Credit: Winona Nelson

Genomes Reveal Humanity's Journey into the Americas

DNA has upended neat and tidy accounts of the peopling of the American continents

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May 1, 2021 |

Our species, *Homo sapiens*, emerged in Africa hundreds of thousands of years ago. From there modern humans followed in the steps of other kinds of humans—*Homo erectus*, Neandertals, Denisovans, and others—as they slowly spread across the planet. But the first *H. sapiens* who entered the Americas went somewhere no member of the human family had ever gone before. The process by which people explored, populated and adapted to the many different environments found across these continents was a momentous undertaking, one which began the rich and complex histories of thousands of different nations and communities.

In their journey into the Americas, the ancestors of present-day Indigenous peoples overcame extraordinary challenges. They survived the bitter cold and arid conditions of a global climatic event between 26,000 and 20,000 years ago known as the Last Glacial Maximum (LGM). They developed relationships with unfamiliar lands and their flora and fauna.

There are many perspectives that aim to explain these events. Indigenous peoples have numerous oral histories of their origins. Passed down from one generation to the next, such traditional knowledge conveys important lessons about the emergence of each group's identity as a people and their relationship with their lands and nonhuman relatives. Some of these histories include migration from another place as part of their origins; others do not. The framework that most Western scientists use in understanding the history of population movements is different. This article will focus on their models for the peopling of the Americas, while respecting and acknowledging that these models stand alongside diverse and ancient oral histories with which they may or may not be congruent.

Archaeologists, biological anthropologists, linguists and paleoclimatologists have long sought to understand humanity's dispersal into the American continents. Their efforts have generated various hypotheses about the origins of Indigenous peoples, not only in terms of who their ancestors were but also when and how they established themselves in these lands. The one that prevailed for decades held that a single group of hunters from East Asia swept into the Americas after the LGM on the trail of big game animals and gave rise to all Indigenous peoples in this part of the world today.

But in the past few decades genetics has also been brought to bear on this chapter of the human story. It is no exaggeration to say that insights from genome studies have revolutionized our understanding. Although many gaps remain in our knowledge, these genetic findings, along with recent archaeological discoveries, have shown that the process of populating the Americas was far more complex than previously understood. Significantly, we now know that multiple ancient populations contributed to the ancestry of Indigenous peoples, not just one.

BEFORE CLOVIS

For much of the 20th century, the so-called Clovis First model of Indigenous origins dominated the field of archaeology. The hypothesis rested on the assumption that distinctive stone tools called Clovis points, found at archaeological sites across North America, marked the first appearance of humans on the continents. These fluted spearpoints appeared abruptly south of where the ice sheets were around 13,000 years ago, during the Late Pleistocene epoch, sometimes in association with the remains of megafauna such as

mastodons, mammoths and bison. From the dates and geographical distribution of Clovis sites, archaeologists inferred that people migrated from Siberia to North America across the now submerged Bering Land Bridge after the LGM, moving swiftly down a corridor along the eastern Canadian Rocky Mountains that had opened up into interior North America as the ice sheets melted. These hunter-gatherers, who lived in small bands and ranged far in pursuit of big game, then spread rapidly southward to populate South America in about 1,000 years.

Ancestral Branches

Ancient and contemporary genomes have revealed a far more detailed picture of the origins of the Indigenous peoples of the Americas than was previously available. Researchers long thought that a single population from East Asia gave rise to the First Peoples, but the genetic evidence shows that multiple groups contributed to their ancestry. Together with archaeological remains found at sites across Beringia, these findings are allowing scientists to start to map the movements of these ancestral populations as they made their way to the Americas.

A Ancient North Siberians contributed ancestry to First Peoples, among other populations. DNA from this group has been recovered from the Mal'ta and Yana Rhinoceros Horn sites.

B An isolated subgroup of East Asians contributed the majority of ancestry to the First Peoples. Around 25,000 years ago these Ancient East Asians and the Ancient North Siberians converged. Exactly where they encountered each other is unknown. Putative traces of humans at Bluefish Caves in the Yukon and Lake E5 and Burial Lake in Alaska hint that they might have met in eastern Siberia. Other possible meeting spots include central and northern Beringia and eastern Eurasia.

C The ancestral population that resulted from this merger went on to split into two branches between about 22,000 and 18,000 years ago. One of these branches, the Ancient Beringians, has no known living descendants. The sites of Upward Sun River and Trail Creek Cave may document their presence in Alaska.

D The other branch, known as the Ancestral Native Americans, gave rise to the First Peoples south of the Laurentide and Cordilleran ice sheets.

Credit: Daniel P. Huffman

Eventually archaeological sites predating the first appearance of Clovis tools came to light. One such site is Monte Verde in southern Chile, which dates to 14,200 years ago. The artifacts found there—tools made of stone, wood and bone—are nothing like the Clovis toolkit. They indicated that more than a millennium before the Clovis technology appeared in North America, other people had made it all the way to the southern tip of South America.

A revolution in molecular biology in the late 20th century enabled scientists to bring new approaches, including the ability to retrieve DNA from ancestral remains, to the question of when humans first populated the American continents. Researchers were able to directly sequence and analyze maternally inherited mitochondrial DNA and paternally inherited Y chromosomes from both contemporary and Ancient Indigenous populations. From these genetic data, they could estimate the timing of major demographic events. The broad outlines of population history emerged: ancestors in Asia, a period of isolation of the ancestors of Indigenous peoples during the peak of the LGM, followed by a rapid population expansion that predated Clovis and Monte Verde by several thousand years. But the picture was only a rough sketch, based on just a couple pieces of the genome. Complete genomes provide many orders of magnitude more information about a person's ancestry than mitochondrial DNA or Y chromosomes do.

It is now relatively easy to sequence complete genomes from living people. Genomes from some contemporary Indigenous peoples reveal genetic variation attributable to contact with Europeans following their arrival in the Americas in 1492. Portions of genomes that are inherited from the First Peoples—Indigenous ancestors who predate European contact—reveal histories extending tens of thousands of years backward in time.

Recovering genomes from the remains of these ancestors can be extremely difficult. The majority of DNA extracted from an ancient bone or tooth will come from soil microorganisms, plants, animals and contemporary humans; the ancient DNA fragments will themselves be scarce and damaged. But recent advances have allowed scientists to retrieve and analyze DNA from even very poorly preserved sources. These developments have greatly increased the number of genomes from ancient peoples, and new methods for analyzing ancient genomes have helped us better understand the stories they tell. Together the ancient and contemporary genomes paint a far more detailed picture of the origins of the First Peoples than the one sketched by the mitochondrial and Y chromosome evidence, showing where different branches of their ancestors came from and when they met up.

AN ANCIENT CONVERGENCE

Singling out any specific moment as the "origin" of "a people" is arbitrary and oversimplified to the point of absurdity. Throughout time, human populations have been composed of people with complex mixtures of different ancestries, each with their own histories. But we have to start this genetic story somewhere, so we will begin it in the Upper Paleolithic period. Approximately 36,000 years ago, a group of people living in what is now East Asia became increasingly isolated from the broader population living in the region. It was a very slow process: they continued to exchange mates with their parent population for more than 11,000 years. By about 25,000 years ago, however, they were genetically distinguishable from the ancestors of contemporary East Asians. This isolated group of Ancient East Asians contributed the majority of ancestry to the First Peoples of the Americas.

All genomic studies rule out the possibility that the First Peoples mixed with Europeans or Africans or any other populations before 1492.

Another ancestral branch emerged around 39,000 years ago and lived at the Yana Rhinoceros Horn site in what is now northeastern Siberia 31,600 years ago. This area is situated in the western part of Beringia—the name given to the region spanning eastern Siberia, western Alaska and the land bridge that once connected them, which now lies under the Bering Strait. Two baby teeth found at Yana give us extraordinary insights into this

population, which geneticists refer to as the Ancient North Siberians. The Ancient North Siberians at Yana were hunter-gatherers who lived in this high-latitude area year-round. The baby teeth came from two boys at Yana who lost them when they were 10 to 12 years old as their permanent molars and canines were emerging. The teeth themselves show that the boys had survived the dangers of infancy. Genomes recovered from the teeth, described by Martin Sikora of the University of Copenhagen and his colleagues in 2019, show that the boys were not close relatives and belonged to a sizable population comprising around 500 breeding individuals. Unlike Neandertals, whose genomes indicate that they had small populations and experienced periodic local extinctions, the Ancient North Siberians appear to have thrived in extremely challenging environments.

The Ancient North Siberians spread throughout northern and central Siberia. Remains of a child who lived at a site known as Mal'ta document their presence in south-central Siberia 24,000 years ago, during the Upper Paleolithic period. DNA recovered from these remains shows that many geographically dispersed populations, including present-day West Eurasians (a group that encompasses Europeans) and the First Peoples of the Americas, have ancestry from the Ancient North Siberians.

The two main branches of the First Peoples' ancestry—the Ancient East Asians and the Ancient North Siberians—converged around 25,000 to 20,000 years ago and interbred. The resulting ancestral population formed shortly after the start of the LGM, during which Siberia had an exceedingly cold climate with limited plants and animals. Humans would have found it very difficult, if not impossible, to live in this environment, and indeed there is essentially no archaeological record in northeastern Siberia between around 29,000 and 15,000 years ago. Many archaeologists infer from this absence that people sought refuge in other regions with more resources and better climates. We do not know exactly what happened, but it

seems likely that the meeting of people from the Ancient East Asian and Ancient North Siberian groups occurred as part of a migration from Siberia in response to this environmental change. The question is: Where did they encounter each other?

They probably did not cross paths in western Beringia: that region appears to have been depopulated after around 29,000 years ago. This leaves eastern Eurasia, central or eastern Beringia, and northern Beringia as possible meeting spots. Genetics does not readily settle this geographical question. The genomes of Indigenous peoples indicate that their ancestors were isolated for several thousand years during the LGM starting shortly after the Ancient East Asians and Ancient North Siberians intermarried. This isolation strongly suggests that the encounter did not take place in eastern Eurasia, where the proximity of other groups would almost certainly have resulted in additional mixing, because that is what humans do. Still, some archaeologists argue that eastern Eurasia is the only region that has extensive and unambiguous archaeological evidence of human presence during this cold period.

Perhaps instead the ancestors of Indigenous peoples rode out the LGM on the southern coast of what would have been central Beringia. Paleoenvironmental reconstructions have shown that it would have had a mild climate, possibly resembling a wetland, because of the proximity of ocean currents. It would have been a relatively comfortable place for people and animals to live when the ice sheets were at their maximum extent. But central Beringia is now underwater and inaccessible, so archaeologists have been unable to look for direct evidence of people there. There are some intriguing hints of a human presence in eastern Beringia, however. Sites in the Yukon and on Alaska's North Slope have yielded putative traces of humans during the LGM. The evidence is not sufficient to convince most archaeologists, but it does call for more attention to be paid to this region.

The Siberian Arctic zone, a region above latitude 66 degrees North that lies north and west of western Beringia, has only recently emerged as another plausible candidate for a refugium during the LGM and thus a place where people from the Ancient East Asian and Ancient North Siberian groups might have come together. Today large parts of this area are underwater, but throughout the LGM it would have been a vast steppe-tundra plain that supported big populations of mammoths, woolly rhinoceros, bison and horses. It would have been a challenging environment for humans. Yet we know from the archaeological and genetic evidence at Yana that they were already well adapted for such Arctic conditions long before the LGM began. Still, as with all other potential refugia besides eastern Eurasia, there is currently very little direct archaeological evidence of humans in this part of the world.

Although we do not know exactly where the Ancient North Siberians and Ancient East Asians joined up, we can infer from genetics what happened next. Immediately after the two groups exchanged genes and while they were isolated from other human groups, a series of complex demographic events occurred very close in time that would ultimately give rise to peoples in

the Americas and Siberia. The ancestral population split into at least two branches between about 22,000 and 18,100 years ago. One branch, named the Ancient Beringians, has no known living descendants. The other, known as the Ancestral Native Americans, gave rise to First Peoples south of the Laurentide and Cordilleran ice sheets.

This branch of Ancestral Native Americans was probably itself subdivided into multiple distinctive groups during the LGM. One of these groups, referred to as Unsampled Population A, has no known archaeological remains to define it, but the present-day Mixe people, who live in Oaxaca, Mexico, seem to have some of its DNA.

A few present-day populations in the Amazon appear to have additional ancestry from a group related to Australasians called Population Y. This link is one of the most puzzling ancestry findings of recent years. Traces of this genetic signal have also turned up in a 40,000-year-old individual from Tianyuan Cave in China. Thus far the evidence suggests that there was once an ancient group widespread throughout Asia that ultimately contributed this ancestry to contemporary Pacific peoples and some Amazonian populations. Researchers are still trying to pin down how many ancient and present-day peoples have this ancestry and where the source population lived.

More important, all genomic studies rule out the possibility that the First Peoples mixed with Europeans or Africans or any other populations before 1492. This conclusion runs contrary to stories of a trans-Atlantic migration promoted by popular television series, but the totality of genetic and archaeological evidence emphatically invalidates those notions.

SOUTHWARD BOUND

After the LGM, Ancestral Native Americans moved southward and split into at least three branches. The first branch to diverge is represented by a single genome from a woman who lived on the Fraser Plateau in British Columbia about 5,600 years ago. Not much else is known about this population. The other two branches encompass all the currently known genetic diversity of populations south of the ice sheets. The Northern Native Americans branch includes the ancestors of Algonquian, Na-Dené, Salishan and Tsimshian peoples. The Southern Native Americans branch includes the ancestors of Indigenous peoples distributed broadly throughout South America, Central America and much of North America.

(Indigenous peoples of the Arctic have additional ancestry from subsequent migrations.) Experts disagree over when, where and how these populations dispersed into the continents. To date, there are three major competing scenarios for this process.

The most conservative archaeologists stand by what is essentially an updated version of the Clovis First model. In their view, the Swan Point site in central Alaska is the key to understanding the peopling of the Americas. Dated to about 14,100 years ago, it is the oldest uncontroversial site in eastern Beringia, and its stone tool technology is said to show clear links to the Diuktai culture in Siberia, as well as Clovis tools. These archaeologists argue that the ancestors of the First Peoples were in northeastern Asia or Siberia during the LGM and did not migrate across the Bering Land Bridge into Alaska until between 16,000 and 14,000 years ago. They maintain that Clovis represents the first successful establishment of humans in the Americas, with people traveling down the so-called ice-free corridor that formed as glaciers retreated, possibly followed by other waves of migration from Siberia. Under this model, sites predating Clovis are either rejected as invalid or attributed to people who did not contribute culturally or biologically to subsequent Indigenous populations.

Other archaeologists emphasize the importance of pre-Clovis evidence, including remains found half a world away from central Alaska at the Page-Ladson site in northern Florida. Described by Jessi Halligan of Florida State University, Michael Waters of Texas A&M University and their colleagues in 2016, this site contains stone artifacts, including a broken knife found in association with 14,450-year-old mastodon bones. The Page-Ladson site is significant to these researchers precisely because of how *insignificant* it would have been at the time: a small watering hole located much farther from the coastline than it is today, with no distinctive features to flag it on the landscape. Humans butchered a mastodon there and carried away its meat and one of its tusks, leaving behind some of its bones, the other tusk and the broken knife. Their visit to the site was evidently brief and purposeful, however; there are no traces of habitation, toolmaking or any other activities. This quick, targeted stop suggests that people had adapted to the landscape well enough to have been familiar with this obscure place and the likelihood of finding food and mastodon tusks for toolmaking there.

Dispersal Scenarios

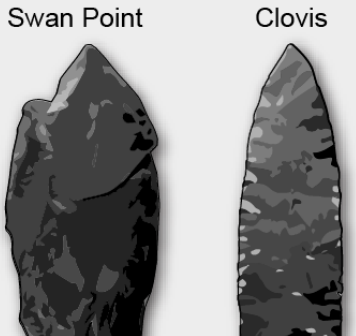
Experts disagree over when, where and how the ancestors of Indigenous peoples dispersed into the American continents. The current debate revolves around three major competing models for this process.

Scenario 1: A Late Peopling

Some archaeologists maintain that the people who made distinctive spearheads initially found in Clovis, N.M., and later discovered at sites such as Anzick in Montana were the first humans to establish themselves successfully in the Americas. The Swan Point site in Alaska figures importantly in their argument because it contains stone tools that appear to link the older Diuktai culture in Siberia to the Clovis culture in North America. Proponents of this so-called Clovis First model hold that people entered the Americas well after the Last Glacial Maximum, traveling down the ice-free corridor that formed as glaciers retreated. These researchers reject pre-Clovis sites as invalid or unrelated to contemporary First Peoples.

Scenario 2: An Early Coastal Peopling

Other archaeologists place great importance on pre-Clovis sites, arguing that they document human presence throughout the Americas well before Clovis technology appeared and before the ice-free corridor opened up. These scholars contend that people probably instead traveled by boat along the western coast starting around 17,000 years ago or possibly as early as 20,000 to 30,000 years ago, if the controversial claims for evidence of such ancient human activity at Pedra Furada and Chiquihuite Cave are to be believed.



Credit: Daniel P. Huffman (*maps*), Jen Christiansen (*artifacts*)

Learning the geography of a place, where resources such as watering holes that attract prey could be reliably found—a process that archaeologists call settling in—takes time. To some experts, Page-Ladson is clear evidence that people were settled in by at least 14,450 years ago, meaning that they would have been in the Americas much earlier. But how much earlier?

There are a number of sites throughout the Americas well below the southernmost margin of the continental ice sheets that date to between about 14,000 and 16,000 years ago. Explaining these sites requires an entirely different paradigm from the late peopling scenario described earlier. For one thing, their antiquity constrains the routes that people could have taken into the Americas. The ice-free corridor between the Laurentide and Cordilleran glaciers did not open until sometime after 14,000 years ago. If people were occupying sites by 14,450 years ago or even earlier, it seems exceedingly unlikely that they could have taken this route. Furthermore, environmental DNA found in lake sediment cores from the middle of the ice-free corridor shows that it would not have been populated by plants or animals until around 12,600 years ago—long after people were already in the Americas. And the earliest direct archaeological evidence of humans within the corridor region itself dates to 12,400 years ago. On balance, the evidence suggests that the first humans to enter the Americas did not take the ice-free corridor in.

The most likely alternative route is via boat along the western coast, which would have become accessible about 17,000 to 16,000 years ago. A coastal route also fits genetic evidence for the Southern Native American expansion better. The best-supported models for

population history currently show that the Southern Native American group diversified rapidly into regional populations throughout North, South and Central America between about 17,000 and 13,000 years ago. Travel by water along the coast would better explain the speed and timing of these population splits than the slower overland route would.

One variant of this early coastal peopling scenario allows that humans may have been present in the Americas during or even slightly before the LGM, perhaps as early as 20,000 to 30,000 years ago. Putative evidence of pre-LGM occupation comes from several sites in Mexico and South America, including Pedra Furada in northeastern Brazil. But most of the archaeological community remains skeptical about these sites, questioning whether they have been dated accurately and whether their supposed artifacts were shaped by humans or natural processes.

This skepticism does not rule out the presence of people in the Americas before the LGM. It simply means that more evidence is needed for confirmation. If people were in the Americas during or just prior to that time, their numbers would probably have been very small, so they would have left a very light archaeological footprint on the landscape. Intriguingly, an early presence might explain the puzzling signal of Population Y ancestry in some Amazonian groups: it could be the result of admixture between peoples dispersing into the Americas after the ice sheets retreated and those already in South America.

The third major scenario is radically different. A small group of scholars believes that people reached this part of the world at an extremely early date. This claim rests in large part on 130,000-year-old mastodon remains excavated from the Cerutti Mastodon site in California. In an analysis published in 2017, Steven Holen of the San Diego Natural History Museum and his colleagues concluded that damage patterns on the bones were the result of butchering. Stones found at the site were interpreted to be manufactured tools. *H. sapiens* is not thought to have begun spreading out of Africa in significant numbers until perhaps 70,000 to 80,000 years ago. If the Cerutti remains really are the product of ancient human activity, they would show not only that humans made their way to the American continents far earlier than previously thought but also that the first people to arrive were probably *Homo erectus* rather than *H. sapiens*.

Most archaeologists reject this argument for multiple reasons, including the possibility that modern construction equipment, rather than early human butchers, smashed the mastodon remains, which were discovered during a road-building project. Furthermore, patterns of variation in contemporary Indigenous genomes do not show separate descent of First Peoples from other humans, nor do they indicate admixture among anatomically modern *H. sapiens* and other kinds of humans in the Americas. If *H. erectus* made it to this corner of the planet, it left neither fossils nor genetic contributions to First Peoples.

As things stand in 2021, most archaeologists and geneticists agree that humans were established in the Americas by at least 14,000 to 15,000 years ago, but they disagree on exactly which pre-Clovis sites are legitimate and therefore how early people may have entered the continents. This diversity of opinions reflects the challenges of working with the archaeological and genetic records, which contain large gaps. Of the three scenarios described here, the second one comes closest to reconciling the archaeological and genetic evidence. But even that model cannot completely account for all the available data.

EMBRACING UNCERTAINTY

As we move forward in studying the peopling of the Americas, we can expect the story to grow even more complicated. At the time of this writing, there are perhaps several dozen publicly available complete genomes from contemporary and ancient Indigenous peoples. These genomes are unevenly distributed; most are from Central and South America and the northern parts of North America. There are few complete genomes from the present-day U.S., the result of Indigenous peoples' justified distrust in researchers. This lack of trust is rooted in the exploitation of Indigenous peoples by physicians and anthropologists who, starting in the earliest days of anthropology, looted ancestors' remains from their resting places. Many used the remains to posit racial classifications that have since been debunked. It is important that geneticists work with Indigenous communities to ensure that the quest for genetic knowledge does not perpetuate further harms.

This geographical gap in our understanding of genetic variation means that we are now in a dynamic period of research in this field. Every new genome sequenced adds tremendously to our knowledge. Investigators are also looking beyond human genomes to DNA from alternative sources such as the bacteria and viruses that are associated with people, as well as human prey and companion species, for clues. This use of nonhuman DNA can potentially illuminate human population movements while respecting the sacredness of Indigenous remains.

There is a good chance that fresh details will emerge that change the models discussed here. This article provides a framework for understanding the significance of these future discoveries. Scientists working within this field have learned to be comfortable with ambiguity and accept that our models are provisional, subject to revision in light of changing evidence. With new tools for DNA analysis and new questions to ask of the data, the future is exciting for studies of the First Peoples and how they triumphed on this last, arduous leg of our species' millennia-long march across the globe.

This article was originally published with the title "Journey into the Americas" in Scientific American 324, 5, 26-33 (May 2021)
doi:10.1038/scientificamerican0521-26

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