REVIEW SUMMARY

ANTHROPOLOGY

Late Pleistocene exploration and settlement of the Americas by modern humans

Michael R. Waters

BACKGROUND: North and South America were the last continents populated by modern humans. The timing of their arrival, the routes they took, their homeland of origin, and how they explored and settled diverse environments filled with now-extinct animals have been debated for over a century. Addressing these questions is key to understanding the development of later prehistoric and contemporary Indigenous cultures.

ADVANCES: The study of the first Americans made slow but steady progress during the 20th century. The first half of the century brought the realization that people had entered the Americas at the end of the Pleistocene. The second half of the century brought the ability to radiocarbon date early sites and the belief that the ~13,000-year-old Clovis lanceolate fluted projectile points associated with mammoth remains represented the first people to enter the continent. This view began to change with the discovery of artifacts dating ~14.2 thousand years (ka) ago at the Monte Verde site in southern Chile. This discovery signaled that people must have been in the Americas before Clovis and that early sites should be present in other parts of the Americas. Initially, many sites proposed to predate Clovis did not stand up to scrutiny, having issues with geological context, dating, or even the archaeological evidence itself. However, the last 30 years have seen an increasing number of sites providing evidence of early occupation that cannot be dismissed. These sites show that people were present and successfully occupying different areas of North and South America between ~15.5 and ~14 ka ago, thereby leading the way to a new understanding of the first Americans.

In the last 15 years, genetic information from contemporary Indigenous Americans and the remains of ancient individuals from Asia and the Americas has transformed our understanding of the ancestry of the first Americans. Genetic studies first concentrated on the analysis of mitochondrial DNA, but in the last decade, technological breakthroughs have permitted the reconstruction of prehistoric genomes. These genomic studies have conclusively shown that the first Americans were the result of ancestral east Asian and northern Eurasian admixture. This founder population made its way to eastern Beringia and after additional population splits traveled south of the continental ice sheets covering Canada sometime between ~17.5 and ~14.6 ka ago. These genetic results agree with the emerging late Pleistocene archaeological record.

OUTLOOK: The key to learning more about the first Americans is investigating archaeological sites with solid geological contexts that are accurately dated. Only rigorously investigated sites using the best practices of archeology, geoarchaeology, and geochronology will provide the primary and pivotal data to interpret the past. Analysis of biomolecules, including DNA, proteins, and lipids from these sites, will enhance environmental reconstructions and archaeological interpretations. This will require time and patience because building archaeological knowledge is a slow process. Genetics is a powerful new tool that has already broadly deciphered the origins and population history of the first Americans. Although the general outline of the ancestry of the Indigenous American genome will likely remain unchanged moving forward, recent genetic studies show even greater genetic complexity during the peopling process, especially once people were south of the ice sheets, and this story will surely change dramatically and quickly with the generation of additional genomes. The ancestral history of the earliest peoples in the Americas will be realized as genetic knowledge from living populations and ancient individuals is combined with archaeological, geological, ethnographic, and oral records. This will require scientists and Indigenous peoples working as partners to uncover the past. ■

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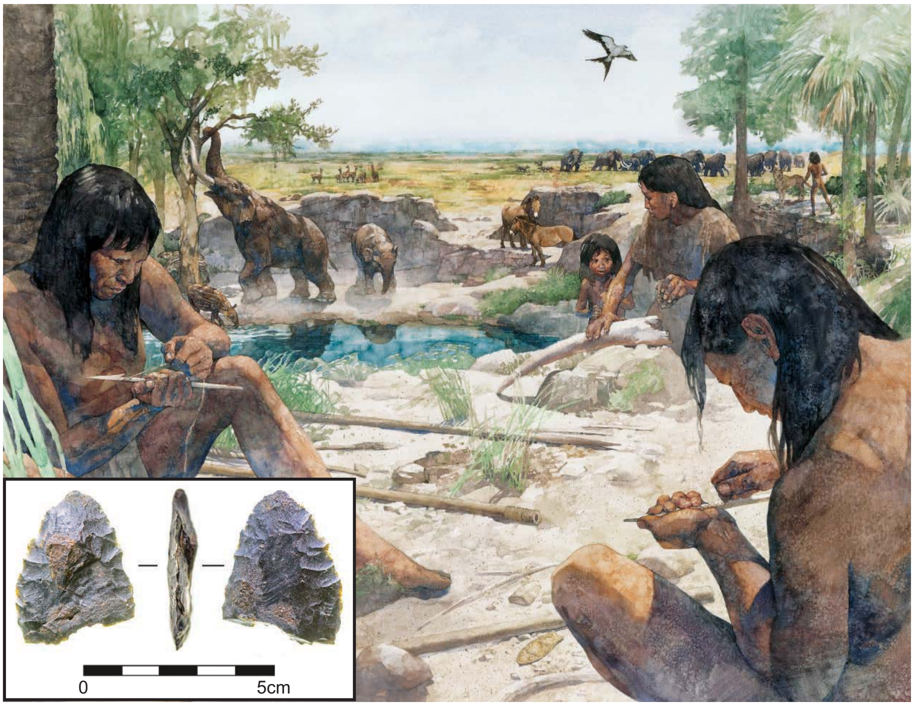

Page-Ladson site, Florida, ~14,550 years ago. Page-Ladson is the oldest radiocarbon-dated site in North America with artifacts of the first Americans, including a bifacial knife (inset), found among the bones of extinct animals.

ART BY GREGORY A. HARLIN, NATIONAL GEOGRAPHIC IMAGE COLLECTION

Email: mwaters@tamu.edu

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REVIEW

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Late Pleistocene exploration and settlement of the Americas by modern humans

Michael R. Waters

North and South America were the last continents to be explored and settled by modern humans at the end of the Pleistocene. Genetic data, derived from contemporary populations and ancient individuals, show that the first Americans originated from Asia and after several population splits moved south of the continental ice sheets that covered Canada sometime between ~17.5 and ~14.6 thousand years (ka) ago. Archaeological evidence shows that geographically dispersed populations lived successfully, using biface, blade, and osseous technologies, in multiple places in North and South America between ~15.5 and ~14 ka ago. Regional archaeological complexes emerged by at least ~13 ka ago in North America and ~12.9 ka ago in South America. Current genetic and archaeological data do not support an earlier (pre–17.5 ka ago) occupation of the Americas.

The discovery of Folsom projectile points with extinct bison and Clovis artifacts with mammoth remains in New Mexico, in the first half of the 20th century, established that people had entered the Americas at the end of the Pleistocene (*1*). Since then, more Clovis sites were found and investigated, radiocarbon dating placed these sites between ~13 and ~12.7 thousand years (ka) ago, and Clovis became accepted as the oldest occupation in the Americas. For decades, archaeological sites proposed to predate ~13 ka ago were rejected because they lacked artifacts, geological context, or secure dates—or had a combination of these problems (*2*). However, over the past 30 years, archaeological investigations in both North and South America revealed occupations predating Clovis that could not be dismissed (*1*, *3*–*5*). In tandem with these archaeological discoveries, genetic studies of contemporary Indigenous Americans and prehistoric individuals provided new perspectives on the origin and population history of the first Americans (*6*). Together, archaeology and genetics are telling a coherent, but complex, story of the first people to enter, explore, and settle the Americas.

Genetic history of the first Americans

Genetic studies of contemporary Indigenous people and ancient individuals from Asia and the Americas reveal an outline of the ancestry of the first humans to settle the Americas, providing age estimates for the timing of population contact, divergence, and migration. Studies of contemporary mitochondrial DNA (mtDNA) and Y-chromosome DNA lineages gave the first genetic insights into Indigenous American population history (*6*). These studies demonstrated that the ancestors of all contemporary Indigenous people had descended from only five maternal lineages (haplogroups A, B, C, D, and X) and two paternal lineages (haplogroups C and Q). These lineages also showed that the founding population came from Asia and experienced a severe genetic bottleneck, in which a small number of people with limited genetic diversity gave rise to all Indigenous people who occupied the continent before European arrival. Further, mtDNA analyses suggested that the source population from which the first Americans were derived had been isolated from Asian lineages, most likely in eastern Beringia, before they dispersed south. After this "Beringian Standstill" (*6*), a small group fissioned from this isolated source population, traveled south of the continental ice sheets that covered most of Canada, and explored and successfully populated North, Central, and South America.

Analysis of the genomes of contemporary Indigenous populations and ancient human remains has built on this framework to provide a deeper understanding of the first American ancestry (*6*–*13*). These genomes show that the ancestral Indigenous American population emerged in Eurasia, descending from a single founding group that split from ancestral East Asians ~36 ka ago, but maintained a high level of gene flow with East Asians until at least ~25 ka ago. This ancestral population also received gene flow from ancient Siberian populations with northern Eurasian ancestry (Mal'ta) until ~25 to ~20 ka ago. Afterward, the ancestral Indigenous American population became isolated from external gene flow.

Sometime between ~22 and ~18.1 ka ago, Ancient Beringians (AB) branched from the ancestral Indigenous Americans, but both populations maintained gene flow between them until at least ~11.5 ka ago, which suggests their close geographic proximity (*11*). This branching took place in either eastern Eurasia or Beringia (*11*). If the split occurred in eastern Eurasia, then these two lineages would have moved together or sequentially into eastern Beringia as weakly structured populations (Fig. 1, A and B), maintaining gene flow between themselves but not with Asian and Siberian populations. Alternatively, the ancestral Indigenous American population could have entered eastern Beringia and then AB emerged (Fig. 1, C and D), ensuring gene flow between them but isolation from Asian or Siberian populations.

Sometime between ~17.5 and ~14.6 ka ago, groups from the ancestral Indigenous American population split into two branches: Northern Native Americans (NNA) and Southern Native Americans (SNA) (*9*, *11*). The location of the divergence of the NNA and SNA branches from the ancestral Indigenous American population most likely occurred either while the groups were migrating south from Beringia or after they had entered unglaciated North America (Fig. 1, A and C) (*9*, *11*, *13*). This is based on the fact that AB do not belong to either the NNA or SNA branches and are equally related to both, and because there was no gene flow between AB and the SNA and NNA populations. Alternatively, the two branches may have diverged in eastern Beringia and then these groups migrated south, but this would have required strong population structure for thousands of years to prevent gene flow among the ancestral Indigenous Americans, AB, and the NNA and SNA groups while in eastern Beringia (Fig. 1, C and D).

The Americas were populated by members of the SNA and NNA branches. These branches emerged sometime between ~17.5 and ~14.6 ka ago, placing a maximum limiting age on the peopling of the unglaciated lands south of the ice sheets. Analysis of mitogenomes places the arrival of humans into unglaciated America at ~16 ka ago (*14*), and Y-chromosome estimates place their arrival sometime between ~19.5 and ~15.2 ka ago (*15*). Genetic analysis of the evolutionary history of dogs, which accompanied the first Americans on their journey from Eurasia to the Americas, provides additional insights about the timing of the arrival of the first Americans (*16*). The dogs that traveled with the first Americans originated in Siberia and split from Siberian dogs sometime between ~17.65 and ~13.7 ka ago. These "precontact" American dogs were south of the ice sheets by sometime between ~16.5 and ~13 ka ago.

Once south of the ice sheets, the NNA branch became geographically restricted to northern North America, whereas most of unglaciated North and South America was peopled by multiple groups of the SNA branch (Fig. 1E) (*9*, *12*, *17*). The earliest SNA individuals, Anzick-1 (12.85 ± 0.05 ka), Spirit Cave (10.95 ± 0.2 ka), and Lagoa Santa (10.4 ± 0.1 ka), have a close genetic relationship and form a clade (*12*). Analysis shows that the common ancestor of Anzick-1 and Spirit

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Center for the Study of the First Americans, Department of Anthropology, Texas A&M University, College Station, TX 77843, USA.
Email: mwaters@tamu.edu

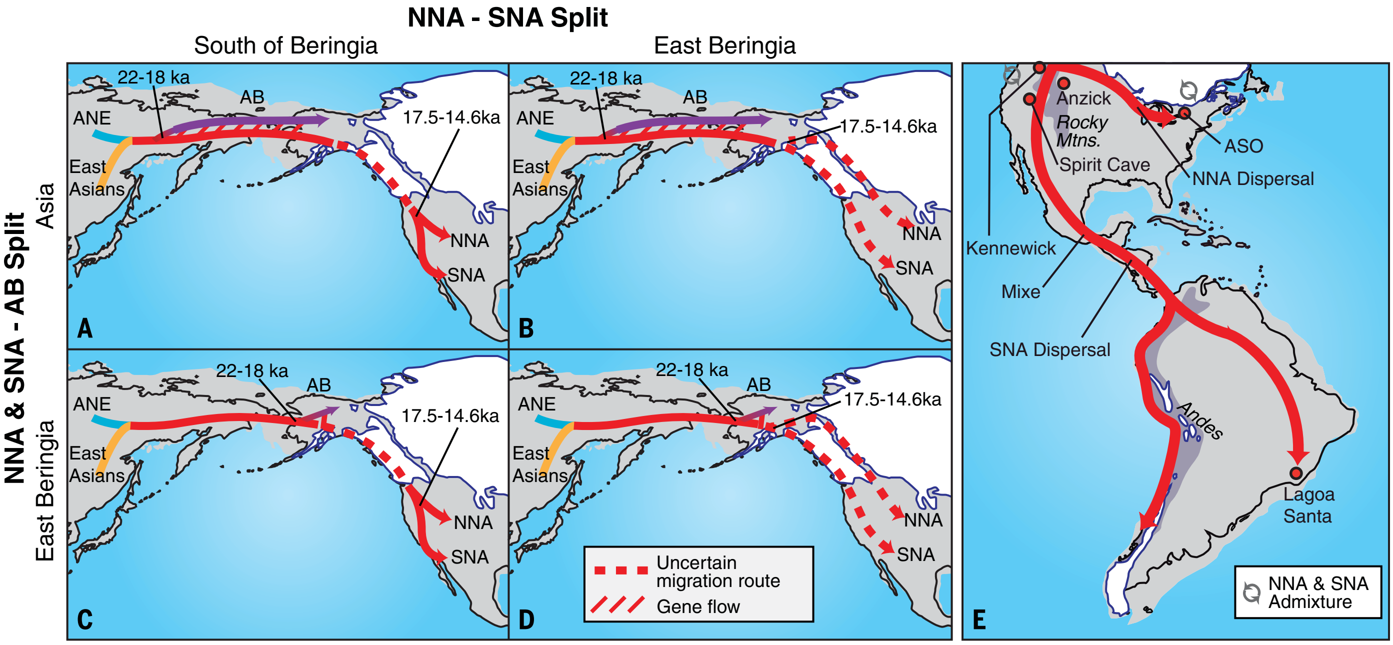


Fig. 1. Maps showing the genetic ancestry of the Indigenous American genome. (**A** to **D**) General population history and the possible locations where population splits and interactions took place. (**E**) Human dispersal, divergence, and contacts within the Americas and the location of important prehistoric genomes. ANE, Ancient Northern Eurasians; ASO, Ancient Southwestern Ontario populations (Algonquians). [Modified from (*11*) with permission]

Cave diverged from the common ancestor of Lagoa Santa and contemporary Central American Mixe sometime between ~14.9 and 13.2 ka ago, and that the Lagoa Santa population diverged from Mixe sometime between ~14.8 and 12.8 ka ago, suggesting that the movement of people from North to South America took hundreds or a few thousand years. Population expansion after the initial entry into the Americas is documented by the rapid radiation of Y-chromosome haplogroup Q-M848 within Q-M3 sometime between ~16.9 and ~13.2 ka ago (*15*). Analysis of genetic variation across South America shows that when early hunter-gatherers reached the northern edge of South America, they advanced southward along two main routes: the Atlantic and Pacific coasts (*12*, *17*, *18*). Contemporary and ancient mitogenomes from the western Andes detected subhaplogroups that originated in South America between ~15.7 and ~13.5 ka ago after initial entry into this region (*19*). Geographic clustering of individual male sublineages of haplogroup Q-M848 in South America suggests that population structure emerged between ~13.9 and ~10.8 ka ago (*15*). In North America, gene flow between the NNA and SNA groups occurred before ~9 ka ago, as documented in the genomes of Kennewick man and ancient Algonquians (Fig. 1E) (*10*, *12*, *13*). The peopling of South America is further complicated by the later entry of SNA groups without Anzick-1 lineage (*17*).

Ancient genomes also reveal several poorly understood population connections. The Lagoa Santa individuals and some contemporary Amazonian tribes share a subtle genetic connection with Indigenous New Guineans, Australians, and Andaman Islanders (*6*, *8*, *12*, *20*). This signal appears to be derived from an extinct ancient ancestor of both groups (Population Y), but does not represent a migration of a group of Australasian ancestors to the Americas (*20*). The contemporary Mixe population carries a distinctive genetic legacy from an outgroup called "Unsampled Population A," which is neither AB, NNA, nor SNA and split from the ancestral Indigenous American population sometime between ~30 and ~22 ka ago in Beringia and mixed with the Mixe population during the early Holocene (*12*). The ~5600-year-old Big Bar remains from British Columbia represent a previously undetected outgroup that split from the ancestral Indigenous American population in Beringia after AB diverged, but before the NNA–SNA split (*12*). These findings show that the Late Pleistocene Beringian population was not homogeneous and even suggests genetic structure between groups in Beringia, perhaps because they were widely dispersed.

Genetic studies conclusively show that the first Americans did not originate from Europe (*9*, *21*) as posited by the Solutrean hypothesis (*22*, *23*). Genetic evidence also does not support a successful occupation of the Americas before ~17.5 ka ago (*11*). Although genetic studies have painted a broad outline of the genetic ancestry of the first Americans, these studies do not provide a clear picture of where population events occurred and provide only broad estimates for the timing of these events. In addition, genetic populations do not equate with archaeologically defined cultures and artifact complexes. Genetically derived interpretations must be understood in the context of Late Pleistocene geographic barriers to human migration and the archaeological evidence left by the earliest Americans.

Late Pleistocene archaeology of Beringia

Yana RHS, in the Siberian Arctic, is the oldest archaeological site in western Beringia (Fig. 2A) (*24*). This ~32,000-year-old site contains an elaborate osseous technology with utilitarian and symbolic artifacts, along with a simple lithic flake-core technology. Although Yana is important to the peopling of Siberia, genomic analysis of human teeth (*25*) reveals that the people of Yana were not directly involved in the peopling of the Americas.

Two sites suggest an early human presence in eastern Beringia. From Lake E5 in northern Alaska (Fig. 2A), human fecal biomarkers found in lacustrine sediments suggest human occupation of the region since ~32 ka ago (*26*). Cutmarks on 15 animal bones dated from ~24 to ~15 ka ago at Bluefish Caves in the Yukon are believed to be the result of human activity (Fig. 2A) (*27*). The absence of stone tools, alternative natural taphonomic explanations for the bone modification, and site formation issues render the evidence from these sites equivocal (*28*).

The first unequivocal evidence of humans in eastern Beringia appears at Swan Point in central Alaska (Fig. 2A). Here, Yubetsu-style wedge-shaped microblade cores were used to make small blades that were inset into osseous projectile points 14.15 ± 0.15 ka ago (Fig. 2E) (*29*). This microblade technology is derived from the Siberian Diuktai culture of central Siberia, which

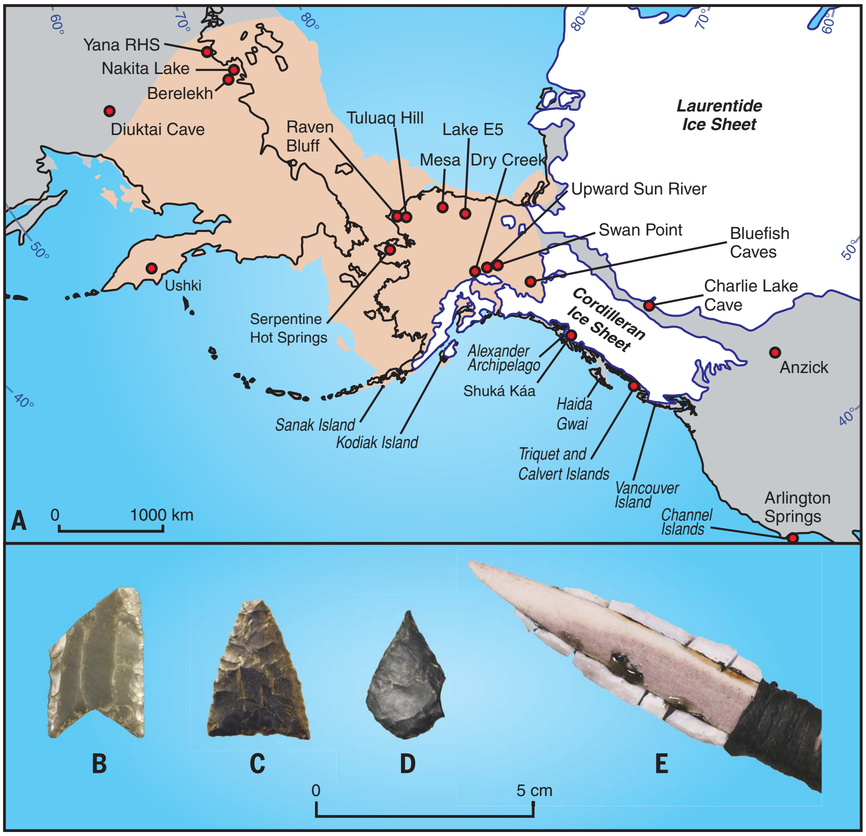


Fig. 2. Map of Beringia and artifacts. (**A**) Map showing Beringia (brown), Laurentide and Cordilleran ice sheets (white), the ice-free corridor between the ice sheets, the Pacific coastal route, and the location of key archaeological and geological sites. Diuktai Cave lies in the core area of the Diuktai culture. Alaskan fluted points were found in dated geological contexts at Serpentine Hot Springs and Raven Bluff. The oldest Sluiceway points are from Tuluaq Hill; Mesa points were defined at the Mesa site. Dry Creek is the type site for the Nenana complex. (**B**) Base of fluted projectile point. (**C** and **D**) Projectile points of the Nenana complex. (**E**) Reconstruction of osseous projectile point with inset microblades.

dates from ~18 to ~12.6 ka ago (29, 30) and is found is western Beringia (31).

Starting ~13.8 ka ago, an assemblage characterized by small triangular or teardrop-shaped Chindadn bifacial projectile points (Fig. 2C and 2D), blade and flake cores, gravers, and unifacial tools, but without microblades and wedge-shaped microblade cores (30, 31), is present in both western and eastern Beringia. This technology appears in Siberia at Berelekh at 13.8 ± 0.2 ka ago and at Nakita Lake at 13.7 ± 0.1 ka ago (Fig. 2A) (31, 32). In Alaska, this assemblage defines the Nenana complex, which ranges from at least ~13.5 to ~12.7 ka ago (30). Sites with microblade technology, burins, and lanceolate bifacial points reappear ~12.5 ka ago. These Denali complex sites are found over large areas of eastern Beringia and with counterparts in western Beringia (11, 30) and are genetically associated with the AB population at the Upward Sun site in Alaska (11).

Across the northern portion of eastern Beringia, the earliest site assemblages are dominated by distinctive lanceolate bifacial projectile points that define the Sluiceway, Mesa, and fluted-point complexes, which together define the Northern Paleoindian tradition (33). Sluiceway projectile points are large, lanceolate forms with convex bases that first appear ~13 ka ago at Tuluaq Hill, Alaska (Fig. 2A), and continued to be made until ~11 ka ago. Mesa projectile points are thick, lanceolate points with a shallow concave base that date from ~12.4 to ~10.9 ka ago. Lanceolate fluted projectile points have deep concave bases with multiple basal flutes and date from ~12.4 to ~12.0 ka ago (Fig. 2B) at the Serpentine Hot Springs and Raven Bluff sites in Alaska (Fig. 2A) (34). No counterparts to these complexes occur in western Beringia. Instead, at ~13.1 ka ago, small-stemmed projectile points were being made in Kamchatka at the Ushki Lake site (35). The Alaskan fluted points and Mesa points represent the later movement of this technology into Alaska from the North American plains (33, 34).

Routes to the south: Moving from Beringia to the unglaciated Americas

The Laurentide and Cordilleran ice sheets reached their maximum extent during the Last Glacial Maximum (LGM, ~26 to ~19 ka ago) and blocked the movement of people from Beringia to unglaciated areas to the south (Figs. 2A and 3). This changed as temperatures rose at the end of the Pleistocene, causing ice margins to melt and create an inland "ice-free" corridor and a Pacific coastal corridor along which humans could travel. Our knowledge about the opening of these corridors is incomplete, but current evidence provides a rough picture of the timing of their development.

The ice-free corridor was open and animals were traversing this passageway by ~13 ka ago. The presence of bison, from a genetically distinct population that developed north of the ice sheets during the LGM, in the central corridor at 13.15 ± 0.15 ka ago and in Edmonton at ~13 ka ago shows that the entire corridor was open by this time (36). Osseous artifacts made of elk at the Anzick site in Montana indicated that elk were present in the northern plains by 12.85 ± 0.05 ka ago (9, 37). Further, shortly after ~13 ka ago, Lake Agassiz was draining northward through the corridor and into the Mackenzie River valley (38). When the entire 2000-km-long corridor initially opened remains uncertain. Cosmogenic ^{10}Be dating of glacial erratics along a 500-km length of the southernmost portion of the interior corridor shows that the Laurentide ice sheet rapidly decoupled from the Cordilleran ice sheet by 14.9 ± 0.9 ka ago (39), placing a maximum limiting age on the opening of the corridor (Fig. 3). Luminescence ages on sand dunes occupying recently deglaciated areas show subsequent rapid retreat of the Laurentide ice margin in the central portion of the corridor (40), coincident with Bølling-Allerød warming from ~14.6 to ~12.9 ka ago (Fig. 3). Age estimates for the opening of the corridor based on the analysis of lake sediments in the Glacial Lake Peace region (41) provide underestimates for the opening of the corridor (42). Erroneous radiocarbon ages from the central portion of the corridor (43) provide overestimates for the opening of the corridor (42). The oldest human presence in the central segment of the corridor is documented at Charlie Lake Cave, where stone tools, including a fluted point, are associated with bison radiocarbon dated to 12.35 ± 0.5 ka ago (Fig. 2A) (44).

The opening of a passage along the Pacific coast is tied to the recessional history of the Cordilleran ice sheet that exposed the continental shelf and extant islands. Paleotemperature proxies from marine sediment cores in the Gulf of Alaska and western British Columbia show that the Cordilleran ice margin began retreating by ~17 ka ago (45). In the Gulf of Alaska, radiocarbon ages from terrestrial records show that Sanak Island was ice free by 15.65 ± 0.25 ka ago and Kodiak Island by 15.95 ± 0.15 ka ago (Fig. 2A) (46). Cosmogenic ^{10}Be ages show that the western margin of the islands of the Alexander Archipelago were free of ice by 17.0 ± 0.7 ka ago (Figs. 2A and 3) (45). Radiocarbon ages on carnivore and ringed seal bones from Shuká Káa Cave on Prince of Wales Island suggest that terrestrial and marine ecosystems were reestablished by 17.2 ± 0.6 ka ago (45). Along the British

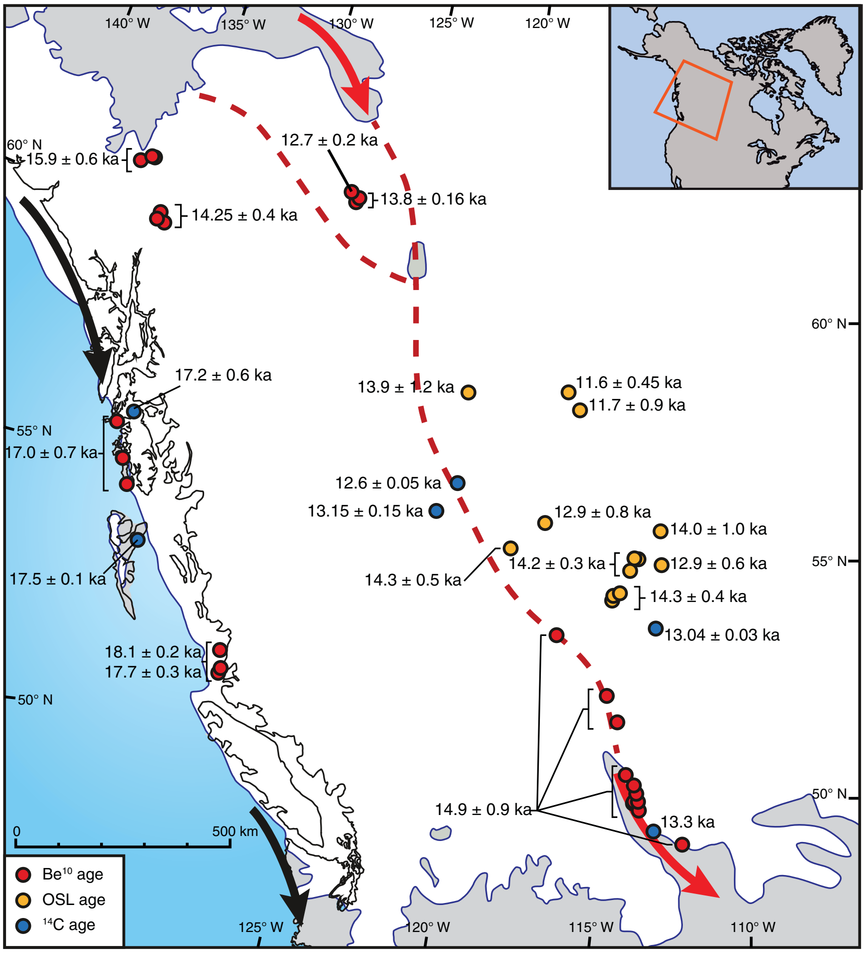


Fig. 3. Map of key dated localities along the inland and coastal corridors. Inland corridor is shown in red and the coastal corridor in black. [Modified from (*42*) with permission]

Columbia coast, the continental shelf between Haida Gwaii and the mainland was ice free and vegetated by 17.5 ± 0.1 ka ago (Fig. 2A) (*47*). Cosmogenic ^{10}Be ages on erratics, bedrock, and moraines show that ice receded from different parts of Calvert Island by 18.1 ± 0.2 and 17.7 ± 0.3 ka ago (Fig. 3) (*48*).

These studies indicate that a coastal route, free of barriers and biologically productive, was minimally available by ~16 ka ago (*45*, *48*). It is hypothesized that a coastal kelp forest existed from Asia to the Americas during the Late Pleistocene and that people moved along this resource-rich "kelp highway" (*49*) using watercraft, but no evidence of Late Pleistocene boat use has yet been found in the archaeological record of the Americas. The earliest inferential evidence of the use of boats comes from the 12,800 ± 100-year-old Arlington Springs human remains on the Channel Islands in California (Fig. 2A) (*50*), because a watercraft would have been necessary to cross the ~8 km of ocean separating the island and the mainland. Alternatively, people may have traversed the northern Pacific coast on foot, subsisting on salmonids along their travels south and using simple watercraft to traverse waterways and other obstacles (*51*, *52*). The earliest radiocarbon-dated sites along the coastal corridor include ~12,600-year-old human footprints and stone artifacts from EjTa-4 on Calvert Island in British Columbia (Fig. 2A), and evidence of ~12,600 to ~12,500-year-old bear hunting at K1 Cave and Gaadu Din 1 Cave on Haida Gwaii (Fig. 2A) (*53*, *54*).

Late Pleistocene archaeology south of the ice sheets

In North and South America, a number of sites dating between ~15.5 and ~13.3 ka ago provide evidence of the first human presence south of the ice sheets (Fig. 4). At these sites, artifacts are found in undisturbed geological contexts that are well dated.

Near the southern margin of the Laurentide ice sheet, at the Hebior site in Wisconsin, four lithic artifacts, including two bifaces, were found among the disarticulated bones of a mammoth in pond clays dating to 14.85 ± 0.15 ka ago (*55*). Also in Wisconsin, the disarticulated remains of another mammoth are associated with two lithic artifacts in pond clays at the Schaefer site that date to 14.65 ± 0.15 ka ago (*56*). Seven butchered horses and one butchered camel were recovered from eolian sediments at the Wally's Beach site in Alberta, Canada. Core and flake tools are associated with these carcasses, which date to 13.3 ± 0.02 ka ago (*57*).

Along the Gulf of Mexico, the Page-Ladson site is buried under 4 m of sediment and is submerged in a midchannel sinkhole along a segment of the Aucilla River in Florida (*58*, *59*). Here, lithic artifacts, including a biface (Fig. 4), are associated with a human-modified mastodon tusk. Seventy-one radiocarbon dates show that these artifacts and modified tusk are ~14,550 years old (*59*).

In the northwest continental United States, five 14,150 ± 50-year-old human coprolites, yielding mtDNA belonging to Indigenous American haplogroups A and B, were recovered from well-stratified and dated deposits at Paisley Caves in Oregon (*60*, *61*). Associated with the coprolites are stone tools and debitage. At the Manis site in Washington, a disarticulated mastodon skeleton was found in pond sediments. The tip of a bone projectile point is embedded into a rib of this animal and dates to 13.77 ± 0.02 ka ago (*62*).

Along Buttermilk Creek in central Texas at the Debra L. Friedkin and Gault sites, stone tools occur beneath layers with Late Prehistoric, Archaic, Late Paleoindian, Folsom, and Clovis artifacts (*63*–*66*). At the Friedkin site, these early artifacts include blades, bladelets, scrapers, bifacial discoidal cores, snap-fracture tools, retouched flakes, expedient tools, ground hematite, 11 complete and fragmentary lanceolate stemmed projectile points, and a triangular lanceolate projectile point with a basally thinned concave base (Fig. 4), along with ~100,000 pieces of debitage. This assemblage occurs in deposits dated between ~15.5 and ~13.5 ka ago by 71 optically stimulated luminescence (OSL) ages (*63*, *64*). At the Gault site, five stemmed and two concave base projectile points (Fig. 4) were dated using the OSL method to ~16 ka ago (*65*, *66*), along with bifaces, blades, blade cores, scrapers, gravers, and other tools and ~150,000 pieces of debitage. Points similar to those from central Texas were excavated from lacustrine deposits associated with mammoth skeletons at the Santa Isabel Iztapan I and II sites in Mexico, which are bracketed by ~14,500- and ~10,800-year-old tephras (Fig. 4) (*67*, *68*).

Along the Pacific coast of South America, at Monte Verde II in southern Chile, structural foundations, hearths, wooden tools, lithic artifacts including bipointed El Jobo projectile points (Fig. 4), bolo stones, medical and edible plants, and animal bones and hides were found on a discrete buried surface (*69*). Radiocarbon ages from hearths within two of the structures date to 14.2 ± 0.1 ka ago (*70*). At the Huaca Prieta site in Peru, 42 artifacts including debitage and edge-retouched flakes and cobbles were buried within multiple discrete layers of alluvium dated from 14.15 ± 0.05 to 13.35 ± 0.05 ka ago (*71*).

The evidence from most of these sites has been criticized (*28*, *72*, *73*). However, the questions raised about each site have been addressed with new data to provide secure evidence that people were in the Americas by ~15 ka ago. Compelling but equivocal evidence of early occupation comes

Fig. 4. Map of key ~15,500- to ~13,300-year-old archaeological sites in the Americas. Diagnostic projectile points and bifaces associated with sites are shown. Rocky Mountains and Andes Mountains are shown in purple. [Modified from (64, 102) with permission]

from Meadowcroft Rockshelter in Pennsylvania and from Arroyo Seco 2 in Argentina (Fig. 4). At Meadowcroft Rockshelter, ~700 artifacts from Stratum IIa, including the lanceolate Miller projectile point, may date between ~15 and ~14 ka ago (74), but the site remains equivocal because of concerns about the early radiocarbon ages from the site (28, 72, 73, 75). Horse and sloth remains associated with lithic artifacts at Arroyo Seco 2 in Argentina suggest repeated episodes of megafauna processing from ~14 to ~13 ka ago (76), but more information about the geological context and site formation processes is needed to make a full evaluation.

Starting ~13 ka ago, the first regional archaeological complexes in North America emerged, the Clovis complex and Western Stemmed Point Tradition (Fig. 5). Clovis is identified by its distinctive biface, blade, and osseous technologies (77). The primary trajectory of biface manufacture is the production of lanceolate, concave base, fluted projectile points (Fig. 5), but also large ovate bifaces that were used as knives or cores. Blades were made from prepared cores and used without modification or were made into end scrapers, knives, gravers, and other tools. Osseous technology includes the use of antler, bone, and ivory to make projectile points, needles, foreshafts for the hafting of stone points, and other tools.

Clovis artifacts are found exclusively south of the continental ice sheets and do not occur in Asia or Beringia (Fig. 5) (77). The densest concentration of Clovis artifacts lies east of the Mississippi River, but these artifacts also occur in high frequencies west of the Mississippi River to the eastern edge of the Rocky Mountains and south into northern Mexico (77–79). Securely radiocarbon-dated Clovis sites range from ~13 to ~12.7 ka ago (37, 79). Two sites, Aubrey in Texas (80) and El Fin del Mundo in Mexico (81), may indicate that Clovis extends to ~13.3 to ~13.4 ka ago; however, the three radiocarbon ages from these sites are problematic (4, 79). If accurate, though, these sites would indicate that the oldest Clovis sites occur in the southernmost portion of the Clovis range. West of the Rocky Mountains, Clovis artifacts are sparse and have been dated only in Arizona to 12.75 ± 0.05 ka ago (79). More abundant in this region are "western-fluted" points, which are morphologically distinct from Clovis, have not been dated, and can cooccur with points of the Western Stemmed Tradition (82–84). Clovis artifacts are absent from the Pacific coast (77, 82, 83) and are also not found in Central or South America (78, 85).

In the Intermountain West, the Western Stemmed Tradition, characterized by lanceolate points with basal stems, dominates the Paleoindian record (Fig. 5) (82, 83). The lithic technology associated with the Western Stemmed Tradition is distinct and appears not to have been derived from Clovis (64, 82–84, 86). The earliest directly dated stemmed points occur at Paisley Caves in Oregon and are minimally dated ~13 to ~12.7 ka ago (86). No points are associated with the ~14,200-year-old occupation at Paisley Caves (60, 61), but the lithic technology represented by the oldest artifacts compares favorably to the Western Stemmed Tradition. At Cooper's Ferry in Idaho, stemmed points are dated to ~13.2 ka ago and possibly earlier (87). At Bonneville Estates Rockshelter in Nevada, charcoal from a hearth in the deepest deposits yielded ages of 12.85 ± 0.05 ka ago (88). No diagnostic artifacts were found associated with this hearth, but the technology represented by the debitage is more consistent with the Western Stemmed Tradition than with Clovis. Together, this evidence shows that the Western Stemmed Tradition is contemporaneous with and perhaps older than Clovis.

In the southern cone of South America, distinctive Fishtail projectile points occur in sites dated between ~12.8 and ~12.2 ka ago (Fig. 5) (89–92). In the deepest layers at Cerro Tres Tatas, (90), Casa del Minero (4), and Piedra Museo (90), Argentina, lithic assemblages with cores, modified flake tools, bifacial knives, scrapers, and choppers without projectile points date to 12.85 ± 0.05 ka ago. At Santa Julia, Chile, a lithic assemblage that included a stemmed bifacial preform dates to 12.9 ± 0.08 ka ago (93). These early sites indicate a human presence coeval with Clovis and may indicate that Fishtail production began ~12.9 ka ago.

Fig. 5. Map of key 13,000- to 12,700-year-old archaeological sites in the Americas. The solid shaded areas in North America indicate the distribution of Clovis. Colors indicate high (brown), moderate (orange), and low (yellow) densities of Clovis artifacts. All radiocarbon-dated Clovis sites are labeled and shown with red dots. The proposed early Clovis sites, Aubrey and El Fin del Mundo, are shown by purple triangles. Hatched region designates the geographic extent of the Western Stemmed Tradition. Key Western Stemmed Tradition sites are indicated by green squares and are labeled. Dark green region in South America designates the highest density of Fishtail projectile points, which occur in lower frequencies in the light green shaded areas. Key Late Pleistocene sites and all dated Fishtail point sites are designated by yellow diamonds. Rocky Mountains and Andes Mountains are shown in purple. Also shown are typical Clovis, Western Stemmed Tradition, and Fishtail projectile points.

Fishtail points also occur in other parts of South America and into Central America (*78*, *85*).

A number of sites from North and South America are proposed to date from ~50 to ~17 ka ago, suggesting that humans entered the Americas before the LGM (*5*). The evidence from most of these sites is problematic, with issues related to geologic context, geochronology, or the absence of definitive human-made artifacts (*1*, *2*, *5*, *28*, *72*, *73*, *94*, *95*). The most promising older sites are the ~18,400- to ~17,100-year-old Cactus Hill site in Virginia (*96*) and the ~31,000- to ~25,000-year-old Miles Point site (*97*) and the >14,500-year-old Parson's Island site (*75*) on and near the Delmarva Peninsula (Fig. 4). At each site, artifacts occur in geologic contexts that may predate Clovis, but issues related to site formation and geochronology are unresolved (*5*, *28*, *72*, *73*).

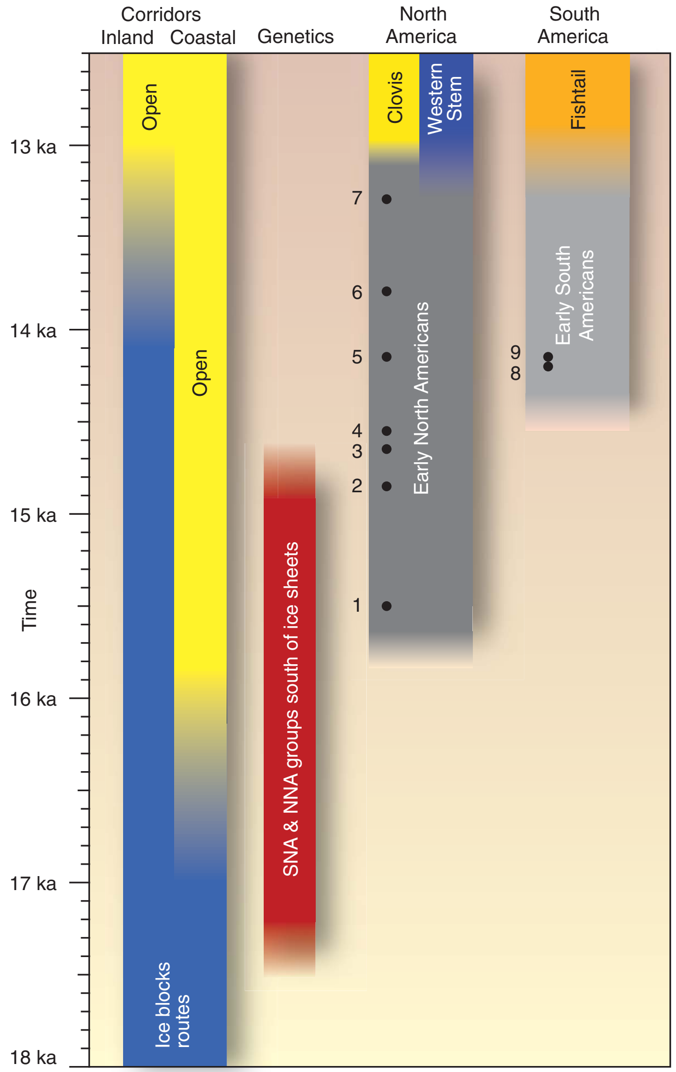
Several paleontological sites in North and South America dating from ~130 to ~13 ka ago with mammoth, mastodon, bison, or sloth remains are suggested to be archaeological sites (e.g., *5*, *28*, *72*, *95*, *98*–*100*). Stone tools are absent from these localities, and the evidence of human activity is based entirely on bone breakage patterns, interpretation of surface marks on bones, and the spatial arrangement of the bones. These sites are equivocal because of the absence of stone tools and because cut marks, spiral fractures, and percussion marks on bone can be created by natural processes (*28*, *72*). Some of these localities may indeed be archaeological sites (*72*), but these sites will remain equivocal until a secure way is found to identify human interaction with carcasses where stone tools are absent.

Discussion

Archaeological and genetic evidence, independently derived using distinctly different methods, converges to tell a complementary story of the first people who explored and settled the Americas at the end of the Pleistocene (Fig. 6). This evidence, much of it obtained in the last few decades, has upended long-held beliefs about the Late Pleistocene peopling of the Americas. The archaeological evidence shows that geographically dispersed populations lived successfully and used biface, blade, and osseous technologies in multiple places in North America by ~15.5 ka ago, with the earliest artifacts appearing in South America by ~14.2 ka ago, documenting the initial arrival and movement of people across the continents of the Western Hemisphere (Fig. 6). In agreement, the genetic evidence indicates that people were south of the continental ice sheets sometime between ~17.5 and ~14.6 ka ago and also shows that there is biological continuity between the first Americans and all Indigenous people who followed (Fig. 6).

Genetic studies clearly show that eastern Asia was the homeland of the first Americans. It is there that we must look for the origins of the blade, biface, and osseous technologies documented in the ~15.5 to ~14 ka assemblages of the Americas. Although the Siberian Upper Paleolithic archaeological record shows clear linkages to later assemblages in eastern Beringia (*30*), Siberian linkages to the Late Pleistocene assemblages south of the ice sheets are less clear. Stronger connections to the earliest assemblages of North America may be found in other parts of Asia, such as Hokkaido, with its diverse Upper Paleolithic assemblages (*101*). Furthermore, the known eastern Beringian assemblages are younger than the earliest sites south of the ice sheets and may be more related to the settlement of eastern Beringia and unrelated to the earliest

Fig. 6. Relationship among geological, archaeological, and genetic data for the first Americans. Diagram shows time estimates for the opening of the inland and coastal routes from Beringia to the Americas, the maximum and minimum estimated time range when SNA and NNA populations entered the Americas, and the early archaeological record of North and South America. Black dots indicate the earliest archaeological sites in North and South America: 1, Debra L. Friedkin and Gault; 2, Hebior; 3, Schaefer; 4, Page-Ladson; 5, Paisley Caves; 6, Manis; 7, Wally's Beach; 8, Monte Verde; and 9, Huaca Prieta.



occupations south of the ice sheets (*52*). This suggests that older sites should occur in Alaska, as suggested by the fecal biomarkers from Lake E5 (*26*), or that the oldest sites are submerged in central Beringia or will be found in the uplifted areas of coastal Alaska and British Columbia (*53*, *54*).

Whereas both corridors into the Americas require more investigation, current evidence favors the Pacific coast as the route taken by the first Americans (Fig. 6). This is based entirely on chronological information showing the early opening of this corridor by ~16 ka ago, but archaeological evidence older than ~12.6 ka ago is absent. The ice-free corridor was definitely open by ~13 ka ago and bison and other animals were passing through it. The corridor may have been open by ~14 ka ago, but if it was, it is difficult to explain why bison waited 1000 years to traverse the corridor. More chronological information is needed from the interior corridor to determine when it unequivocally opened, and a search for early sites should be undertaken along both corridors.

The archaeological evidence from North America shows that regionally distinct assemblages, Clovis and the Western Stemmed Tradition, first appeared by ~13 ka ago as people adapted to rapidly changing climates and major floral and faunal reorganizations (Fig. 6). The origin and chronological and technological relationships between these complexes are unclear. Artifacts of Clovis and the Western Stemmed Tradition are technologically distinct, and it would be difficult to derive one from the other (*82*–*84*, *86*). Evidence from sites in the Intermountain West suggest that stemmed points may predate Clovis (*86*, *87*). Sites in Texas show that stemmed points have deep time depth in North America and may indeed be the earliest point style in North America brought by the first migrants (*64*, *66*). There is little doubt that Clovis originated south of the continental ice sheets by ~13 ka ago and we should look for the origins of Clovis in the biface, blade, and osseous technologies that make up the ~15,500- to ~14,000-year-old North American assemblages. There are hints of this transition at the Debra L. Friedkin and Gault sites in Texas (*64*, *66*). Stemmed points are present in the earliest assemblages of South America with the ~14,200-year-old stemmed El Jobo points at Monte Verde, Chile, followed by stemmed Fishtail points. The Fishtail complex of South America is minimally dated to ~12.8 ka ago and may date back to ~12.9 ka ago. It is undetermined whether this type was independently invented in South America from the earlier biface technology or if Fishtail points are descended from one or both North American point traditions.

The archaeological and genetic evidence shows that the peopling of the Americas was a complex process that we are only beginning to understand. For the rest of this century, we need to find and excavate sites of the first Americans in Beringia and across the Americas. Datable Late Pleistocene sites will be difficult to find because of issues of site preservation and visibility. Erosional processes have removed volumes of Late Pleistocene sediments from many locations and with it any potentially early sites. Deep burial hampers finding early sites, and sea-level rise has submerged the early archaeological record on the continental shelves. However, the known Late Pleistocene sites show that there are places where this record is preserved and accessible. When found, excavated, and properly dated, the archaeological data from these sites will provide the key empirical evidence needed to learn more about the first people to enter and settle the Americas. These sites will also yield the remains of ancient Americans. The genomes from these individuals, especially those tied to the archaeological record, will better define the movement of people across the landscape as they settled the Americas.

Finally, we must always remember that we are investigating the ancestors of contemporary Indigenous peoples and as such, we should strive to include Indigenous Americans in our studies as partners in our quest to uncover their past. Collaboration between scientists and Indigenous peoples will enrich our understanding of the story of the first Americans.

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Late Pleistocene exploration and settlement of the Americas by modern humans

Michael R. Waters

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How humans colonized the Americas

The arrival and spread of humans across the American continent is a research topic of abiding interest. Numerous archaeological finds in recent years have led to a reappraisal of the timing of the first occupations, before the Clovis culture of 13,000 years ago. Genetic research––especially genomic research over the past 5 years––also points to probable earlier dates for the founder populations that spread from Beringia ~15,000 years ago. Waters reviews these research advances and provides signposts to the promise of future genomic studies for enriching our knowledge of the ancestral history of humans in the Americas.

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