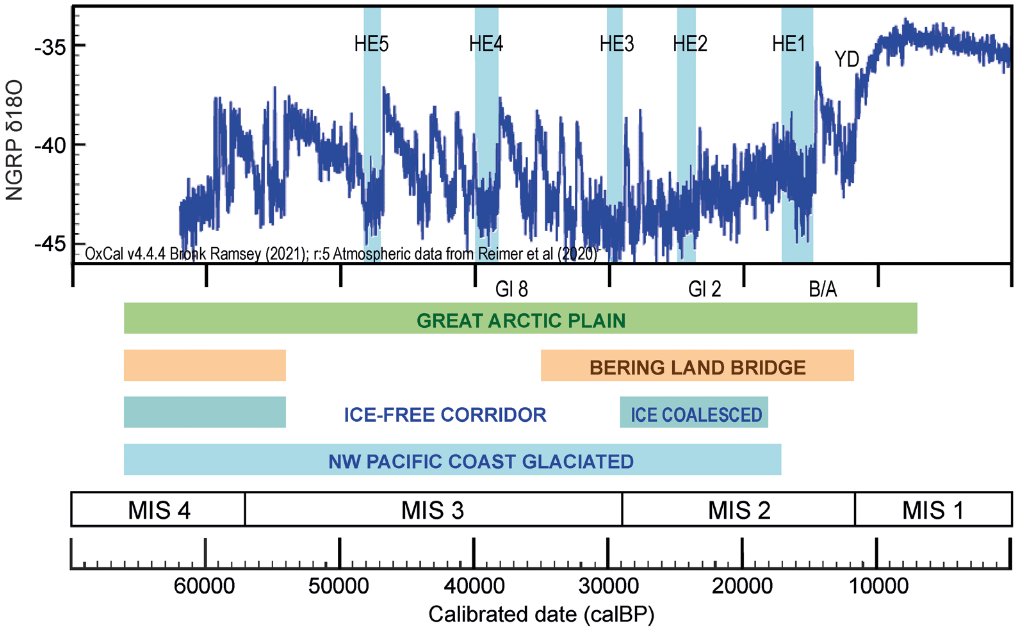

Fig. 2. Paleoclimate record for the past 60,000 years, based on the NGRIP oxygen-isotope core, calibrated with the IntCal20 radiocarbon calibration curve, showing Heinrich Events 5–1, the Younger Dryas, and several interstadials (adapted from OxCal v4.4.4 [Bronk Ramsey, 2021])

Higher GMSL during MIS 3 implies reduced terrestrial ice during the same interval, and a newly revised chronology for the North American ice sheet complex (comprising the *Cordilleran*, *Laurentide*, and *Innuitian* glaciers) shows a greatly reduced ice volume for 45–40 ka (i. e., coinciding with high sea level). During this period, the Laurentide ice sheet devolved into several smaller glaciers, and much of the NW Pacific coast of North America was unglaciated (due to shrinkage of the Cordilleran glacier). Rapid readvance of

[8] *Slobodin S. B., Anderson P. M., Glushkova O. Y., Lozhkin A. V.* Western Beringia // Human Colonization of the Arctic: The interaction between early migration and the paleoenvironment. London, 2017. P. 241–298.

[9] See: *Hopkins D. M.* Cenozoic history of the Bering Land Bridge // Science. 1959. Vol. 129. P. 1519–1528.

ice began during *Heinrich Event 4* (HE 4) after 40 ka and by 35–30 ka, the Laurentide ice sheet was reconstituted, and the NW Pacific coast again was glaciated[10].

Despite regrowth of the Cordilleran and Laurentide ice sheets after 40 ka, an ice-free corridor (>250 km wide at its narrowest point) existed 35–30 ka between the two glaciers, which did not coalesce until after 30 ka (see: Fig. 2). Thus, at a time when humans occupied the western arctic lowlands of Beringia (*Yana River site complex*) and are tentatively documented in eastern arctic Beringia, interior access from the latter to mid-latitude North America probably was possible[11]. On the other hand, access to mid-latitude North America via the NW Pacific coast seems to have been blocked by ice at this time (35–30 ka). Also, potentially significant for Beringia was the faunal exchange with the Northern Plains of North America before 30 ka[12].

New research indicates that deglaciation of the NW Pacific coast began as early as 18 ka, and a viable coastal route between southern Beringia and mid-latitude North America may have been available by 17 ka[13]. Equally important with respect to human settlement is early retreat of the ice on the southern coast of Alaska (<18 ka), which would have facilitated movement from the southern BLB to the NW Pacific coast before the rapid rise in sea level (<16 ka). Deglaciation of the Copper River Valley in southern Alaska by 16 ka provided another possible route from the Beringian interior to the NW Pacific coast (and suggests that the occupants of Beringia could have bypassed the southern BLB altogether)[14].

The reopening of the corridor between the Cordilleran and Laurentide ice sheets appears to have taken place after 14 ka. A narrow ice-free corridor apparently extended from the Yukon to southern Alberta (roughly 2,000 km in length) at 13.8 ± 0.5 ka[15] and might have allowed limited movement of people from the interior of Beringia to the Northern Plains before 13 ka (movement of bison through the corridor is thought to have occurred <13.4 ka)[16].

[10] *Dalton A. S., Stokes C. R., Batchelor C. L.* Evolution of the Laurentide and Innuitian ice sheets prior to the Last Glacial Maximum (115 ka to 25 ka) // Earth-Science Reviews. 2020. Vol. 224. P. 103875.

[11] *Pitulko V. V., Pavlova E. Y.:* 1) Geoarchaeology and Radiocarbon Chronology of Stone Age Northeast Asia. College Station, 2016; 2) Colonization of the Eurasian Arctic. Encyclopedia of the World's Biomes. Vol. 2. [s. l.], 2020. P. 374–391; 3) Colonization of the Arctic in the New World. Encyclopedia of the World's Biomes // Ibid. P. 392–408; *Vachula R. S., Huang Y., Russell J. M. et al.* Sedimentary biomarkers reaffirm human impacts on northern Beringian ecosystems during the Last Glacial period // Boreas. 2020. Vol. 49 (3). P. 514–525.

[12] *Heintzman P. D., Froese D., Ives J. W. et al.* Bison phylogeography constrains dispersal and viability of the Ice Free Corridor in western Canada // Proceedings of the National Academy of Sciences. 2016. Vol. 113. P. 8057–8063.

[13] *Lesnek A. J., Briner J. P., Lindqvist C. et al.* Deglaciation of the Pacific coastal corridor directly preceded the human colonization of the Americas // Science Advances. 2018. Vol. 4. P. eaar5040.

[14] *Dalton A. S., Margold M., Stokes C. R. et al.* An updated radiocarbon-based ice margin chronology for the last deglaciation of the North American Ice Sheet Complex // Quaternary Science Reviews. 2020. Vol. 234. P. 106223.

[15] Ibid, supplemental information. P. 12; *Clark J., Carlson A. E., Reyes A. V. et al.* The age of the opening of the Ice-Free Corridor and implications for the peopling of the Americas // Proceedings of the National Academy of Sciences. 2022. Vol. 119. P. e2118558119.

[16] Movement of bison from the south (Northern Plains) is dated at 13.4 ka and from the north (Beringia) at 13 ka (*Heintzman P. D., Froese D., Ives J. W. et al.* Bison phylogeography constrains dispersal… P. 8057–8063).

The human paleo-genomic framework

Recent paleo-genomic research reveals that two major lineages occupied Northeast Asia and Beringia before 15 ka, and it now appears that both may have settled the Western Hemisphere. One of the lineages (East Asian) is descended from the initial movement of modern humans into Northeast Asia and is represented today by the Han population. The other lineage has west Eurasian roots but expanded into Siberia after HE 4 that dates to 40–38 ka (Fig. 3). The relationship between the two lineages is complex and includes multiple episodes of genic exchange. Although living Native Americans are primarily descended from the East Asian lineage, they carry as much as 30–40 % of the west Eurasian genome.

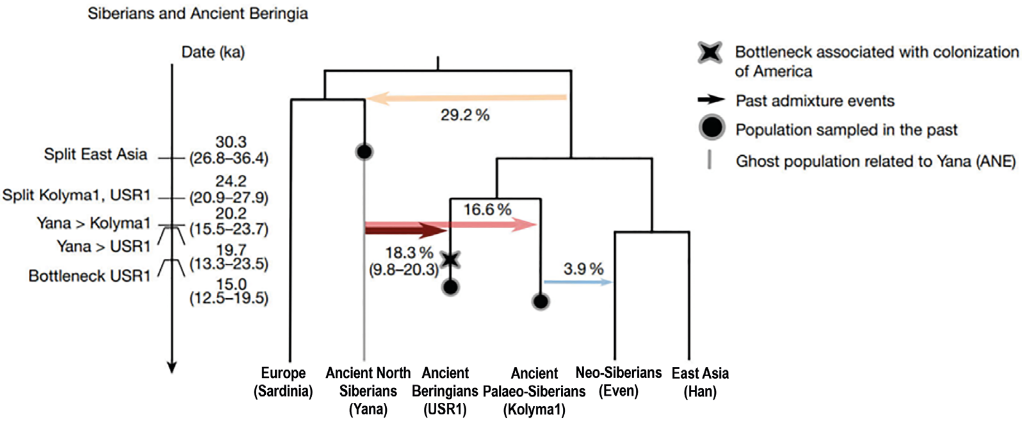

Fig. 3. Paleo-genomic model of Northeast Asian and Beringian lineages, illustrating early split between west Eurasian lineage (left) and East Asian lineage (right) [Sikora M. et al. 2019, fig. 2b]. Reprinted by permission from Springer-Nature, Nature, copyright 2019

The earliest known representatives of the East Asian lineage are found at *Tianyuan Cave* (40 ka) in northern China and at *Salkhit* (~34 ka) in northeastern Mongolia. Both reflect early admixture with the Denisovans (also evident among Native Americans), and the Salkhit woman carries a significant contribution from west Eurasians, presumably as a result of the eastward movement of the latter <38 ka[17].

The HE 4 cold interval (40–38 ka) was followed by a protracted interstadial (GI 8) that apparently promoted rapid human population growth in the most biologically productive area of northern Eurasia. People in southwest Europe expanded eastward <38 ka and occupied the central East European Plain 38–32 ka (e. g., *Kostenki*)[18]. Their earliest known

[17] *Qin P., Stoneking M.* Denisovan ancestry in east Eurasian and Native American populations // Molecular Biology and Evolution. 2015. Vol. 32 (10). P. 2665–2674; *Yang M. A., Gao X., Theunert C. et al.* 40,000-year-old individual from Asia provides insight into early population structure in Eurasia // Current Biology. 2017. Vol. 27. P. 3202–3208; *Massilani D., Skov L., Hajdinjak M. et al.* Denisovan ancestry and population history of early East Asians // Science. 2020. Vol. 370. P. 579–583; *Yang M. A., Fan X., Sun B. et al.* Ancient DNA indicates human population shifts and admixture in northern and southern China // Science. 2020. Vol. 369. P. 282–288.

[18] *Fu Q., Posth C., Hajdinjak M. et al.* The genetic history of Ice Age Europe // Nature. 2016. Vol. 534. P. 200–205; *Sikora M., Seguin-Orlando A., Sousa V. C. et al.* Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers // Science. 2017. Vol. 358 (6363). P. 659–662.

Fig. 4. Map of Northeast Asia showing the location of archaeological sites and non-archaeological localities that have yielded human remains and ancient genomes. Illustration prepared by L. K. Takahashi and E. Y. Pavlova

representatives in Northeast Asia (*Ancient North Siberians* [ANS]) are found at the Yana River site complex in western arctic Beringia dating to ~34–32 ka[19] (see: Fig. 3). Younger representatives of the same lineage (*Ancient North Eurasians* [ANE]) are found in southern Siberia during and after the LGM at *Mal'ta* (~24 ka) and *Afontova Gora* (~17 ka)[20].

The East Asian lineage (*Ancient Paleo-Siberians* [APS]) subsequently expanded north into Siberia and western arctic Beringia, although the timing of the latter remains to be

[19] *Sikora M., Pitulko V. V., Sousa V. C. et al.* The population history of northeastern Siberia since the Pleistocene. P. 182–188.

[20] *Raghavan M., Skoglund P., Graf K. E. et al.* Upper Palaeolithic Siberian genome reveals dual ancestry of Native Americans // Nature. 2013. Vol. 505. P. 87–91.

determined. They are present in the Amur River Basin as early as 33 ka (late MIS 3) and at the end of the LGM (19 ka)[21]. The East Asian lineage is also present at *Khaiyrgas Cave* in the Lena Basin (at latitude 59° North) at 16.9–16.5 ka and at *Ust-Kyakhta-3* near Lake Baikal at 14.2 ka[22]. Although the Amur Basin finds are not associated with artifacts, the human remains from Khaiyrgas Cave and Ust-Kyakhta-3 are associated with microblades produced from small wedge-shaped cores. Because older (radiocarbon-dated) levels at Khaiyrgas Cave also contain microblade technology, we conclude that the East Asian APS population probably is present in the Lena Basin as early as ~24 ka corresponding to the GI 2 Interstadial[23] (Fig. 4).

The people who dispersed widely in mid-latitude North America and South America <15 ka (*Ancient Native Americans* [ANA]) diverged from their East Asian source population ~24–19 ka, but it is unclear whether the split occurred in Beringia or somewhere in Northeast Asia (e. g., Lena Basin)[24]. The East Asian APS population was present in western arctic Beringia by 15 ka (and may have been present in eastern arctic Beringia as early as 24 ka)[25]; they are ancestral to northern North American groups (e. g., Inuit, Aleut, Dene-speakers) and may be considered Native Americans or “First Peoples”, along with the ANA population. A related East Asian population (*Ancient Beringians*) that was present in eastern Beringia 12–9 ka is now believed to represent a group that diverged from the North American ANA population[26].

The settlement of Beringia

In our earlier publication, we concluded that Neanderthals and other non-modern human taxa were unable to occupy high-latitude environments in northern Eurasia — due to cold climate and/or low plant and animal productivity — and thus were excluded from the Western Hemisphere via Beringia (which lies above latitude 60° North). We concluded that modern humans, on the other hand, were able — at the time of their dispersal above latitude 45° North — to occupy most habitats in northern Eurasia, including arctic Beringia, and that the primary variable in the timing of their dispersal in the Western Hemisphere was the advance and retreat of glaciers in northern North America. Their successful adaptation to high-latitude environments was based on the ability to design technologies of

[21] *Mao X., Zhang H., Qiao S. et al.* The deep population history of northern East Asia from the Late Pleistocene to the Holocene // Cell. 2021. Vol. 184. P. 1–11.

[22] *Yu H., Spyrou M. A., Karapetian M. et al.* Paleolithic to Bronze Age Siberians reveal connections with First Americans and across Eurasia. P. 1–14; *Kılınç G. M., Kashuba N., Koptekin D. et al.* Human population dynamics and *Yersina pestis* in ancient northeast Asia. P. eabc4587.

[23] *Stepanov A. D., Kirillin A. S., Vorobiev S. A. et al.* Peshchera Khaiyrgas na Srednei Lene (rezultaty issledovanii 1998–1999 gg.) // Drevnie Kultury Severo-Vostochnoi Azii. Astroarkheologiya. Paleoinformatika. Novosibirsk, 2003. P. 98–113; *Kuzmin Y. V., Kosintsev P. A., Stepanov A. D. et al.* Chronology and faunal remains of the Khaiyrgas Cave (Eastern Siberia, Russia) // Radiocarbon. 2017. Vol. 59 (2). P. 575–582.

[24] *Sikora M., Pitulko V. V., Sousa V. C. et al.* The population history of northeastern Siberia since the Pleistocene. P. 182–188.

[25] *Bourgeon L., Burke A., Higham T.* Earliest human presence in North America dated to the Last Glacial Maximum: New radiocarbon dates from Bluefish Caves, Canada // PLoS ONE. 2017. Vol. 12. P. e0169486–e0169486; *Pitulko V. V., Pavlova E. Y., Nikolskiy P. A.* Revising the archaeological record of the Upper Pleistocene Arctic Siberia: Human dispersal and adaptations in MIS 3 and 2 // Quaternary Science Reviews. 2017. Vol. 165. P. 127–148.

[26] *Ning C., Fernandes D., Changmai P. et al.* The genomic formation of First American ancestors in East and Northeast Asia // bioRxiv. 2020. doi.org/10.1101/2020.10.12.336628

comparable complexity to those of recent hunter-gatherers, including insulated clothing and highly effective hunting weaponry, including mechanical projectiles[27].

Some new research provides additional support for both conclusions. Even in mid-latitude northern Eurasia, Neanderthal populations were small and stressed with high inbreeding coefficients. The recent analysis of a whole Neanderthal genome from *Chagyrskaya Cave* in the Altai Mountains (52° North) revealed a local population composed of less than 60 individuals (smaller than the estimated size of Neanderthal populations in central Europe)[28]. By comparison, the modern human population in western arctic Beringia 34–32 ka (Yana River site complex) was significantly larger (effective population size of ~500) with a low inbreeding coefficient[29].

Some new research indicates that modern humans were designing both insulated clothing and mechanical projectile weaponry during the early phase of their dispersal in northern Eurasia. Eyed needles (and traces of a mechanical drill) now are dated to ~45 ka at *Denisova Cave* (Altai Mountains), while the use of mechanical projectile weaponry recently has been reported from the same time range in southern Europe (Italy)[30]. Self-acting mechanical devices used by modern humans in northern Eurasia >40 ka probably included snares and/or traps for harvesting small mammals (e. g., hare)[31].

Collectively, these technologies allowed modern humans to inhabit places where (a) mean January temperatures were at or below –10 °C (with winter clothing), and (b) plant and animal productivity were low (by increasing dietary breadth and foraging efficiency and success rate). Also significant is new evidence for LGM occupation of areas previously suspected to have been abandoned under conditions of extreme cold and aridity during 26.5–19 ka, including the central East European Plain (52° North) and the Lena Basin (59° North)[32].

Beringian Environments. During past periods of cold climate, when growth of terrestrial ice sheets lowered global sea level, large areas of continental shelf were exposed in both the Northern and Southern Hemispheres. These areas included the *Bering-Chukchi*

[27] *Hoffecker J.F., Pitulko V.V., Pavlova E.Y.* Climate, technology and glaciers: The settlement of the Western Hemisphere. P.327–355; *Pitulko V.V., Pavlova E.Y.* Upper Palaeolithic Sewing Kit from the Yana Site, Arctic Siberia // Stratum plus. 2019. No. 1. P.157–224; *Pitulko V.V., Pavlova E.Y., Nikolskiy P.A.* Mammoth ivory technologies in the Upper Palaeolithic: a case study based on the materials from Yana RHS, Northern Yana-Indighirka lowland, Arctic Siberia // World Archaeology. 2015. Vol.47 (3). P.333–389.

[28] *Mafessoni F., Grote S., de Filippo C. et al.* A high-coverage Neandertal genome from Chagyrskaya Cave // Proceedings of the National Academy of Sciences. 2020. Vol.117. P.15132–15136. — Comparable data on the Denisovans currently is lacking; we assume that their population ecology was similar to that of the Neanderthals.

[29] *Sikora M., Pitulko V.V., Sousa V.C. et al.* The population history of northeastern Siberia since the Pleistocene. P.182–188. — The pattern suggests that low biological productivity — not cold climate — was the key variable limiting the distribution of Neanderthal populations in northern Eurasia.

[30] *Douka K., Slon V., Jacobs Z. et al.* Age estimates for hominin fossils and the onset of the Upper Palaeolithic at Denisova Cave // Nature. Vol.565. P.640–644; *Sano K., Arrighi S., Stani C. et al.* The earliest evidence for mechanically delivered projectile weapons in Europe // Nature Ecology & Evolution. 2019. Vol.3. P.1409–1414.

[31] *Hoffecker J.F., Hoffecker I.T.* Technological complexity and the global dispersal of modern humans // Evolutionary Anthropology. 2017. Vol.26. P.285–299.

[32] *Stepanov A.D., Kirillin A.S., Vorobiev S.A. et al.* Peshchera Khaiyrgas na Srednei Lene (rezultaty issledovanii 1998–1999 gg.). P.98–113; *Kuzmin Y.V., Kosintsev P.A., Stepanov A.D. et al.* Chronology and faunal remains of the Khaiyrgas Cave (Eastern Siberia, Russia). P.575–582; *Pryor A.J.E., Beresford-Jones D.G., Dudin A.E. et al.* Chronology and function of a new circular mammoth bone structure from Kostenki 11 // Antiquity. 2020. Vol.94 (374). P.323–341.

Platform between Chukotka and western Alaska, and the *East Siberian Artic Shelf*, which adjoins the arctic coast of central and eastern Siberia (see: Fig. 1). The former lies at a lower elevation than the latter, and a land connection between Chukotka and Alaska does not emerge until sea level has fallen to 53 meters below its current level. A significant portion of the East Siberian Arctic Shelf is less than 40 meters below the current sea level and was exposed at times when most of the Bering-Chukchi Platform was submerged[33] (see: Fig. 2).

As originally defined, *Beringia* was limited to the areas of exposed continental shelf described above[34]. Beginning in the 1960s, its geographic boundaries were expanded into areas above modern sea level in Northeast Asia and Alaska/Yukon, and today Beringia is widely defined as extending from the Mackenzie River in NW Canada (approximate LGM margin of Laurentide ice sheet) westward to the Kolyma River or Verkhoyansk Mountains[35]. In terms of human settlement, the western boundary now appears to be an arbitrary one. The exposed East Siberian Arctic Shelf, which extends from the Taimyr Peninsula (arctic coast of central Siberia) to the northern Bering-Chukchi Platform is a more credible unit of human geography.

Before 15 ka, human settlement in Beringia appears to have been largely confined to the exposed East Siberian Arctic Shelf (sometimes labeled the *Great Arctic Plain* [GAP]) and adjoining lowlands along the arctic coast of Northeast Asia (e.g., Yana-Indighirka Lowland, Kolyma Basin) and the North Slope of Alaska[36]. Rapid growth and dispersal of the ANA population in the Western Hemisphere <15 ka probably reflects the presence of people on the NW Pacific coast of North America >15 ka and possibly much earlier, given the constraints on movement between the Cordilleran and Laurentide ice sheets >13.8 ± 0.5 ka[37] (see: Fig. 2). We conclude that people probably also occupied the adjoining southern margin of the exposed Bering-Chukchi Platform (or southern *Bering Land Bridge* [BLB]) at some point >15 ka.

The two areas of exposed continental shelf and adjoining lowlands supported very different environments due to contrasts in available moisture. The GAP was extremely dry owing to retreat of the coast, exacerbated by the effects of the north Eurasian ice sheet during the LGM[38]. As a result, the wet, cold, and unproductive soils that are typical of the arctic tundra zone were replaced with dry and productive soils (warmed by 24-hour sunlight during the summer months) more characteristic of the steppe zone[39].

The warm, dry soils supported a steppe-tundra biome populated by a diverse array of large mammals, including mammoth, horse, bison, saiga, musk ox, and reindeer[40].

33 *Slobodin S. B., Anderson P. M., Glushkova O. Y., Lozhkin A. V.* Western Beringia. P. 241–298.

34 *Hultén E.* Outline of the History of Arctic and Boreal Biota During the Quaternary Period. New York, 1937. P. 34.

35 See, for example: *Hoffecker J. F., Elias S. A.* Human Ecology of Beringia. New York, 2007. P. 2–5.

36 *Schirrmeister L., Hubberten H.-W., Rachold V., Grosse G.* Lost world — Late Quaternary environment of periglacial Arctic shelves and coastal lowlands in NE-Siberia // 2nd International Alfred Wegener Symposium. Bremerhaven, 2005.

37 *Clark J., Carlson A. E., Reyes A. V. et al.* The age of the opening of the Ice-Free Corridor and implications for the peopling of the Americas. P. e2118558119.

38 *Stauch G., Lehmkuhl F.* Quaternary glaciations in the Verkhoyansk Mountains, Northeast Siberia // Quaternary Research. 2010. Vol. 74. P. 145–155.

39 *Guthrie R. D.* Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammoth tooth pits, buckles, and inside-out Beringia // Quaternary Science Reviews. 2001. Vol. 20. P. 549–574.

40 *Sher A. V., Kuzmina S. A., Kuznetsova T. V., Sulerzhitsky L. D.* New insights into the Weichselian environment and climate of the East Siberian Arctic, derived from fossil insects, plants, and mammals // Ibid.

The temporal distribution of dated large-mammal bones, however, suggests significant fluctuations in their numbers. Intervals of extreme cold and aridity probably triggered population declines (due to reduced plant productivity), while interstadials would have promoted population growth — at least until increased moisture led to formation of peat bogs and tundra soils (*paludification*)[41].

Climates on the southern BLB were wetter and warmer due to the influence of the North Pacific Ocean[42]. The effects on soils and vegetation (herbaceous tundra) probably were enhanced by poor drainage on the relatively flat Bering-Chukchi Platform, and there is evidence for widespread peat formation[43]. While at least some of the steppe-tundra mammals found on the GAP were present on the southern BLB (e. g., mammoth), terrestrial resources for a human population most likely were significantly poorer than those of arctic Beringia.

On the other hand, some resources not available on the GAP may have been present on the southern BLB, including seasonal concentrations of waterfowl (attracted to ponds and wetlands during the early summer months) and driftwood accumulations on the shore (?). Most important in the context of human settlement before 15 ka, the southern coast provided access to marine resources. While marine productivity in the North Pacific was comparatively low during the LGM (26.5–19 ka), waters along parts of the southern BLB coast apparently were "fertilized" by runoff from early deglaciation in Alaska 15.7–14.7 ka during *Heinrich Event 1* (HE 1) and rose to peak levels during the *Bølling/Allerød* (GI 1) interstadial (14.7–12.9 ka)[44].

Before Heinrich Event 4 (47–40 ka). Although definitive evidence for human settlement of Beringia currently does not antedate 35 ka, we suspect that modern humans were present on the GAP before 40–38 ka (HE 4). This is based on the fact that people were present, at least on a seasonal basis, in arctic and sub-arctic Eurasia during the first half of MIS 3: they are found near the Arctic Circle in northeast Europe roughly 40 ka[45] and in sub-arctic western Siberia as early as 45,000 years ago[46], that is during GI 12 (47–45 ka). They also are found in arctic Siberia, near the mouth of the Yenisei River, where traces

2005. Vol. 24 (5–6). P. 533–569; *Zimov S. A., Zimov N. S., Tikhonov A. N., Chapin III F. S.* Mammoth steppe: a high productivity phenomenon // Ibid. 2012. Vol. 57. P. 26–45; *Pitulko V. V., Pavlova E. Y., Nikolskiy P. A.* Revising the archaeological record of the Upper Pleistocene Arctic Siberia. P. 127–148.

41 *Mann D. H., Groves P., Reanier R. E. et al.* Life and extinction of megafauna in the ice-age Arctic // Proceedings of the National Academy of Sciences. 2015. Vol. 112. P. 14301–14306.

42 *Yurtsev B. A.* Problemy pozdnekainozoiskoi paleogeografii Beringii v svete botaniko-geograficheskikh dannykh // Beringiya v Kainozoe. Vladivostok, 1976. P. 101–120; *Rae J. W. B., Gray W. R., Wills R. C. J. et al.* Overturning circulation, nutrient limitation, and warming in the Glacial North Pacific // Scientific Advances. 2020. Vol. 6. P. eabd1654.

43 *Elias S. A., Crocker B.* The Bering Land Bridge: A moisture barrier to the dispersal of steppe-tundra biota? // Quaternary Science Reviews. 2008. Vol. 27. P. 2473–2483; *Treat C. G., Kleinen T., Broothaerts N. et al.* Widespread global peatland establishment and persistence over the last 130,000 y // Proceedings of the National Academy of Sciences. 2019. Vol. 116 (11). P. 4822–4827.

44 *Kohfeld K. E., Chase Z.* Controls on deglacial changes in biogenic fluxes in the North Pacific Ocean // Quaternary Science Reviews. 2011. Vol. 30. P. 3350–3363; *Rae J. W. B., Gray W. R., Wills R. C. J. et al.* Overturning circulation, nutrient limitation, and warming in the Glacial North Pacific. P. eabd1654; *Wang R., Kuhn G., Gong X. et al.* Deglacial land-ocean linkages at the Alaskan continental margin in the Bering Sea // Frontiers in Earth Science. 2021. Vol. 9. P. 712415.

45 *Pavlov P., Roebroeks W., Svendsen J. I.* The Pleistocene colonization of northeastern Europe: a report on recent research // Journal of Human Evolution. 2004. Vol. 47. P. 3–17.

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

of a mammoth kill are dated to ~49.3–45.2 ka[47]. Nevertheless, evidence for people on the GAP before 35 ka — both within and beyond the conventional boundaries of Beringia — remains scarce and problematic[48].

Late MIS 3 (35–29 ka). The earliest firmly documented settlement of Beringia took place after 35 ka on the GAP. It is represented by a cluster of open-air sites near the mouth of the Yana River (*Yana River site complex*) that have yielded thousands of stone and non-stone artifacts, and a large quantity of associated faunal remains, including steppe bison, reindeer, hare, and mammoth[49]. Calibration of radiocarbon dates with the IntCal20 curve shows a concentration of ages around 34.5–31.5 ka, coinciding with the GI 6 and GI 5 interstadials[50] (Fig. 5).

Fig. 5. Map of Beringia ~35–29 ka showing location of the Yana River site complex and the two lakes in eastern arctic Beringia that have yielded biomarker evidence for a human presence at the same time. The Ancient North Siberians (ANS) lineage occupied western arctic Beringia (Great Arctic Plain [GAP]) during this period. Illustration prepared by L. K. Takahashi and E. Y. Pavlova

[47] *Pitulko V. V., Tikhonov A. N., Pavlova E. Y. et al.* Early human presence in the Arctic: Evidence from 45,000-year-old mammoth remains // Science. 2016. Vol. 351. P. 260–263.

[48] *Gelvin-Reymiller C., Reuther J. D., Potter B. A. et al*. Technical aspects of a worked proboscidean tusk from Inmachuk River, Seward Peninsula, Alaska // Journal of Archaeological Science. 2006. Vol. 33. P. 1088–1094; *Pitulko V. V., Tikhonov A. N., Pavlova E. Y. et al.* Early human presence in the Arctic. P. 260–263.

[49] *Pitulko V. V., Nikolskiy P., Basilyan A., Pavlova E.* Human Habitation in Arctic Western Beringia prior to the LGM // Paleoamerican Odyssey. College Station, 2013. P. 13–44; *Pitulko V., Pavlova E., Nikolskiy P.* Revising the archaeological record of the Upper Pleistocene Arctic Siberia. P. 127–148; *Pitulko V. V.* Yana B area of the Yana site: some observations done during the excavations of 2015 through 2018 // Prehistoric Archaeology. Journal of Interdisciplinary Studies. 2019. No. 1. P. 64–91.

[50] *Pitul'ko V. V., Pavlova E. Y.* Geoarchaeology and Radiocarbon Chronology of Stone Age Northeast Asia. P. 58–59; *Reimer P. J., Austin W. E. N., Bard E. et al.* The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP) // Radiocarbon. 2020. Vol. 62 (4). P. 725–757.

The Yana River sites also yielded ancient DNA from several human teeth, and whole-genome analyses of two of the teeth revealed that the people in Beringia at this time (designated *Ancient North Siberians*) belonged to the west Eurasian lineage (see earlier discussion). The lineage also is represented by human remains from LGM and post-LGM sites in southern Siberia and contributed as much as 30 % of the Native American genome[51].

Sediment cores extracted from two lakes in the northern Brooks Range provide tentative evidence for a human presence in eastern arctic Beringia (North Slope of Alaska) in the form of biomarker data after 35 ka[52] (see: Fig. 5). Although the biomarker data, which includes fecal sterols and polycyclic aromatic hydrocarbons (traces of burning), is considered problematic, the timing coincides with re-emergence of a land connection between western and eastern Beringia (as well as interior access to the northern Plains of North America). Dated large mammal remains suggest food resources on the North Slope were comparable to those of the Yana River area[53].

Last Glacial Maximum (26.5–19 ka). The two brief warm intervals associated with the Yana River sites (GI 6/GI 5) were followed by an extended cold period (HE 3), dating to ~30–29 ka and marking the end of MIS 3. After two more brief interstadials (GI 4/GI 3), a period of extreme and sustained cold ensued (i. e., the LGM) between 26.5 ka and 19 ka, interrupted by another brief interstadial (GI 2) about 24–23 ka[54]. Several lines of evidence suggest that temperatures in arctic Beringia were relatively mild during the LGM[55].

Although definitive traces of human settlement in Beringia 30–15 ka are lacking, there is some problematic evidence for people in both western and eastern arctic Beringia during this interval. The latter includes biomarker data from the two lakes in the Brooks Range mentioned above, one of which (*Burial Lake*) exhibits a peak in the fecal sterol data ~24 ka (i. e., GI 2)[56]. Additionally, the spread of people throughout mid-latitude North America and South America after 15 ka indicates their presence in Beringia at some earlier point in time, most likely in the coastal zone of the southern BLB and adjoining NW Pacific coast (Fig. 6).

Evidence from the Yana-Indighirka Lowland dates to the early LGM (27.6–25.6 ka) and includes a mammoth rib and bear bone with possible tool cut-marks, an ivory core fragment and worked ivory fragment, and mammoth scapula with a perforation. A mammoth scapula with a perforation was recovered from Wrangel Island, which represent-

[51] *Sikora M., Pitulko V. V., Sousa V. C. et al.* The population history of northeastern Siberia since the Pleistocene. P. 182–188.

[52] *Vachula R. S., Huang Y., Russell J. M. et al.* Sedimentary biomarkers reaffirm human impacts on northern Beringian ecosystems during the Last Glacial period. P. 514–525.

[53] *Mann D. H., Groves P., Reanier R. E. et al.* Life and extinction of megafauna in the ice-age Arctic. P. 14301–14306.

[54] *Andersen K. K., Svensson A., Johnsen S. J. et al.* The Greenland ice core chronology 2005, 15–42 ka. Part 1: Constructing the time scale // Quaternary Science Reviews. 2006. Vol. 25 (23–24). P. 3246–3257.

[55] *Alfimov A. V., Berman D. I.* Beringian climate during the Late Pleistocene and Holocene // Quaternary Science Reviews. 2001. Vol. 20. P. 127–134; *Daniels W. C., Russell J. M., Morrill C. et al.* Lacustrine leaf wax hydrogen isotopes indicate strong regional climate feedbacks in Beringia since the last ice age // Ibid. 2021. Vol. 269. P. 107130.

[56] *Vachula R. S., Huang Y., Russell J. M. et al.* Sedimentary biomarkers reaffirm human impacts on northern Beringian ecosystems during the Last Glacial period. P. 514–525.

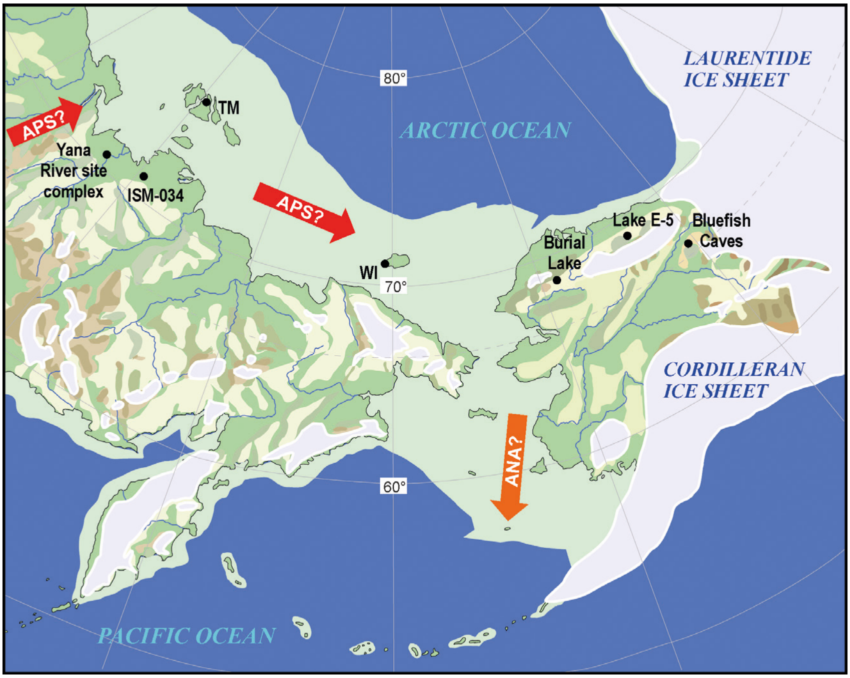

Fig. 6. Map of Beringia during the LGM (26.5–19 ka) showing location of Bluefish Caves and the two lakes in eastern arctic Beringia that have yielded biomarker evidence for a human presence at this time. The Ancient Paleo-Siberians (APS) lineage occupied arctic Beringia, or Great Arctic Plain, after the LGM, but also may have been present during the LGM, while the Ancient Native Americans (ANA) lineage probably occupied the southern Bering Land Bridge/North-West Pacific coast >15 ka. Legend for the site names: ISM-034 — Ilyn-Syalakh 034 site; TM — Tabayuryakh Mammoth; WI — Wrangel Island. Illustration prepared by L. K. Takahashi and E. Y. Pavlova

ed an upland area on the northeastern GAP, dating to 27.2–26.1 ka[57]. Mammoth bones with possible cut marks also are reported from the New Siberian Islands (another upland area in the central plain), dating to the early — or before the beginning of — the LGM (28–24 ka)[58].

In addition to the biomarker data from the Brooks Range, evidence from eastern arctic Beringia comprises stone and bone artifacts and cut-marked large-mammal bones in buried stratigraphic context at *Bluefish Caves* in the northern Yukon (see: Fig. 6). The pollen-stratigraphy suggests that the layers have not been mixed. The artifacts include a

[57] *Pitulko V., Pavlova E., Nikolskiy P.* Revising the archaeological record of the Upper Pleistocene Arctic Siberia. P. 127–148; *Pavlova E. Y., Pitulko V. V.* Late Pleistocene and early Holocene climate changes and human habitation in the arctic western Beringia based on revision of palaeobotanical data // Quaternary International. 2020. Vol. 549. P. 5–25.

[58] *Potapova O., Pavlov I., Plotnikov V. et al.* A new woolly mammoth (*Mammuthus primigenius* Blumenbach, 1799) from Kotelny Island, Novosibirsk Archipelago, Russia. Conference: 80th Society of Vertebrate Paleontology Annual Meeting (October 12–16, 2020). [s. l.], 2020. P. 273; *Pavlov I., Suzuki N.* Tabayuriakhsky mammoth (*Mammuthus primigenius* Blum., 1799), from the island of Kotelny, Novosibirskiy archipelago // Arctic and Subarctic Natural Resources. 2020. Vol. 25 (2). P. 56–66.

Fig. 7. Map of Beringia during the Bølling-Allerød Interstadial (14.7–12.9 ka) showing location of sites mentioned in the text. The Duvanny Yar locality, which yielded human remains [Lee E. J. et al. 2018] and ancient DNA of Ancient Paleo-Siberians (APS) lineage [Sikora M. et al. 2019] dates to ~10 ka. Illustration prepared by L. K. Takahashi and E. Y. Pavlova

microblade core, core tablet, and burin recovered from the lower loess unit in Cave II and dated to ~24–23 ka (i. e., GI 2). A flaked mammoth bone fragment recovered from the same context yields an older radiocarbon age (~28 ka)[59]. The occupation may be at least tentatively attributed to the East Asian APS lineage, based on the association of the latter with microblade technology (see above).

Bølling/Allerød Interstadial (14.7–12.9 ka). Although *Urez-22* on the Yana-Indighirka interfluve, which contains microblades, may date to the end of the HE 1 cold interval, most >13-ka sites in Beringia date to the B/A (GI 1) interstadial[60]. In addition to sites in the Yana-Indighirka Lowland (e. g., *Berelekh, Nikita Lake, Ilin-Syalakh*[61]), they

[59] *Bourgeon L., Burke A., Higham T.* Earliest human presence in North America dated to the Last Glacial Maximum. P. e0169486–e0169486; *Bourgeon L.:* 1) Préhistoire Béringienne: Étude archéologique des Grottes du Poisson-Bleu (Yukon). Collection Mercure. 2018. No. 179; 2) Revisiting the mammoth bone modifications from Bluefish Caves (YT, Canada) // Journal of Archaeological Science: Reports. 2021. Vol. 37. P. 102969.

[60] *Pavlova E. Y., Pitulko V. V.* Late Pleistocene and early Holocene climate changes and human habitation in the arctic western Beringia based on revision of palaeobotanical data // Quaternary International. 2020. Vol. 549. P. 5–25.

[61] *Pitulko V. V., Basilyan A. E., Pavlova E. Y.* The Berelekh "graveyard": new chronological and stratigraphical data from the 2009 field season // Geoarchaeology. 2014. Vol. 29. P. 277–299; *Pitulko V. V., Pavlova E. Y., Basilyan A. E.* Mass accumulations of mammoth (mammoth 'graveyards') with indications of past human activity in the northern Yana-Indighirka lowland, Arctic Siberia // Quaternary International. 2016. Vol. 406. P. 202–217.

Fig. 8. Map of the NW Pacific coast of North America at ~13.8 ka showing a narrow ice-free corridor in western Canada and the margin of the continental shelves (coastlines reduced from this margin at 13.8 ka) and suggested dispersal of ANA groups from NW Pacific coastal areas north into southern and eastern Beringia (including Kamchatka) and south into mid-latitude North America. Illustration prepared by L. K. Takahashi and E. Y. Pavlova

include sites in central Kamchatka (*Ushki* site complex)[62], central Alaska (e. g., *Swan Point*, *McDonald Creek*, *Dry Creek*, *Walker Road*) and the *Little John* site in the southern Yukon[63] (Fig. 7). With the exception of the lowest layer at Swan Point, the Bølling/Allerød (B/A) interstadial levels at these sites lack evidence for microblade technology, instead yielding various small bifacial stone points (stemmed, triangular, and teardrop-shaped).

Although various authors have linked the B/A interstadial sites to the initial settlement of the Western Hemisphere[64], it now is apparent that they all post-date the beginning of the dispersal of the ANA population in mid-latitude North America. We conclude

[62] *Dikov N. N.* Drevnie Kul'tury Severo-Vostochnoi Azii. Moscow, 1979.

[63] *Hoffecker J. F., Elias S. A.* Human Ecology of Beringia. P. 101–161; *Potter B. A., Holmes C. E., Yesner D. R.* Technology and Economy Among the Earliest Prehistoric Foragers in Interior Eastern Beringia // Paleoamerican Odyssey. College Station, 2013. P. 81–103; *Pitulko V., Pavlova E., Nikolskiy P.* Revising the archaeological record of the Upper Pleistocene Arctic Siberia. P. 127–148.

[64] *Dikov N. N.* Drevnie Kul'tury Severo-Vostochnoi Azii. Moscow, 1979; *Hoffecker J. F., Powers W. R., Goebel T.* The colonization of Beringia and the peopling of the New World // Science. 1993. Vol. 259. P. 46–

that these sites probably represent movements of people into or within Beringia during the B/A interstadial. The population movements conceivably were driven by (a) inundation of continental shelf areas <16 ka (including the southern BLB coast), and (b) the rapid growth of population along the NW Pacific coast, supported by a rise in marine productivity (see above).

We suspect the latter generated population expansion to the north — as well as towards mid-latitude North America — resulting in the simultaneous spread of people into southern and central Beringia. Conceivably, the NW Pacific coast was a source for the Tanana Valley sites via the deglaciated Copper River system, while the similarities between the stemmed points in Kamchatka and early stemmed points in mid-latitude North America (*Western Stemmed Tradition*) may reflect a common NW Pacific coast source[65] (Fig. 8). The issue may be resolved by discovery and analysis of aDNA from human remains associated with the sites that contain various bifacial point types, which should represent the ANA population (versus their APS source population)[66].

Younger Dryas (12.9–11.3 ka). The *Younger Dryas* (YD) cold interval (or GS 1 stadial) is associated with significant change in the Beringian archaeological record. During this interval, assemblages containing wedge-shaped microblade cores spread throughout most of western and eastern Beringia[67]. The industry probably is derived from arctic Beringia, where it is documented by 15 ka (*Urez-22)* and possibly much earlier (see above), and its southward spread into subarctic Beringia may be related to the colder climates of the YD period[68].

Although aDNA from human remains has yet to be recovered from microblade assemblages of YD age, the association of both older and younger (i.e., post-YD) sites in Northeast Asia and northern North America with the East Asian APS lineage suggests that the YD microblade assemblages are an archaeological proxy for the spread of the APS population. At several stratified sites (e. g., *Ushki*, *Dry Creek*), microblade assemblages of YD age replace older assemblages containing various bifacial point types[69].

Another significant development in the archaeological record during the YD is the spread of assemblages containing various lanceolate point types found on the North American Plains (sometimes labeled *Northern Plano*) in eastern Beringia. Since the 1950s, this phenomenon has been attributed to the northward movement of Plains bison hunters into the Yukon and Alaska[70]. More recently, it has been linked to an expansion of bison habitat in the arctic/subarctic during the dry conditions of the YD cold interval (and the northward movement of steppe bison through the reopened ice-free corri-

53; *West F. H.* The Archaeological Evidence // American Beginnings: The Prehistory and Paleoecology of Beringia. Chicago, 1996. P. 537–559.

65 *Ponkratova I. Y., Davis L. G.* Technological characterization of late Pleistocene-aged stemmed points from the Ushki Lake site, Layer VII, Kamchatka, Russia // Conference: 27th EAA Annual Meeting (Kiel Virtual, 2021). Prague, 2021. P. 620.

66 By contrast, any human remains found in sites/layers containing traces of microblade technology should represent the APS population (from which the ANA population is estimated to have diverged ~20–19 ka).

67 *Hoffecker J. F., Elias S. A.* Human Ecology of Beringia. P. 162–204.

68 *Pitulko V., Pavlova E., Nikolskiy P.* Revising the archaeological record of the Upper Pleistocene Arctic Siberia. P. 127–148.

69 *Hoffecker J. F., Elias S. A.* Human Ecology of Beringia. P. 163–198.

70 *Willey G. R.* An Introduction to American Archaeology. Vol. 1. Englewood Cliffs, 1966. P. 70–71.

dor)[71]. Recent identification of the North American ANA population as the parent lineage of the *Ancient Beringian* population in eastern Beringia, which is associated with lanceolate points of YD age at *Upward Sun River* in central Alaska, supports the "Northern Plano model"[72].

Beringia and the settlement of the Western Hemisphere

Recent paleo-genomics research reveals that living First Peoples of the Western Hemisphere are primarily descended from an East Asian lineage (APS) that was present in Northeast Asia during the LGM, although they reflect a significant genomic contribution from a west Eurasian lineage (ANS/ANE) that also was present in Siberia during the LGM. A west Eurasian group (ANS) was at least briefly in arctic Beringia during 35–30 ka. Either East Asian APS or its daughter lineage *Ancient Native Americans* (ANA) entered Beringia before 15 ka, when the latter began to disperse in mid-latitude North America (the APS/ANA split is estimated to have taken place 24–19 ka). The APS population, which is present in Beringia no later than 10 ka, also is ancestral to the living northern peoples of the Western Hemisphere[73].

Integration of the archaeological record with the paleo-genomic framework has become possible during the past several years, as human remains associated with artifact assemblages yield whole genomes. As noted earlier, East Asian APS groups are consistently associated with microblade technology during both the late Pleistocene and Holocene, while the west Eurasian lineage (ANS/ANE) is linked to other Siberian middle and late Upper Paleolithic industries. The ANA lineage is associated with a variety of traditions and complexes during initial dispersal and settlement in the Western Hemisphere (15–12 ka)[74].

Although evidence for people in Beringia before 35 ka remains problematic, we conclude that this is possible, if not likely, given the documented presence of modern humans

[71] *Hoffecker J. F.* Assemblage variability in Beringia: The Mesa factor // From the Yenisei to the Yukon: Interpreting Lithic Assemblage Variability in Late Pleistocene/Early Holocene Beringia. College Station, 2011. P. 165–178.

[72] *Potter B. A., Irish J. D., Reuther J. D., McKinney H. J.* New Insights into Eastern Beringian Mortuary Behavior: A Terminal Pleistocene Double Infant Burial at Upward Sun River // Proceedings of the National Academy of Sciences. 2014. Vol. 111. P. 17060–17065; *Ning C., Fernandes D., Changmai P. et al.* 2020. The genomic formation of First American ancestors in East and Northeast Asia. https://doi.org/10.1101/2020.10.12.336628. The Ancient Beringian lineage also is identified from an isolated tooth in *Trail Creek Cave 9* (Seward Peninsula, Alaska) dating to the early Holocene (9 ka), but it is not directly associated with any artifacts (*Moreno-Mayar J. V., Vinner L., de Barros Damgaard P. et al.* Early human dispersal within the Americas. Science. 2018. Vol. 362. P. eaav2621).

[73] *Moreno-Mayar J. V., Vinner L., de Barros Damgaard P. et al.* Early human dispersal within the Americas // Science. 2018. Vol. 362. P. eaav2621; *Flegontov P., Altınışık N. E., Changmai P. et al.* Palaeo-Eskimo genetic ancestry and the peopling of Chukotka and North America // Nature. 2019. Vol. 570. P. 236–240; *Sikora M., Pitulko V. V., Sousa V. C. et al.* The population history of northeastern Siberia since the Pleistocene. P. 182–188; *Yu H., Spyrou M. A., Karapetian M. et al.* Paleolithic to Bronze Age Siberians reveal connections with First Americans and across Eurasia // Cell. 2020. Vol. 181. P. 1–14.

[74] *Raghavan M., Skoglund P., Graf K. E. et al.* Upper Palaeolithic Siberian genome reveals dual ancestry of Native Americans. P. 87–91; Paleoamerican Odyssey / eds K. E. Graf, C. V. Ketron, M. R. Waters. College Station, 2013; *Yu H., Spyrou M. A., Karapetian M. et al.* Paleolithic to Bronze Age Siberians reveal connections with First Americans and across Eurasia. P. 1–14; *Kılınç G. M., Kashuba N., Koptekin D. et al.* Human population dynamics and *Yersina pestis* in ancient northeast Asia. P. eabc4587.

in subarctic and arctic Eurasia before 40 ka. If Beringia was inhabited before 38 ka, its occupants presumably were early representatives of the East Asian lineage (e. g., Tianyuan Cave), because the west Eurasian lineage did not move into Northeast Asia until after 38 ka[75].

While much of the East Siberian Arctic Shelf was exposed 45–38 ka (i. e., large mammal resources of the GAP were probably available), the BLB was almost entirely inundated by high sea level at this time. Accordingly, the Bering Strait might have been a barrier to the settlement of eastern Beringia and the Western Hemisphere as a whole. On the other hand, we note that the narrow strait (further reduced in width by a GMSL of -40 meters) would not have constituted an absolute barrier comparable to the coalesced Laurentide and Cordilleran ice sheets during the LGM. Even without watercraft, movement across the Bering Strait would have been possible during colder months over seasonal ice (and with land visible on the opposite side under conditions of adequate lighting). Mid-latitude North America was accessible, in turn, from eastern Beringia via a wide interior corridor throughout this interval[76].

The west Eurasian ANS population moved into western arctic Beringia before or during two brief interstadials (GI 6 and GI 5) between 35–31 ka that preceded the HE 3 cold period (30–29 ka). Their stone artifacts were primarily made on large flakes (e. g., side-scrapers), but also included a number of small "precision" tools[77]. Although the sites are concentrated in the Yana-Indighirka Lowland, they probably ranged across large areas of the GAP. Analysis of aDNA suggests an "effective population size" (N_e) of about 500 individuals[78]. Large mammal biomass probably was at peak levels during the interstadials due to increased plant productivity. The BLB was exposed during 35–30 ka, and there is tentative evidence for people in eastern arctic Beringia at this time (although no information on possible genomic or cultural affiliations)[79].

A revised glacial chronology for MIS 3 indicates that an ice-free corridor (at least 250 km in width) between the Laurentide and Cordilleran ice sheets remained open 35–30 ka, potentially allowing movement of people from eastern Beringia to mid-latitude North America[80]. The recent discovery of human footprints in ancient lakeshore sediments dating to 23–21 ka in New Mexico may indicate that such a movement of people occurred during this interval (because both interior and coastal access to mid-latitude North America was blocked after 30 ka)[81]. The low visibility of the North American pop-

[75] *Massilani D., Skov L., Hajdinjak M. et al.* Denisovan ancestry and population history of early East Asians. P. 579–583; *Yang M. A., Fan X., Sun B. et al.* Ancient DNA indicates human population shifts and admixture in northern and southern China. P. 282–288.

[76] *Pico T., Creveling J. R., Mitrovica J. X.* Sea-level records from the U. S. mid-Atlantic constrain Laurentide Ice Sheet extent during Marine Isotope Stage 3. P. 15612; *Dalton A. S., Stokes C. R., Batchelor C. L.* Evolution of the Laurentide and Innuitian ice sheets prior to the Last Glacial Maximum (115 ka to 25 ka). P. 103875.

[77] *Pitul'ko V. V., Pavlova E. Y.* Geoarchaeology and Radiocarbon Chronology of Stone Age Northeast Asia.

[78] *Sikora M., Pitulko V. V., Sousa V. C. et al.* The population history of northeastern Siberia since the Pleistocene. P. 182–188.

[79] *Vachula R. S., Huang Y., Russell J. M. et al.* Sedimentary biomarkers reaffirm human impacts on northern Beringian ecosystems during the Last Glacial period. P. 514–525.

[80] *Dalton A. S., Stokes C. R., Batchelor C. L.* Evolution of the Laurentide and Innuitian ice sheets prior to the Last Glacial Maximum (115 ka to 25 ka). P. 103875.

[81] *Bennett M. R., Bustos D., Pigati J. S. et al.* Evidence of humans in North America during the Last Glacial Maximum // Science. 2021. Vol. 373. P. 1528–1531.

ulation may reflect the constraints of the corridor on its size and long-term stability (the population may have become extinct after 21 ka).

It is not clear if Beringia was abandoned during the HE 3 cold interval (30–29 ka) and/or the early LGM (26.5–24 ka), or if the current lack of definitive evidence for their presence is due to low archaeological visibility. If the human population contracted at this time, its reduced size and density would contribute to its low visibility in the archaeological record. Brief interstadials during 29–27 ka (GI 4 and GI 3) and 24–23 ka (GI 2) probably created an environment on the GAP similar to that during GI 6 and GI 5. As noted above, both interior and coastal access to mid-latitude North America was blocked by ice sheets after 30 ka[82].

Either the East Asian APS lineage or its daughter ANA population entered Beringia before 15 ka (based on widespread dispersal of the ANA population in the Western Hemisphere from Beringia after 15 ka). It is not clear (a) where the split (at 20–19 ka) between the APS and ANA populations took place (i. e., in Northeast Asia or Beringia); (b) when either group entered Beringia, although both were present in Beringia at some point after 15 ka; and (c) by what route either or both groups entered Beringia. Did the East Asian lineage enter Beringia via the GAP and/or the Northeast Asian coastal zone?

The integration of paleo-genomics and archaeology reveals a significant development in the settlement of the Western Hemisphere. At some point in the process of spreading into Beringia and dispersing in the Americas, the East Asian lineage (APS/ANA) abandoned their microblade technology (associated with a northern interior foraging economy) and designed a new set of stone artifacts. Because it now appears most likely that most or all the ANA population dispersed out of Beringia via the NW Pacific coast, the shift in technology probably reflects a corresponding shift from northern interior to coastal diet and economy.

The conclusion that the ANA population accessed mid-latitude North America primarily or exclusively via the NW Pacific coast is based on the apparent lack of a viable interior route from Beringia until after this population had spread widely across North America (~14 ka)[83]. Although a narrow ice-free corridor (~2,000 km long and <100 km wide at its narrowest point) is reported after 14 ka, it either blocked the movement of people from interior Beringia or constrained their numbers so severely that they had little impact on the ANA population in mid-latitude North America. By contrast, the NW Pacific coast was subject to early deglaciation (~18 ka) and may have represented a viable migration route as early as 17 ka[84]. Most importantly, the NW Pacific coast was rich in marine resources, which reached peak productivity levels during the B/A interstadial (14.7–12.9 ka)[85]. These rich marine resources may be necessary to account for the rapid growth and dispersal of the ANA population[86].

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82 *Dalton A. S., Margold M., Stokes C. R. et al.* An updated radiocarbon-based ice margin chronology for the last deglaciation of the North American Ice Sheet Complex. P. 106223.

83 Ibid.

84 *Lesnek A. J., Briner J. P., Lindqvist C. et al.* Deglaciation of the Pacific coastal corridor directly preceded the human colonization of the Americas. P. eaar5040.

85 *Kohfeld K. E., Chase Z.* Controls on deglacial changes in biogenic fluxes in the North Pacific Ocean. P. 3350–3363.

86 *Llamas B., Fehren-Schmitz L., Valverde G. et al.* Ancient mitochondrial DNA provides high-resolution time scale of the peopling of the Americas // Science Advances. 2016. Vol. 2. P. e1501385.

A credible scenario for First Peoples settlement of Beringia and the Western Hemisphere is that the East Asian APS lineage entered Beringia from the Lena Basin (e. g., Khaiyrgas Cave) via the GAP during the GI 2 interstadial (24–23 ka), when large mammal populations probably were at high levels. The reported microblade core in the lowest level at Bluefish Caves in eastern arctic Beringia (along with the biomarker data from the northern Brooks Range) supports this scenario. Occupation of the southern BLB conceivably corresponds to the APS/ANA split 24–19 ka, while the relatively poor resources of the interior BLB may have encouraged a growing dependence on coastal resources, intensified by onset of HE 1 after 18 ka[87]. Early deglaciation of the NW Pacific coast opened a new coastal habitat for the ANA population, where much of their maritime economy probably was developed.

Evidence for high-latitude genetic adaptation in the APS population during the LGM provides additional support for this scenario. An arctic "genetic signature", represented by high frequencies of genes related to control of polyunsaturated fatty acid levels and melanin production (i. e., adaptations to a high protein/fat diet and low UV radiation/vitamin D deficiency), is found throughout the Indigenous population of the Western Hemisphere. The arctic signature indicates that the APS ancestors of the latter occupied areas above latitude 66° North for an extended period before divergence of the two populations >19 ka (i. e., during the LGM)[88]. The only unglaciated area of the Arctic during the LGM was the GAP and adjoining lowlands of northeastern Siberia and North Slope of Alaska, most of which lies within Beringia.

We conclude, as in our earlier publication, that the advance and retreat of large glaciers was the primary variable in the timing and routes of human settlement of the Americas[89]. The environments of Beringia were not a barrier for modern humans, who dispersed in Northeast Asia <50 ka. Rather, we suspect that the rich steppe-tundra fauna of GAP attracted people to the Arctic Zone during late MIS 3 and at some point during MIS 2. The settlement of Beringia (i. e., movement east of the Verkhoyansk Mountains) probably was a secondary consequence of the occupation of the GAP. The marine biota of the southern BLB coast provided an alternative source of food and materials for people in a less rich terrestrial habitat and probably encouraged their spread southward into the NW Pacific coast.

A revised glacial/sea-level chronology, new paleo-genomics research, and some new archaeological discoveries suggest a more complex pattern, however, to modern human settlement of Beringia and the Western Hemisphere than envisioned in our earlier publication. Late MIS 3 glaciers probably did not block access to mid-latitude North America, although they may have limited severely the size and long-term stability of any population

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[87] *Wooller M.J., Saulnier-Talbot E., Potter B.A. et al.* A new terrestrial palaeoenvironmental record from the Bering Land Bridge and context for human dispersal // Royal Society Open Science. 2018. Vol. 5. P. 180145.

[88] *Fumagalli M., Moltke I., Grarup N. et al.* Greenlandic Inuit show genetic signatures of diet and climate adaptation // Science. 2015. Vol. 349. P. 1343–1347; *Amorim C.E.G., Nunes K., Meyer D. et al.* Genetic signature of natural selection in first Americans // Proceedings of the National Academy of Sciences. 2017. Vol. 114. P. 2195–2199; *Hlusko L.J., Carlson J.P., Chaplin G. et al.* Environmental selection during the last ice age on the mother-to-infant transmission of vitamin D and fatty acids through breast milk // Proceedings of the National Academy of Sciences. 2018. Vol. 115 (19). P. E4426–E4432; *Niedbalski S.D., Long J.C.* Novel alleles gained during the Beringian isolation // Scientific Reports. 2022. Vol. 12. P. 4289.

[89] *Hoffecker J.F., Pitulko V.V., Pavlova E.Y.* Climate, technology and glaciers: The settlement of the Western Hemisphere. P. 327–355.

in the latter, and it now appears that a small population (probably derived from the west Eurasian lineage that occupied eastern arctic Beringia >30 ka) was present south of the LGM ice sheets. The coalesced Laurentide and Cordilleran ice sheets blocked interior access to mid-latitude America for the East Asian lineage (APS/ANA) until 13.8 ± 0.5 ka (and possibly later due to the length and narrow width of the ice-free corridor). Early deglaciation of the NW Pacific coast (<18 ka) provided early access to mid-latitude North America for the ANA population and the resource base for their rapid growth and expansion 15–13 ka.

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