ANTHROPOLOGY

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Current evidence allows multiple models for the peopling of the Americas

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Some recent academic and popular literature implies that the problem of the colonization of the Americas has been largely resolved in favor of one specific model: a Pacific coastal migration, dependent on high marine productivity, from the Bering Strait to South America, thousands of years before Clovis, the earliest widespread cultural manifestation south of the glacial ice. Speculations on maritime adaptations and typological links (stemmed points) across thousands of kilometers have also been advanced. A review of the current genetic, archeological, and paleoecological evidence indicates that ancestral Native American population expansion occurred after 16,000 years ago, consistent with the archeological record, particularly with the earliest securely dated sites after ~15,000 years ago. These data are largely consistent with either an inland (ice-free corridor) or Pacific coastal routes (or both), but neither can be rejected at present. Systematic archeological and paleoecological investigations, informed by geomorphology, are required to test each hypothesis.

INTRODUCTION

Investigation of the peopling of the Americas has generated decades of scholarly studies, increasingly illuminated by paleoecological and particularly paleogenetic research. There are currently several models of the peopling process differing with respect to timing, routes, and affiliation with modern (and ancient) populations in Asia and the Americas (Fig. 1). One perspective that has become prominent in the last decade is of an early entry (~25,000 to 15,000 years ago) into the Americas via a Pacific coastal migration. This perspective further implies ecological adaptations (for example, the kelp highway hypothesis) and, more recently, typological relationships (stemmed points) (*1*–*5*). We believe that this perspective, although commonly disseminated in the popular press (*6*–*8*), is a prematurely narrow interpretation of current evidence, which yields far less certainty. Some proponents (*1*) also assert that there is near-complete agreement among archeologists on these issues, but the most recent relevant survey (*9*) shows that archeologists remain divided, with substantial numbers thinking migrants used both interior and coastal routes, as well as strong skepticism for several proposed pre-Clovis sites. More nuanced consideration of the proposed alternatives can also be found (*10*–*12*). Here, we evaluate the claims made in (*1*) and elsewhere with respect to the current genetic, archeological, and paleoecological data and identify model constraints. We also suggest avenues of further research to refine models of the peopling of the Americas. Due to multiple dating techniques presented in this paper, we use years ago for calibrated radiocarbon dates, OSL and cosmogenic dates, and genetic age estimates. All of these are roughly comparable.

GENETIC AND ARCHEOLOGICAL CONGRUENCE

Genetic studies provide independent information on the timing and nature of Native American ancestral divergence from northeast Asian populations, genetic isolation, and expansion into the Americas. The most recent comprehensive ancient mitogenomic analysis (*13*) indicates that Native American ancestors diverged from Siberian populations between 24,900 and 18,400 years ago with population expansion associated with female lineage diversification sometime between ~16,000 to 13,000 years ago. These results are consistent with a large-scale genomic study based on mostly modern Native American and Siberian data (*14*). We should be careful to insist on confidence intervals rather than relying on mean or median estimates, because the former more accurately reflect the precision of the data. This approach also results in consistency with a wider range of colonization models rather than narrowly limiting the options. Models of diversification should encompass migration from the geographic location of the ancestral Native American population, which is currently unknown, but probably includes expansion into northeastern Siberia and Beringia. As a possible working hypothesis, if Native American ancestors were situated in southern Siberia 20,000 years ago, then the post–16,000-year expansion must include migration into northeast Asia.

Genetic analyses dependent on data from modern populations do not bear directly on the geographic locations of the divergence events (*13*). For instance, the data used to generate the Beringian Incubation

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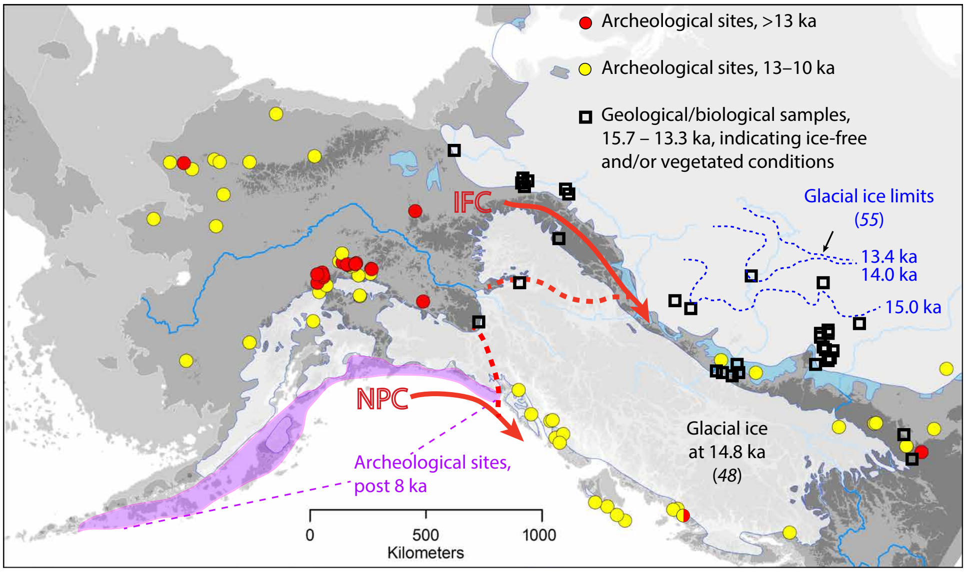

Fig. 1. Northwest North America with archeological sites older than 10,000 calibrated years before the present (Supplementary Materials) and proposed colonization routes: IFC and NPC. Glacial ice extent (white) from (*48*), and archeological site and geological sample locations summarized in (*12*, *78*). Laurentide Ice Sheet limits (dotted lines) from (*55*). ka, thousand years; IFC, ice-free corridor; NPC, North Pacific coast.

Model only require that Native American ancestors were geographically isolated from wherever the East Asian/Siberian ancestors inhabited during the time of isolation (*15*). The genetic data do not require that this isolation occurred in central or eastern Beringia—it could range across a vast area, from Cis-Baikal to Hokkaido. So far, complete nuclear genomes from ancient samples produced in recent years (*16*–*18*) are not able either to substantially narrow the divergence estimate or to clarify spatial routes of the initial peopling.

A recent analysis of the 11,500-year-old Upward Sun River 1 genome (*19*) suggests that Native Americans descend from a single population that separated from East Asians by 26,100 to 23,900 years ago, with two deep branches: an Ancient Beringian population that split off ~22,000 to 18,000 years ago and a second branch that split into northern and southern lineages ~17,500 to 14,600 years ago (*19*). Earlier gene flow between ancestral Native Americans and Ancient North Eurasians (ANEs) (represented by Mal'ta and Afontova individuals) between ~25,000 and 20,000 years ago strongly suggests geographic proximity of these groups, somewhere in southern Siberia, where all ANE individuals have been located (see fig. S1 for localities and regions mentioned in the text). The record of human remains in northeast Asia is very sparse, but they have been recovered at Yana RHS, dating to ~27,000 years ago (*20*). Unfortunately, no ancient DNA analysis has yet been published, but Yana's location at the extreme western edge of Beringia will make it difficult to draw firm conclusions about populations present in the rest of western, central, and eastern Beringia, for example, for 1500 to 2000 km to the southern Beringian coasts or 2500 km to Alaska. The lack of an unequivocal human presence in the entire region during the Last Glacial Maximum (LGM) between the Yana occupation (during a warm period) and the clear expansion of Diuktai Culture (Late Upper Paleolithic) populations moving from south to north after 16,000 years ago suggests a temporary expansion of Middle Upper Paleolithic populations followed by later contraction during the LGM followed by expansion after the onset of deglaciation (*21*, *22*).

The locations of ancestral Native Americans between ~20,000 and 15,000 years ago remain unknown, but two scenarios have been proposed (*19*). Scenario 1 posits that the split of Ancient Beringians and other Native Americans occurred in northeast Asia/Siberia, while scenario 2 posits that this split occurred in eastern Beringia (Alaska). Current archeological and paleoecological data support scenario 1. There is no secure evidence of ~20,000-year-old American sites, while there is abundant evidence of human occupation in northeast Asia (for example, southern Siberia, Amur basin, Primor'ye, and Japanese archipelago) (fig. S1) (*23*). The LGM is regionally characterized by very cold and arid conditions with evidence for depopulation of north Asia and no evidence throughout Eurasia for northward expansions of humans (*24*, *25*). Previous genetic models of Native American demography indicate a bottleneck during this period, with expansion only after 16,000 to 13,000 years ago (*13*, *26*). We observe a clear pattern of human expansion from Siberia to Beringia around 16,000 to 14,000 years (*12*) and the first unequivocal and widespread occupations south of glacial ice in the Americas after 13,500 years ago, associated with Clovis and Fishtail complex technologies (*27*–*29*). We note that both point types are continent-wide in North and South America, respectively. They are the only point types with such broad distributions and are consistent with colonizing processes (*30*–*32*), although they might also represent communication of ideas among low-density early populations.

We have firmer geographic constraints on these populations after about 12,600 years ago. Ancient Beringians, associated with the Denali complex/Paleoarctic tradition, were in Alaska and adjacent areas between 12,500 and 6000 years ago (*19*). Although the northern lineage (including Na-Dene, Algonquian, Salish, Tsimshian, and Haida) appears constrained to northern North America (*33*), the southern lineage directly links with Clovis (Anzick) (*16*–*18*). However, we have no direct genetic evidence arising from populations associated with pre-Clovis sites linking them with later Native Americans. Thus, we should be careful to distinguish potential failed migrations versus the direct ancestors of Clovis and later Paleoindians.

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We also note that pre-Clovis sites continue to vary in site integrity, that is, clear associations of secure dates and unambiguous cultural materials. There appear to be relatively few technological or adaptive connections among the proposed pre-Clovis sites, or with (later) unequivocal Paleoindian complexes, represented by hundreds of sites and thousands of artifacts across the Americas (*34*, *35*). However, analyses by (*36*) have shown that currently dated Clovis sites represent a sample that came from a population of sites that date to a time span covering 1070 to 835 years. This suggests that it is possible that some pre-Clovis sites after ~15,000 years ago may represent Clovis ancestors or are Clovis sites that lack diagnostic artifact types.

POTENTIAL MIGRATION ROUTES

We review here issues with both North Pacific coast (NPC) and ice-free corridor (IFC) routes of colonization of mid-continental North America (Fig. 1). We note that an NPC route could originate along southern Beringia or from interior Beringia. The IFC route has several potential branches funneling in from the north. These include a route west of the Mackenzie River between the northern sections of the Laurentide and Cordilleran Ice Sheets, or through the Liard and Peace River areas, which also deglaciated early (*37*).

A coastal colonization route remains a viable hypothesis; however, several issues relating to the proposed coastal migration have been typically ignored (*12*). Contrary to commonly asserted claims, the entire late Pleistocene coast was not submerged due to rising sea levels. A comprehensive meta-analysis (*38*) reviewing paleoecoastal geomorphology from Puget Sound to the Alaska Peninsula indicated that more than half of the northwest Pacific coastal regions retained preserved pre-Clovis–aged shorelines (Fig. 2). Surveys in these regions have so far failed to discover sites securely dated to older than ~12,600 years ago (1600 years later than the earliest unequivocal sites in interior Beringia), contradicting common assertions of an early coastal migration (*12*). A few potential earlier sites that have been reported recently, including Triquet Island, remain unreported in peer-reviewed sources. Calvert Island cultural materials including human footprints are associated with bracketing ages of between 13,300 and 12,700 years ago (Stratum X) and 12,650 years ago (Stratum IX) (*39*). Hunter Island (*40*) contains materials that may date to ~13,500 years ago or to the Younger Dryas (both radiocarbon dates come from the same layer and do not overlap). Similarly, Kildit Narrows contains scattered materials from a charcoal-rich layer with three nonoverlapping associated dates of ~13,600, 12,800, and 10,700 years ago (*40*). In the latter two cases, the association of the cultural materials and dates is unclear.

Throughout most (~2000 km) of the hypothetical NPC route, from Yakutat Bay to the Aleutians, the earliest human occupations post-date 8000 years ago (more than 6000 years after the earliest interior Beringian occupations), long after shorelines stabilized, and using technology derived from earlier interior traditions (Fig. 1) (*41*, *42*). Furthermore, the Siberian Diuktai Culture (~18,000 to 12,000 years ago) is terrestrial, while there is no evidence for coastal or maritime economies along the northwest Pacific coast from the Kuriles, Kamchatka, Chukotka, or the Okhotsk Sea coast until the middle Holocene (*43*). East Beringian obsidian distribution patterns show long-distance east-west movement of obsidian from interior sources between 14,000 and 13,000 years ago, while coastal sources were only used 4900 to 2300 years after the earliest interior use, and no coastal obsidian has been found substantially inland (*12*). If Paleoindian ancestors moved along the southern coastal edge of Beringia, we would expect earlier sites in adjacent Pacific drainages (for example, Copper and Susitna rivers) and later occupations in the deep interior (for example, Tanana and Yukon rivers). Extant data show the earliest occupations along the Tanana River (~14,200 years ago), later expansion of related technologies into the Pacific drainages (~12,000 years ago), and much later expansion to the coast (~8000 years ago). All these patterns are inconsistent with an initial coastal migration along the southern edge of Beringia before 16,000 years ago (*12*).

More research is required to assess resource bases along the NPC route. Some coastal refugia have been identified in the southern part of the coastal route [for example, (*44*, *45*)], whereas the record is sparse to the north, including the Alexander Archipelago, southern coastal Alaska, the Alaska Peninsula, and the Aleutians [see review in (*12*)]. Anadromous fish could have been a stable resource for humans, but the earliest evidence of salmon fishing is in interior Alaska (*46*, *47*). Other complications to a coastal route include the potential

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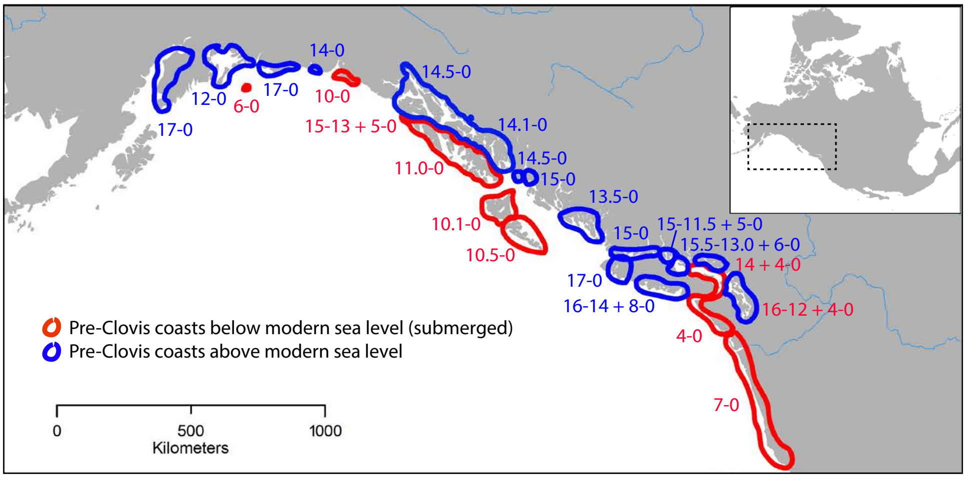

Fig. 2. Sea-level curves by region and periods above modern sea level (in thousands of calibrated years before the present) (that is, pre-Clovis occupations would be potentially accessible if they are extant), adapted from data in (*38*, *79*).

presence of sea ice (pack and drift), recurrent volcanism, and potential reduction in kelp richness and abundance in periglacial environments (*12*). The ecological viability of large stretches of the coastal route has not been fully evaluated yet, and more work needs to be done before we can identify the time periods when this region could support human populations from the Aleutian area to Puget Sound. Alternatively, another potential entry to the NPC from southwestern Yukon is constrained by the deglaciation of the White Pass, estimated between 13,500 and 13,000 years ago (*48*), likely too late to serve as a route for Paleoindian ancestors.

The enigmatic record at Bluefish Cave raises the possibility of population pulses into eastern Beringia as early as 24,000 years ago (*49*). We note that if there was successful settlement in the LGM, we should see more abundant evidence of sites in the succeeding millennia, which we do not. In contrast, a substantial continuous record begins ~14,200 years ago at Swan Point CZ4b with multiple hearth features and overlapping dates on hearth charcoal and associated fauna, which represents an East Beringian branch of the geographically extensive Siberian Diuktai Culture (*50*). East Beringian tradition populations around 15,000 to 14,000 years ago would be adapted to expanding habitat in the northern funnels of the IFC. The southern funnel of the IFC had a detectable human presence by 13,300 years ago (Fig. 1), where a camel and horses were butchered in an earliest Clovis or pre-Clovis time range in Alberta's St. Mary Reservoir (*51*–*53*).

Any evaluation of the IFC must rest on a secure geological foundation, involving a vast region affected by intense glacial and paraglacial dynamics that challenge geologists and paleoecologists. The IFC region has received episodic attention over the last several decades. There is currently, however, an almost unprecedented level of earth science interest in the central portion of the IFC, applying methods previously unavailable [from mapping using light detection and ranging (LIDAR) data to the increased use of luminescence and cosmogenic nuclide dating techniques on nonbiological materials] and leaving its geological framework in a fluid state of understanding. Timing of the LGM and subsequent deglacial sequences vary considerably in northern and southern corridor regions (*54*). Currently evolving geoarcheological and paleoecological studies of interior routes indicate that IFC deglaciation initiated by 19,000 years ago. A series of 76 ^{10}Be surface exposure cosmogenic nuclide ages reveal that intermediate and high elevation sites in the Peace River Corridor bottleneck were ice-free between 15,000 and 14,000 years ago, while 22 luminescence dates on eolian sand indicate that a broad subaerially exposed landscape was present by at least ~15,000 years ago (and possibly earlier) and that glacial lakes had already substantially drained (Fig. 3) (*37*, *55*–*57*). Figure 1 illustrates the locations of these key late Pleistocene (and pre-Clovis) geological and paleoecological samples. At least two routes into the Peace River Corridor have been proposed: one along the east side of the Mackenzie Mountains (solid red line in Fig. 1), and the other to the west of the Mackenzie Mountains through the Yukon Plateau and Pelly River valley to the Liard River (dotted red line in Fig. 1) (*58*).

Moreover, ^{14}C dates on taiga vole indicate vegetated conditions in some areas of the bottleneck by at least 14,870 years ago (*59*), and a poplar fragment from Boone Lake in the uplands of northwestern Alberta (*60*) indicates the presence of trees by at least 13,500 years ago. These data suggest a vegetated Corridor well before minimum age estimates of ecological viability derived from the presence of bison and horse at 13,100 years ago (*61*, *62*) and plant macrofossils and environmental DNA at Charlie Lake at 12,600 years ago (*63*) (Fig. 3). Beyond the IFC region, other researchers have identified alternative inland routes through unglaciated Cordilleran areas (*64*–*66*), where resources such as sheep may have persisted through the LGM (*67*). Collectively, these data indicate that the Corridor and adjacent interior areas could have emerged as a potential route for ancestral Native Americans as early as 15,000 to 14,000 years ago, and that movements in either direction along the entire length of the Corridor

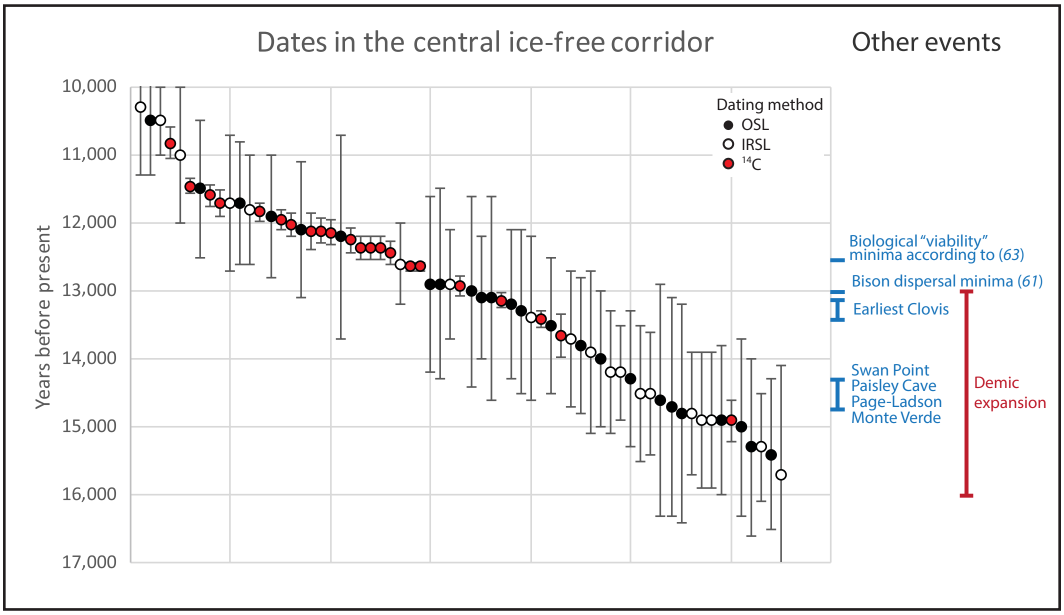

Fig. 3. Chronology of the central IFC. OSL and IRSL dates indicate minima ages of deglaciation and pro-glacial lake drainage (*55*), and calibrated ^{14}C dates indicate minima dates for fauna and vegetation (*12*, *35*, *61*, *63*, *80*–*82*). Demic expansion estimates of Native American ancestors from (*13*). All dates are shown with 1 SD.

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were feasible well before Clovis times (*12*, *68*). Both pathways, interior and coastal, allow viable hypotheses that need not be mutually exclusive and should be further tested.

STEMMED POINTS AS CULTURAL DIAGNOSTICS

Several authors (*1*, *3*) have suggested that a variety of stemmed points in different contexts represent a coastal expansion before 16,000 years ago. This hypothesis is at a nascent stage, rather than [as expressed in (*1*)] the strongest hypothesis on offer. Stemming is a widespread form of haft design innovated numerous times across multiple continents and is thus not an appropriate derived character on which to base a hypothesis of cultural affiliation. No detailed technological analysis has established empirical validity to connect these disparate assemblages. Proponents have noted (*7*) that stemmed points, crescents, and shell middens date between 12,200 and 11,400 years ago before the present (cal yr B.P.), about 1000 to 2000 years after widespread Beringian and Clovis sites. Terrestrially oriented subsistence practices are evident across North America several centuries before the appearance of evidence for coastal adaptations. All the well-dated early coastal sites from North America are younger than the earliest Clovis sites. Two early near-coastal sites in South America, Monte Verde and Huaca Prieta (*69*, *70*), have few technological connections with later Paleoindian groups, including the Western Stemmed tradition of western North America.

Contrary to previous assertions (*1*, *3*), Ushki Lake and Paisley Cave stemmed points are dissimilar to Jomon tanged points in key ways; despite the map symbols, these points come from interior sites reflecting terrestrial adaptations. The Channel Islands sites are not associated with dated stemmed points (and stemmed points in California are not well dated). Triquet Island, apparently dating to after earlier interior Beringian sites, may prove to be an early coastal site, but results for it have not yet been published in a peer-reviewed journal. Several other published coastal sites in this region have been argued by some to contain pre-Clovis archeology, but they have problems including unclear association with human occupation or multiple nonoverlapping dates on the same strata (*12*). There is still debate on the dating of some of the Western Stemmed Tradition material (*71*–*73*), as most of the securely dated sites postdate Clovis by a considerable margin.

CONCLUSIONS

There are widespread patterns that remain unexplained by the coastal hypothesis: Numerous data indicate that the only early populations known in Siberia, Russian Far East, and Beringia had terrestrially oriented economies and technologies (*74*, *75*), including Ushki Lake, cited by (*1*) as part of a coastal migration of stemmed point using populations. Ubiquitous Paleoindian industries are also generally terrestrial (*76*), with relatively limited evidence of coastal exploitation in lower-latitude areas (*2*). East Beringian obsidian distributional analyses show an early reliance on interior sources, with exploitation of coastal sources thousands of years later (*12*). The empirical patterning points toward successful terrestrial adaptations and movement in Siberia, Beringia, and the Americas south of the ice sheets.

Although a wide variety of data summarized here suggest a preponderance of evidence for the IFC route over the NPC route, we do not take a dogmatic position here—both remain viable colonization pathways. Current genetic data provide a relatively wide window of constraints for location of the genetic isolation of Native American ancestors, and later expansion from Siberia into the Americas (and possibly northeast Asia) around 16,000 to 13,500 years ago. As geneticists and archeologists and indigenous communities work together in a respectful and mutually beneficial manner, the opportunities to analyze additional human remains to infer population history in the Americas grow. In parallel, systematic paleogenetic analyses of securely dated sediments (*77*) could potentially directly reveal human presence.

Current archeological data fit with terrestrial or coastal migrations (or both) that probably occurred well after the LGM, most probably after 16,000 years ago and before the widespread Paleoindian occupations around 13,500 years ago. This configuration of the empirical evidence explains the absence of consensus among archeologists and other scientists regarding both routes and timing of the peopling of the Americas, and should prompt us to continue systematic, geomorphologically targeted investigations along both pathways.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/8/eaat5473/DC1

Table S1. Late Pleistocene and Early Holocene components illustrated in Fig.1.

Fig. S1. Locations mentioned in the text.

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