



The Late Pleistocene Dispersal of Modern Humans in the Americas

Ted Goebel, *et al.*
Science **319**, 1497 (2008);
DOI: 10.1126/science.1153569

The following resources related to this article are available online at www.sciencemag.org (this information is current as of August 22, 2008):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/cgi/content/full/319/5869/1497>

This article **cites 48 articles**, 9 of which can be accessed for free:

<http://www.sciencemag.org/cgi/content/full/319/5869/1497#otherarticles>

This article has been **cited by** 5 article(s) on the ISI Web of Science.

This article has been **cited by** 2 articles hosted by HighWire Press; see:

<http://www.sciencemag.org/cgi/content/full/319/5869/1497#otherarticles>

This article appears in the following **subject collections**:

Anthropology

<http://www.sciencemag.org/cgi/collection/anthro>

Information about obtaining **reprints** of this article or about obtaining **permission to reproduce this article** in whole or in part can be found at:

<http://www.sciencemag.org/about/permissions.dtl>

The Late Pleistocene Dispersal of Modern Humans in the Americas

Ted Goebel,^{1*} Michael R. Waters,² Dennis H. O'Rourke³

When did humans colonize the Americas? From where did they come and what routes did they take? These questions have gripped scientists for decades, but until recently answers have proven difficult to find. Current genetic evidence implies dispersal from a single Siberian population toward the Bering Land Bridge no earlier than about 30,000 years ago (and possibly after 22,000 years ago), then migration from Beringia to the Americas sometime after 16,500 years ago. The archaeological records of Siberia and Beringia generally support these findings, as do archaeological sites in North and South America dating to as early as 15,000 years ago. If this is the time of colonization, geological data from western Canada suggest that humans dispersed along the recently deglaciated Pacific coastline.

Explaining when and how early modern humans entered the New World and adapted to its varied environments is one of anthropology's most exciting and enduring questions. Until recently, it was generally believed that about 13.5 thousand years ago (ka) (1) the first migrants spread rapidly from Beringia to Tierra del Fuego in a few centuries, passing through an interior ice-free corridor in western Canada, becoming Clovis, and hunting to extinction the last of the New World's megamammals (2). Today, we realize that the peopling of the Americas was a much more complex process, because of two significant developments during the past decade. Molecular geneticists, using refined methods and an ever-increasing sample of living populations and ancient remains, are now capable of providing reliable information on the Old World origins of the first Americans, the timing of their initial migration to the New World, and the number of major dispersal events. Archaeologists have found new sites and reinvestigated old ones using new methods, to test whether a pre-13.5-ka population existed in North and South America, and to explain how early populations colonized its unpeopled landscapes (Fig. 1). Here, we review these developments and present a working model explaining the dispersal of modern humans across the New World. We focus primarily on molecular genetic, archaeological, and human skeletal evidence. We do not review the contributions of historical linguistics, because most linguists today are pessimistic about the use of their data

to reconstruct population histories beyond about 8 ka (3).

The Genetic Evidence

All human skeletal remains from the Americas are anatomically modern *Homo sapiens*; thus, the peopling of the New World is best understood in the context of the evolution and dispersal of modern humans in the Old World. Modern human dispersal from Africa across Eurasia began by about 50 ka (4, 5) and culminated with colonization of the Americas. Evidence from nuclear gene markers, mitochondrial (mt)DNA, and Y chromosomes indicates that all Native Americans came from Asia (6, 7). Molecular genetic diversity among modern Native Americans fits within five mtDNA (A, B, C, D, and X) and two Y-chromosome (C and Q) founding haplogroups, and all of these are found among indigenous populations of southern Siberia, from the Altai to Amur regions (8–10). Of these haplogroups, only X is known from both central Asia and Europe; however, X is a large, diverse haplogroup with many lineages, and the lineage found in Native American populations is distinct from those in Eurasia (6, 11). Ancient DNA from early American skeletal remains (12, 13) and human coprolites (14) link the present and the past; these, too, have only yielded Native American haplogroups of Asian origin. Based on the modern and ancient DNA records, then, Asia was the homeland of the first Americans, not Europe, lending no support to the recently proposed "Solutrean hypothesis," that the progenitors of Clovis were derived from an Upper Paleolithic population on the Iberian Peninsula (15, 16).

Using contemporary mtDNA and Y-chromosome variation as a clock, geneticists calculate that modern humans dispersed into greater central Asia by 40 ka (4, 17, 18), setting the stage for the colonization of the Americas. Corroborating human skeletal evidence of this event, however, is scarce. The earliest modern human remains in

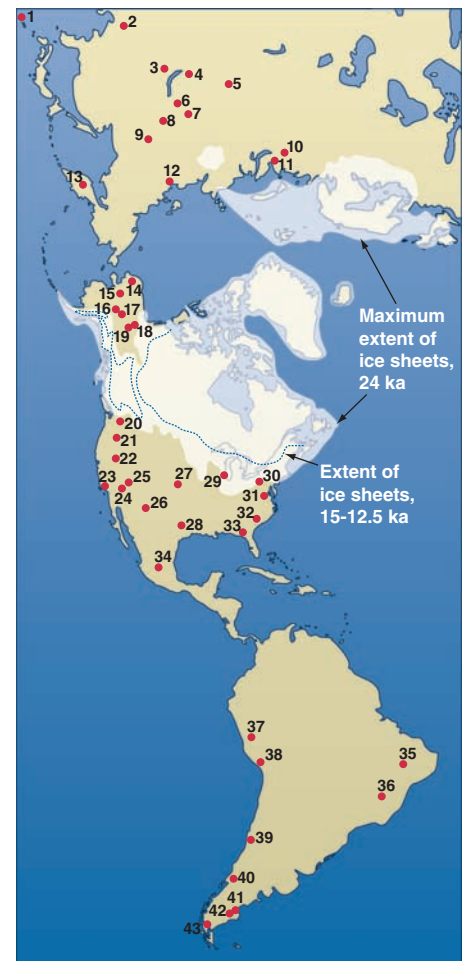


Fig. 1. Map showing location of archaeological sites mentioned in text (1, Yamashita-cho; 2, Tianyuan Cave; 3, Studenoe-2; 4, Mal'ta; 5, Nizhniy Idzhir; 6, Alekseevsk; 7, Nepa-1; 8, Khaergas Cave; 9, Diuktai Cave; 10, Byzovaia; 11, Mamontovaya Kurya; 12, Yana RHS; 13, Ushki; 14, Tuluq; 15, Nogahabara I; 16, Nenana; 17, Swan Point; 18, Old Crow; 19, Bluefish Caves; 20, Kennewick; 21, Paisley Caves; 22, Spirit Cave; 23, Arlington Springs; 24, Calico; 25, Tule Spring; 26, Pendejo Cave; 27, La Sena and Lovewell; 28, Gault; 29, Schaefer, Hebior, and Mud Lake; 30, Meadowcroft Rockshelter; 31, Cactus Hill; 32, Topper; 33, Page-Ladson; 34, Tlapacoya; 35, Pedra Furada; 36, Lagoa Santa; 37, Pikimachay; 38, Quebrada Jaguay; 39, Quebrada Santa Julia; 40, Monte Verde; 41, Piedra Museo; 42, Cerro Tres Tatas and Cuevo Casa del Minero; 43, Fell's Cave).

Siberia are from Mal'ta and date to only 24 ka (19). In nearby eastern Asia, though, modern human fossils from Tianyuan Cave and Yamashita-cho are dated to the critical period, 39 to 36 ka (20), and in Siberia, archaeological evidence suggests that modern humans entered the region by 45 to 40 ka, when initial Upper Paleolithic technologies, tool forms, items of personal adornment, and art appeared for the first time (21). In Europe, archaeologists link the emergence of such behaviors to the spread of modern humans from southwestern Asia (22).

¹Center for the Study of the First Americans, Department of Anthropology, Texas A&M University, 4352 TAMU, College Station, TX 77843–4352, USA. ²Center for the Study of the First Americans, Departments of Anthropology and Geography, Texas A&M University, 4352 TAMU, College Station, TX 77843–4352, USA. ³Department of Anthropology, University of Utah, Salt Lake City, UT 84122–0060, USA.

*To whom correspondence should be addressed. E-mail: goebel@tamu.edu

Establishing when central Asian and Native American haplogroup lineages last shared a common ancestor has proven to be difficult. Current coalescent estimates based on variation in extant mtDNA lineages set the event at 25 to 20 ka (4) or less than 20 ka (23), after the last glacial maximum (LGM), and estimates based on Y-chromosome variability suggest that divergence occurred after 22.5 ka, possibly as late as 20 to 15 ka (7, 24, 25). The differences in calculations are the result of several issues, including potential variation in mutation rates, variable and sometimes circular techniques of calibrating coalescent times to calendar years, time-dependency of mutation and/or substitution rates, and effects of genetic drift on the original founding population (4, 26).

New analyses of haplogroup subclades help to resolve when modern humans subsequently spread from Beringia to the rest of the Americas. Three subclades of mtDNA subhaplogroup C1 are widely distributed among North, Central, and South Americans but absent in Asian populations, which suggests that they evolved after the central Asian–Native American split, as the first Americans were dispersing from Beringia (27). The estimated date of coalescence for these subclades is 16.6 to 11.2 ka, which suggests that the colonization of the Americas south of the continental ice sheets may have occurred sometime during the late-glacial period, thousands of years after the initial splitting of Asian and Native American lineages. Genetic simulation studies and analyses of the geographic structure of Native American mtDNA haplogroups further suggest that colonization from Beringia occurred earlier in this time frame (about 16 ka) than later, because late-entry, rapid-spread models (like the Clovis-First model) are not capable of generating the observed geographic distribution of genetic patterns in extant populations (28, 29).

The cranial morphology of the earliest Americans [i.e., “Paleoamericans” like Kennewick (Washington), Spirit Cave (Nevada), and Lagoa Santa (Brazil)] is significantly different from that of more recent Native Americans (30). Given the assumption that craniometric variation is neutral and therefore phylogenetically significant, the differences could reflect two successive migrations stemming from two geographically or temporally distinct sources (31–33). Accordingly, Paleoamericans came to the New World first and were later replaced by ancestors of modern Native Americans.

Genetic data do not support this model. All major Native American mtDNA and Y-chromosome haplogroups emerged in the same region of central Asia, and all share similar coalescent dates, indicating that a single ancient gene pool is ancestral to all Native American populations (6, 10, 16). Similarly, all sampled native New World populations (from Alaska to Brazil) share a unique allele at a specific microsatellite locus that is not found in any Old World populations (except Koryak and Chukchi of western

Beringia), which implies that all modern Native Americans descended from a single source population (34). This history is further supported by ancient DNA studies showing that Paleoamericans carried the same haplogroups (and even subhaplogroups) as modern Native groups (12–14). Thus, although the Paleoamerican sample is still small, the morphological differences are likely the result of genetic drift and natural selection (30), not separate migrations.

A separate but related problem is whether some modern Native American populations resulted from migrations that occurred after initial human dispersal. Phylogenetic analyses of haplogroup lineages cannot easily discriminate between a single migration and multiple migrations of genetically distinct but closely related populations. For this, we need identification of specific mtDNA and Y-chromosome haplogroup subclades through analysis of the entire molecule (as well as detailed studies of nuclear genome variation). A recent study investigating mtDNA subclade distributions across Siberia (11) recognized two subclades of haplogroup D2, one among central Siberian groups (D2a) and the other among Chukchi, Siberian Eskimos, and Aleuts (D2b). These subclades share a coalescent date of 8 to 6 ka, which suggests that middle-Holocene ancestors of modern Eskimo-Aleuts spread from Siberia into the Bering Sea region and not vice versa, which supports earlier interpretations based on dental evidence (35).

The Archaeological Evidence

To colonize the Americas, modern humans had to learn to subsist in the extreme environments of the Siberian Arctic. They did this by 32 ka. The evidence comes from the Yana Rhinoceros Horn site (RHS), which is located along the lower Yana River in northwest Beringia and contains a frozen, well-preserved cultural layer with stone artifacts and remains of extinct fauna (36). Most interesting are bi-beveled rods on rhinoceros horn and mammoth ivory, signs of a sophisticated Upper Paleolithic technology. Sites of similar age occur in subarctic central Siberia (Nepa, Alekseevsk) and arctic European Russia (Mamontovaya Kurya, Byzovaia) (21, 37), which suggests that people had become well-equipped to handle life in the far north shortly after arriving in south Siberia (22). Their spread into the Arctic occurred during a time of relatively warm climate before the LGM.

As yet, no unequivocal traces that the early people of Yana RHS explored farther east onto the Bering Land Bridge and crossed into Alaska and northwest Canada have been found, but hints of an early human presence may include the 28-ka mammoth-bone core and flake recovered from Bluefish Caves (Yukon Territory) and even older bone materials from along the nearby Old Crow River (38). These bones, however, lack associated stone artifacts and might be the result of natural bone breakage (39). Instead, the earliest reliable archaeological evidence from

eastern Beringia comes from Swan Point (central Alaska), where a distinctive microblade and burin industry dates to 14 ka (40). The Swan Point artifacts share many technological qualities with late Upper Paleolithic sites in central Siberia (e.g., Studenoe-2, Nizhnii Idzhir, Khaergas Cave, Diuktai Cave) and appear to document the dispersal of microblade-producing humans from Siberia to Beringia during the late glacial.

After 14 ka, the Beringian archaeological record becomes much more complicated. The best-documented industries for this time are the Nenana complex of central Alaska (dating to 13.8 to 13 ka) and the early Ushki complex of Kamchatka (13 ka) (22, 41). These complexes contain small bifaces and unifaces made on blades and flakes, but they lack microblades and burins. The Sluiceway-Tuluq complex (northwest Alaska) also may be contemporaneous to Nenana but is technologically distinct from it (22). These sites contain large lanceolate bifaces that appear to date to about 13.2 ka. Another site, Nogahabara I (west Alaska), contains a mixed array of artifacts (lanceolate bifaces, notched bifaces, and microblade cores) reportedly dated to 13.8 to 12.7 ka (42); however, this site must be viewed with caution because the artifacts and bones used for dating are from near-surface and surface contexts in a sand dune blowout, a context notorious for artifact redeposition and mixing. After 13 ka, microblade and burin technologies reappear, sometimes in combination with bifacial point technologies. Perhaps these changes through time and across space relate to cultural differences and population turnovers, but more likely they represent the development of a unique human adaptation to the rapidly changing shrub-tundra environment of late-glacial Beringia (22). A small number of undated fluted points similar to Clovis occur in Alaska (39), but their relation to Clovis points found south of the continental ice sheets is unknown and may represent the backward flow of technologies (or people) from mid-latitude North America to Beringia at the very end of the Pleistocene (22, 39).

Since 40 ka, the Cordilleran and Laurentide ice sheets covered much of Canada, but during warmer periods they retreated sufficiently to create ice-free corridors along the Pacific coast and Plains east of the Canadian Rockies. These corridors were the conduits through which the first humans spread from Beringia to the Americas. When humans arrived in arctic Siberia at Yana RHS 32 ka, contracted ice sheets left wide-open corridors through which humans could have passed, but by 24 ka the ice sheets had grown sufficiently to clog both passageways (43). Although isolated ice-free refugia probably existed in both corridors throughout the LGM, humans probably did not occupy these areas until the corridors reopened during the late glacial. Timing of the reopening of the coastal and interior corridors is still debated, because of imprecise dating and because the various

Cordilleran glaciers reacted differently to climate change (43). Nonetheless, the coastal corridor appears to have become deglaciated and open to human habitation by at least 15 ka, whereas the interior corridor may not have opened until 14 to 13.5 ka (44, 45). The archaeological records of both corridors are still inadequate for addressing questions about the initial peopling of the Americas; however, the presence of human remains dating to 13.1 to 13 ka at Arlington Springs, on Santa Rosa Island off the coast of California, indicates that the first Americans used watercraft (46).

Clovis and its contemporaries. Discussion of the early archaeological record south of the Canadian ice sheets starts with Clovis, the best-documented early complex in the Americas. Radiocarbon dates obtained over the last 40 years from Clovis sites across North America suggested that the complex ranged in age from 13.6 to 13 ka (2); however, evaluation of the existing dates and new ^{14}C assays reveals that Clovis more precisely dates from 13.2–13.1 to 12.9–12.8 ka (47), a shorter and younger time span for Clovis than earlier thought. The current evidence suggests Clovis flourished during the late Allerød interstadial and quickly disappeared at the start of the Younger Dryas stadial. The apparent simultaneous appearance of Clovis across much of North America suggests that it rapidly expanded across the continent, but the overlap in ^{14}C dates between regions of North America makes it impossible to determine a point of origin or direction of movement.

With recently excavated Clovis assemblages, especially from the southeastern United States and Texas, we know unequivocally that Clovis is characterized by not only bifacial technology but also distinctive Upper Paleolithic blade technology (Fig. 2) (15, 48). The principal diagnostic artifact of Clovis is its lanceolate fluted projectile point, not just because of its form but also the technology used to produce it. Other tool forms were equally important, especially formal stone tools like end scrapers, as well as cylindrical rods made on ivory, antler, or bone. These rods were beveled at one or both ends and functioned as fore-shafts or projectile points, respectively (48).

Traditionally, Clovis has been thought to represent a population of mobile hunter-gatherers because individual Clovis tools had multiple functions and were highly curated, which suggests that they were part of a conveniently transported tool kit (2). Many Clovis tools were made on high-quality stones like chert and obsidian procured hundreds of kilometers from where they were eventually discarded (48). Clovis sites are small and typically represent mammoth or mastodon kills, short-term camps, or caches. In the southeastern United States and Texas, however, enormous scatters of Clovis artifacts have been found that possibly represent quarry-habitation sites habitually used by Clovis people, from which they did not range great distances.

At the Gault site (Texas), of 650,000 excavated artifacts (mostly debitage), 99% are made from local, on-site cherts; rare nonlocal materials are from sources only 70 km away (49).

Clovis points have long been known to be associated with remains of mammoth and mastodon (2), but the importance of proboscideans in Clovis subsistence remains uncertain. Optimal foraging theory has been used to predict that humans would not become proboscidean-hunting specialists (50), and certainly the recurrence of bison, deer, hares, reptiles, and amphibians indicates that, in some contexts, Clovis people did more than hunt mammoth and mastodon (51). However, at least 12 unequivocal Clovis proboscidean kill and butchery sites are known (52), an unusually high number for such a short period of time, given that there are only six proboscidean kill sites for the entire Eurasian Upper Paleolithic (53). In most areas of North America, Clovis people hunted mammoth and mastodon regularly, and they likely played some

role in their extinction. It is not surprising that they also subsisted on a variety of other foods.

Most Clovis sites are in North America. Few Clovis artifacts have been found in Central and South America (54). Instead, a different complex of archaeological sites may mark this era south of Panama. At least six sites in South America (Cerro Tres Tetras, Cueva Casa del Minero, and Piedra Museo in Argentina and Fell's Cave, Quebrada Santa Julia, and Quebrada Jaguay in Chile) have multiple dates that overlap the known age of Clovis (47, 55, 56). These sites mostly contain undiagnostic flake tools and bifaces, but distinctive Fishtail points (some with fluted bases) were found in deposits dating to 13.1 to 12.9 ka at Fell's Cave and Piedra Museo. Although it has been suggested that Fishtail points postdate Clovis and were derived from it (54), the two may have shared an earlier, as yet unidentified progenitor. Among the newest Clovis-aged localities in South America is Quebrada Santa Julia, a stratified site with a well-preserved

living floor and hearth dating to 13.1 ka (57). Associated with the hearth were a broken, nondiagnostic, fluted biface, several flake tools, a core, and nearly 200 flakes, as well as remains of extinct horse. Quebrada Santa Julia provides an unambiguous association of fluting technology and extinct fauna in South America.

Early occupations. Since the discovery and definition of Clovis, researchers have searched for evidence of an even older occupation of the Americas, but most sites dating before Clovis investigated between 1960 and 1995 [e.g., Calico (California), Tule Springs (Nevada), Pendejo Cave (New Mexico), Pedra Furada (Brazil), Pikimachay Cave (Peru), and Tlapacoya (Mexico)] have not held up to scientific scrutiny (2, 39). Perhaps the best candidate is the Monte Verde site (Chile), which contains clear artifacts in a sealed context and is dated to 14.6 ka (58). Despite criticism (59), its acceptance by most archaeologists means synchronous and possibly earlier sites should exist in North America. A few localities dating between 15 and 14 ka now seem to provide compelling evidence of an occupation before Clovis.

In the northern United States, the Schaefer and Hebior sites (Wisconsin) provide strong evidence of human proboscidean hunting or scavenging near the margin of the Laurentide ice sheet between 14.8 and 14.2 ka (60, 61). At each site, disarticulated remains of a single mammoth were sealed in pond clay and associated with unequivocal

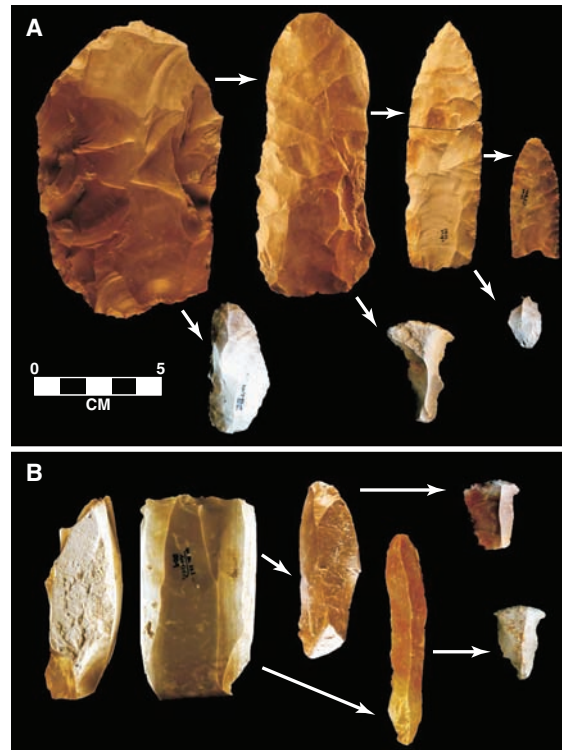


Fig. 2. The distinctive Clovis biface and blade technologies (schematic diagram with approximate scale). Clovis fluted points were manufactured by reduction of a large blank through a succession of stages including removal of broad thinning flakes across the entire face of the biface, end thinning at all stages, and final fluting of the finished piece (A). Thinning flakes were often utilized as tools. Clovis blades were detached from conical and wedge-shaped cores (B), the main distinction being that conical cores have blade removals around their entire circumference while wedge-shaped cores have a single front of blade removals. Blades are long, parallel-sided, curved in longitudinal cross section, and triangular or trapezoidal in transverse cross section; they were often used as tools. These specific artifacts are made on Edwards chert from the Gault site, Texas.

stone artifacts. The bones bear consistent signs of butchering—cut and pry marks made by stone tools (61). Critics suggest that the bone breakage and surface marring is the result of natural processes (2); however, it is difficult to reject the evidence from these sites because of the consistent patterning of the marks, low-energy depositional context, and associated stone tools. Even earlier evidence of humans in Wisconsin is suggested by what appear to be cut and pry marks on the lower limb bones of a mammoth recovered from Mud Lake. These bones date to 16 ka, but stone tools are absent (61).

Three other sites—Meadowcroft Rockshelter (Pennsylvania), Page-Ladson (Florida), and Paisley Cave (Oregon)—may provide additional evidence of humans in North America by about 14.6 ka. At Meadowcroft Rockshelter, artifacts occur in sediments that may be as old as 22 to 18 ka (62), but it is the record post-dating 15.2 ka that is especially interesting. This is the uppermost layer of lower stratum IIa, which produced a small lanceolate biface and is bracketed by dates of 15.2 and 13.4 ka. Acceptance of the site, however, hinges on resolution of dating issues (63).

At Page-Ladson, early materials occur in a buried geologic context within a sinkhole that is now submerged by the Aucilla River. Seven pieces of chert debitage, one expedient unifacial flake tool, and a possible hammerstone were associated with extinct faunal remains, including a mastodon tusk with six deep grooves at the point where the tusk emerged from the alveolus of the cranium (64). These grooves are interpreted to have been made by humans as the tusk was removed from its socket. Seven ^{14}C dates for this horizon average about 14.4 ka, which suggests human occupation of the sinkhole during the late Pleistocene when the water table was lower than it is today. Page-Ladson may contain evidence of pre-Clovis humans, but, despite extensive reporting on the site, more details on artifact contexts and site formation processes are needed to permit objective evaluation of the record.

At Paisley Cave, three human coprolites are directly ^{14}C dated to about 14.1 ka (14). The human origin of the coprolites is supported by ancient mtDNA analyses that showed they contained haplogroups A and B, but a complete report is not yet available.

The evidence for humans in the Americas even earlier than 15 ka is less secure, but recently has been presented for four sites: Cactus Hill (Virginia), La Sena (Nebraska), Lovewell (Kansas), and Topper (South Carolina). Cactus Hill is a sand-dune site with late prehistoric,

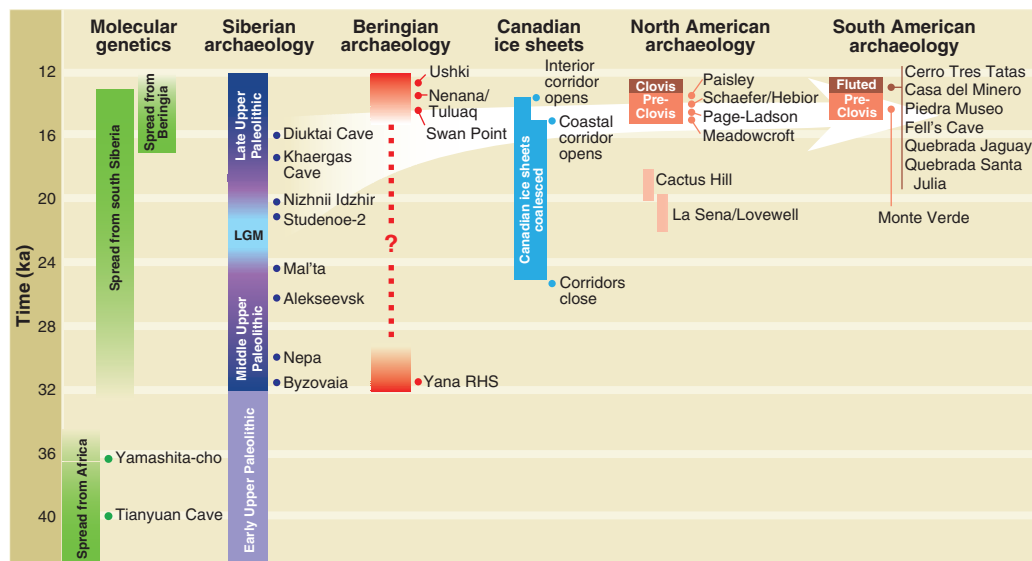


Fig. 3. Combined, the molecular genetic and archaeological records from Siberia, Beringia, and North and South America suggest humans dispersed from southern Siberia shortly after the last glacial maximum (LGM), arriving in the Americas as the Canadian ice sheets receded and the Pacific coastal corridor opened, 15 ka.

Archaic, and Clovis levels. Potentially older artifacts, including small prismatic blade cores, blades, and two basally thinned bifacial points were recovered 10 to 15 cm below the Clovis level (65). Three ^{14}C dates ranging from 20 to 18 ka are reported from the levels below Clovis, but there are also dates of 10.3 ka and later. Charcoal samples were not recovered from hearth features but occur as isolated fragments at the same level as the artifacts. The younger dates indicate translocation of charcoal from overlying sediments, and the older charcoal could be derived from sediments underlying the cultural layer (59, 63), but luminescence dates on the aeolian sands correlate with the older ^{14}C results and indicate minimal mixing of the sediments (66). Even though much information has yet to be published about this site, the potential presence of a biface and blade assemblage stratigraphically below the site's Clovis assemblage is compelling.

An even older occupation has been proposed based on taphonomically altered mammoth bones at the La Sena and Lovewell sites that date from 22 to 19 ka (67). Neither site has yielded stone tools or evidence of butchering; however, many of the leg bones display percussion impact and flaking, which suggests that they were quarried and flaked by humans while they were in a fresh, green state, within a few years of the death of the animals. Clovis people periodically flaked bone in this fashion, as did Upper Paleolithic Beringians (2, 22); however, in those contexts humans left behind stone tools, whereas at La Sena and Lovewell stone tools are absent.

Currently, the oldest claim for occupation of North America is at the Topper site, located on a Pleistocene terrace overlooking the Savannah River. Clovis artifacts at Topper are found at the

base of a colluvial deposit, and older artifacts are reported in underlying sandy alluvial sediments dated to about 15 ka (68). The proposed early assemblage is a smashed core and micro-lithic industry. Cores and their removals show no negative bulbs, and flakes and spalls were modified into small unifacial tools and “bend-break tools,” possibly used for working wood or bone. In 2004, similar-looking material was found in older alluvial deposits dating in excess of 50 ka (69). Given that the assemblage was not produced through conventional Paleolithic technologies and that the putative artifacts could have been produced through natural processes (specifically thermal spalling), evaluation of this site must await a complete lithic analysis.

Combining the Genetic and Archaeological Evidence

Unquestionably, the human skeletal evidence across the Americas shows that the New World was populated by *Homo sapiens*. Although the crania of these early people look different from modern Native Americans, modern and ancient DNA studies show that they were genetically related. The earliest inhabitants of the Americas hailed from south Siberia (between the Altai Mountains and Amur valley) and ultimately descended from a population of modern humans who dispersed from Africa by 50 ka and appeared in central Asia by 40 ka. Thus, a maximum limiting age can be placed on the entry of people into the New World of no earlier than 40 ka. Any claims for an earlier migration should be viewed with skepticism.

Current molecular evidence implies that members of a single population left Siberia and headed east to the Americas sometime between about 30 and 13 ka (Fig. 3). Most studies suggest this event occurred after the LGM, less than 22 ka. Recent

analyses of mtDNA and nuclear sequence data further suggest a dispersal south from Beringia after 16.6 ka (27), from a founding population of less than 5000 individuals (70). The genetic record has not revealed multiple late-Pleistocene migrations, but does distinguish a Holocene dispersal of Eskimo-Aleuts from northeast Asia. There is nothing in the modern or ancient genetic records to suggest a European origin for some Native Americans.

At first glance, the genetic evidence would seem to mesh well with the traditional view that Clovis represents the first people to enter the Americas. Redating of Clovis from 13.2–13.1 to 12.9–12.8 ka indicates it is not only centuries younger than the late-glacial complexes of Alaska but also younger than even the most conservative estimate for the opening of the interior Canadian corridor. The Clovis-First model, however, requires all American sites older than Clovis to be rejected, and this appears to be no longer possible. The Clovis-First model does not explain the apparent synchronicity between Clovis and the early Paleo-Indian sites of South America. Finally, a late-entry and rapid dispersal of humans across the New World is inconsistent with the distribution of genetic variation observed in Native American populations today.

Humans possibly colonized the Americas before the LGM. They occupied western Beringia by 32 ka, and no glacial ice sheets would have blocked passage through western Canada during this relatively warm time. However, there is still no unequivocal archaeological evidence in the Americas to support such an early entry.

The most parsimonious explanation of the available genetic, archaeological, and environmental evidence is that humans colonized the Americas around 15 ka, immediately after deglaciation of the Pacific coastal corridor. Monte Verde, Schaefer, and Hebior point to a human presence in the Americas by 14.6 ka. Human occupations at Meadowcroft, Page-Ladson, and Paisley Cave also appear to date to this time. Together these sites may represent the new basal stratum of American prehistory, one that could have given rise to Clovis. Most mtDNA and Y-chromosome haplogroup coalescence estimates predict a 15-ka migration event, and it may correlate to the post-LGM dispersal of microblade-producing populations into northern Siberia and their eventual appearance in Beringia during the late glacial. The first Americans used boats, and the coastal corridor would have been the likely route of passage since the interior corridor appears to have remained closed for at least another 1000 years. Once humans reached the Pacific Northwest, they could have continued their spread southward along the coast to Chile, as well as eastward along the southern margin of the continental ice sheets, possibly following traces of mammoth and mastodon to Wisconsin. Clovis could have originated south of the continental ice sheets, and the dense Clovis quarry-campsites in the southeastern United States may

be the result of a longer occupation there than in other regions. Alternatively, Clovis could be the result of a second dispersal event from Beringia to America—from the same ancestral gene pool as the first dispersing population—when the interior ice-free corridor opened, about 13.5 ka.

The peopling of the Americas debate is far from resolved. To move forward, we must continue to take an interdisciplinary scientific approach to the problem. Archaeological investigations will provide the empirical evidence of the first Americans, but this evidence must be objectively and rigorously evaluated. Geoarchaeological investigations have and will play a major role by documenting the geological and geochronological context of sites and developing predictive models to find early sites. The sparse evidence for pre-13 ka occupation of the Americas may be a problem of sampling and artifact recognition. Genetic studies will also be key as more is learned about modern and ancient haplogroup subclades in combination with full mtDNA genome sequencing and identification of patterns of nuclear DNA variation. The empirical data from these fields and other disciplines will ultimately provide the evidence needed to build and test models to explain the origins and dispersal of the first Americans.

References and Notes

- All ages are presented as ka (thousands of calendar years ago). Dates relating to genetic events are in calendar years based on coalescent methods. Dates relating to archaeological events are derived by calibrating radiocarbon ages. Radiocarbon dates younger than 21,000 ¹⁴C years ago were calibrated with Calib 5.0.1 (IntCal04 curve); older dates were calibrated by using CalPal Online (CalPal 2007 HULU curve).
- G. A. Haynes, *The Early Settlement of North America: The Clovis Era* (Cambridge Univ. Press, Cambridge, 2002).
- J. N. Hill, in *The Settlement of the American Continents: A Multidisciplinary Approach to Human Biogeography*, C. M. Barton, G. A. Clark, D. R. Yesner, G. A. Pearson, Eds. (Univ. of Arizona Press, Tucson, 2004), pp. 39–48.
- P. Forster, *Philos. Trans. R. Soc. London B Biol. Sci.* **359**, 255 (2004).
- M. Metspalu, T. Kivisild, H.-J. Bandelt, M. Richards, R. Villems, *Nucleic Acids Mol. Biol.* **81**, 181 (2006).
- D. A. Merriwether, in *Environment, Origins, and Population*, D. H. Ubelaker, Ed., *Handbook of North American Indians*, vol. 3, W. C. Sturtevant, Ed. (Smithsonian Institution Press, Washington, DC, 2006), pp. 817–830.
- T. M. Karafet, S. L. Zegura, M. F. Hammer, in *Environment, Origins, and Population*, D. H. Ubelaker, Ed., *Handbook of North American Indians*, vol. 3, W. C. Sturtevant, Ed. (Smithsonian Institution Press, Washington, DC, 2006), pp. 831–839.
- M. V. Derenko et al., *Am. J. Hum. Genet.* **69**, 237 (2001).
- E. B. Starikovskaya et al., *Ann. Hum. Genet.* **69**, 67 (2005).
- S. L. Zegura, T. M. Karafet, L. A. Zhivotovskiy, M. F. Hammer, *Mol. Biol. Evol.* **21**, 164 (2004).
- M. Derenko et al., *Am. J. Hum. Genet.* **81**, 1025 (2007).
- B. M. Kemp et al., *Am. J. Phys. Anthropol.* **132**, 605 (2007).
- D. G. Smith, R. S. Malhi, J. A. Eshleman, F. A. Kaestle, B. M. Kemp, in *Paleoamerican Origins: Beyond Clovis*, R. Bonnicksen, B. T. Lepper, D. Stanford, M. R. Waters, Eds. (Center for the Study of the First Americans and Texas A&M Univ. Press, College Station, TX, 2005), pp. 243–254.
- D. L. Jenkins, in *Paleoindian or Paleoarchaic? Great Basin Human Ecology at the Pleistocene/Holocene*

- Transition, K. E. Graf, D. N. Schmitt, Eds. (Univ. of Utah Press, Salt Lake City, 2007), pp. 57–81.
- B. Bradley, D. Stanford, *World Archaeol.* **36**, 459 (2004).
- S. Wang et al., *PLoS Genet.* **3**(11), e185 (2007).
- R. S. Wells et al., *Proc. Natl. Acad. Sci. U.S.A.* **98**, 10244 (2001).
- D. Comas et al., *Eur. J. Hum. Genet.* **12**, 495 (2004).
- M. P. Richards, P. B. Pettit, M. C. Stiner, E. Trinkaus, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 6528 (2001).
- H. Shang, H. Tong, S. Zhang, F. Chen, E. Trinkaus, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 6573 (2007).
- T. Goebel, *Evol. Anthropol.* **8**, 208 (1999).
- J. F. Hoffecker, S. A. Elias, *Human Ecology of Beringia* (Columbia Univ. Press, New York, 2007).
- T. G. Schurr, S. T. Sherry, *Am. J. Hum. Biol.* **16**, 420 (2004).
- M.-C. Bortolini et al., *Am. J. Hum. Genet.* **73**, 524 (2003).
- M. Seielstad et al., *Am. J. Hum. Genet.* **73**, 700 (2003).
- S. Y. W. Ho, G. Larson, *Trends Genet.* **22**, 79 (2006).
- E. Tamm et al., *PLoS ONE* **2**(9), e829 (2007).
- A. G. Fix, *Am. J. Phys. Anthropol.* **128**, 430 (2005).
- D. H. O'Rourke, M. G. Hayes, S. W. Carlyle, *Hum. Biol.* **72**, 15 (2000).
- J. F. Powell, *The First Americans: Race, Evolution, and the Origin of Native Americans* (Cambridge Univ. Press, Cambridge, 2005).
- R. L. Jantz, D. W. Owsley, *Am. J. Phys. Anthropol.* **114**, 146 (2001).
- R. González-José et al., *Am. J. Phys. Anthropol.* **128**, 772 (2005).
- W. A. Neves, M. Hubbe, L. B. Piló, *J. Hum. Evol.* **52**, 16 (2007).
- K. B. Schroeder et al., *Biol. Lett.* **10.1098/rsbl.2006.0609** (2007).
- J. H. Greenberg, C. G. Turner II, S. L. Zegura, *Curr. Anthropol.* **27**, 477 (1986).
- V. V. Pitulko et al., *Science* **303**, 52 (2004).
- P. Pavlov, J. I. Svendsen, S. Indrelid, *Nature* **413**, 64 (2001).
- R. E. Morlan, *Quat. Res.* **60**, 123 (2003).
- E. J. Dixon, *Bones, Boats, and Bison: Archeology and the First Colonization of Western North America* (Univ. of Utah Press, Salt Lake City, 1999).
- C. E. Holmes, B. A. Crass, paper presented at the 30th annual meeting of the Alaska Anthropological Association, Fairbanks, 27 to 29 March 2003.
- T. Goebel, M. R. Waters, M. A. Dikova, *Science* **301**, 501 (2003).
- D. Odess, J. T. Rasic, in *American Antiquity* **72**, 691 (2007).
- J. J. Clague, R. W. Mathewes, T. A. Ager, in *Entering America: Northeast Asia and Beringia before the Last Glacial Maximum*, D. B. Madsen, Ed. (Univ. of Utah Press, Salt Lake City, 2004), pp. 63–94.
- C. A. S. Mandryk, H. Josenhans, D. W. Fedje, R. W. Mathewes, *Quat. Sci. Rev.* **20**, 301 (2001).
- A. S. Dyke, in *Quaternary Glaciations—Extent and Chronology, Part II: North America*, J. Ehlers, P. L. Gibbard, Eds. (Elsevier, Amsterdam, 2004), pp. 373–424.
- J. R. Johnson, T. W. Stafford Jr., G. J. West, T. K. Rockwell, American Geophysical Union Joint Assembly, Acapulco, 22 to 25 May 2007, *Eos* **88**(23), Jt. Assem. Suppl., Abstr. PP42A-03.
- M. R. Waters, T. W. Stafford Jr., *Science* **315**, 1122 (2007).
- K. B. Tankersley, in *The Settlement of the American Continents: A Multidisciplinary Approach to Human Biogeography*, C. M. Barton, G. A. Clark, D. R. Yesner, G. A. Pearson, Eds. (Univ. of Arizona Press, Tucson, 2004), pp. 49–63.
- M. B. Collins, in *Foragers of the Terminal Pleistocene in North America*, R. B. Walker, B. N. Driskell, Eds. (Univ. of Nebraska Press, Lincoln, 2007), pp. 59–87.
- D. A. Byers, A. Ugan, *J. Archaeol. Sci.* **32**, 1624 (2005).
- M. D. Cannon, D. J. Meltzer, *Quat. Sci. Rev.* **23**, 1955 (2004).
- D. K. Grayson, D. J. Meltzer, *J. Archaeol. Sci.* **30**, 585 (2003).
- T. Surovell, N. Waguespack, P. J. Brantingham, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 6231 (2005).
- J. E. Morrow, C. Gnecco, Eds., *Paleoindian Archaeology: A Hemispheric Perspective* (Univ. Press of Florida, Gainesville, 2006).
- L. Miotto, M. C. Salemm, *Quat. Int.* **109-110**, 95 (2003).

56. D. H. Sandweiss *et al.*, *Science* **281**, 1830 (1998).
57. D. Jackson, C. Méndez, R. Seguel, A. Maldonado, G. Vargas, *Curr. Anthropol.* **48**, 725 (2007).
58. T. D. Dillehay, Ed., *Monte Verde: A Late Pleistocene Settlement in Chile*, vol. 2, *The Archaeological Context and Interpretation* (Smithsonian Institution Press, Washington, DC, 1997).
59. S. J. Fiedel, *J. Archaeolog. Res.* **8**, 39 (2000).
60. D. J. Joyce, *Quat. Int.* **142-143**, 44 (2006).
61. D. F. Overstreet, in *Paleoamerican Origins: Beyond Clovis*, R. Bonnichsen, B. T. Lepper, D. Stanford, M. R. Waters (Center for the Study of the First Americans, Texas A&M Univ. Press, College Station, TX, 2005), pp. 183–195.
62. J. M. Adovasio, D. R. Pedler, in *Entering America: Northeast Asia and Beringia before the Last Glacial Maximum*, D. M. Madsen, Ed. (Univ. of Utah Press, Salt Lake City, 2004), pp. 139–158.
63. C. V. Haynes Jr., in *Paleoamerican Origins: Beyond Clovis*, R. Bonnichsen, B. T. Lepper, D. Stanford, M. R. Waters, Eds. (Center for the Study of the First Americans, Texas A&M Univ. Press, College Station, TX, 2005), pp. 113–132.
64. S. D. Webb, Ed., *First Floridians and Last Mastodons: The Page-Ladson Site in the Aucilla River* (Springer, Dordrecht, The Netherlands, 2005).
65. J. M. McAvoy, L. D. McAvoy, Eds., *Archaeological Investigations of Site 44SX202, Cactus Hill, Sussex County, Virginia* (Research Report Series No. 8, Virginia Department of Historic Resources, Richmond, 1997).
66. J. K. Feathers, E. J. Rhodes, S. Huot, J. M. McAvoy, *Quat. Geochronol.* **1**, 167 (2006).
67. S. R. Holen, *Quat. Int.* **142-143**, 30 (2006).
68. A. C. Goodyear, in *Paleoamerican Origins: Beyond Clovis*, R. Bonnichsen, B. T. Lepper, D. Stanford, M. R. Waters (Center for the Study of the First Americans, Texas A&M Univ. Press, College Station, TX, 2005), pp. 103–112.
69. A. C. Goodyear, *Legacy: S. Carolina Inst. Archaeol. Anthropol.* **9-1/2**, 1 (2005).
70. A. Kitchen, M. M. Miyamoto, C. J. Mulligan, *PLoS One* **3**, e1596 (2008).
71. We thank J. Enk, S. Fiedel, K. Graf, H. Harpending, G. Haynes, E. Marchani, J. O'Connell, A. Scola, and J. Tackney for comments on early drafts of this paper. C. Pevny assisted in preparation of Fig. 2.

10.1126/science.1153569