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Genomic evidence for the Pleistocene and recent population history of Native Americans

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How and when the Americas were populated remains contentious. Using ancient and modern genome-wide data, we find that the ancestors of all present-day Native Americans, including Athabascans and Amerindians, entered the Americas as a single migration wave from Siberia no earlier than 23 thousand years ago (KYA), and after no more than 8,000-year isolation period in Beringia. Following their arrival to the Americas, ancestral Native Americans diversified into two basal genetic branches around 13 KYA, one that is now dispersed across North and South America and the other is restricted to North America. Subsequent gene flow resulted in some Native Americans sharing ancestry with present-day East Asians (including Siberians) and, more distantly, Australo-Melanesians. Putative 'Paleoamerican' relict populations, including the historical Mexican Pericúes and South American Fuego-Patagonians, are not directly related to modern Australo-Melanesians as suggested by the Paleoamerican Model.

It is generally agreed that ancestral Native Americans are descendants of Siberian peoples who traversed the Bering Land Bridge (Beringia) from northeast Asia in Late Pleistocene times, and though consensus has yet to be reached, it is mostly conceded that the Clovis archaeological complex, dating to ca. 13 KYA, does not represent the first migration as long supposed (*1*–*7*). Archaeological evidence accumulated over the last two decades indicates that people were south of the North American continental ice sheets more than a millennium earlier and had reached as far south as southern South America by at least ca. 14.6 KYA (*1*–*3*). Interpretations differ, however, regarding the precise spatiotemporal dynamics of the peopling process, owing to archaeological claims for a significantly earlier human presence pre-dating the Last Glacial Maximum (LGM; ca. 20 KYA) (*8*–*10*), and conflicting interpretations of the number and timing of migrations from Beringia based on anatomical and genetic evidence (*11*–*16*). Much of the genetic evidence is from studies of mitochondrial DNA (mtDNA) and Y-chromosome, which as single, uniparentally inherited loci are particularly subject to genetic drift and sex-biased demographic and cultural practices.

Among the principal issues still to be resolved regarding the Pleistocene and recent population history of Native Americans are: (i) the timing of their divergence from their Eurasian ancestors; (ii) whether the peopling was in a single wave or multiple waves, and, consequently, if the genetic differences seen between major subgroups of Native Americans (e.g., Amerindian and Athabascan) result from different migrations or in situ diversification in the Americas (*5*, *6*, *17*, *18*); (iii) if the migration involved ca. 15,000 years of isolation in the Bering Strait region, as proposed by the Beringian Incubation Model to explain the high frequency of unique and widespread American mitogenomes and private genetic variants (*19*–*22*); and, finally, (iv) if there was post-divergence gene flow from Eurasia and possibly even population replacement in the Americas, the latter suggested by the apparent differences in skull morphology between some early (‘Paleoamerican’) remains and those of more recent Native Americans (*23*–*27*). We address these issues using genomic data derived from modern populations, supplemented by ancient specimens that provide chronologically controlled snapshots of the genetics of the peopling process as it unfolded.

We sequenced 31 genomes from present-day individuals from the Americas, Siberia and Oceania to an average depth of ca. 20X: Siberians – Altai (*n* = 2), Buryat (*n* = 2), Ket (n=2), Koryak (*n* = 2), Sakha (*n* = 2), Siberian Yupik (*n* = 2); North American Native Americans – Tsimshian (*n* =); southern North American and Central and South American Natives – Pima (*n* = 1), Huichol (*n* = 1), Aymara (*n* = 1), Yukpa (*n* = 1); and, Oceanians – Papuan (*n* = 14) (*28*) (Table S1). All the genome-sequenced present-day individuals were previously genotyped using single nucleotide polymorphism (SNP) chips (*4*, *29*–*35*) except for the Aymara individual that was SNP chip genotyped in this study (tables S3 and S4). They were selected on the basis of their ancestry profiles obtained with *ADMIXTURE* (*36*) to best represent their respective populations, and to minimize recent genetic admixture from populations of western Eurasian origin (*28*). For populations represented by more than one individual, we also verified from the genotype data that the sequenced individuals did not represent close relatives (*28*). We additionally sequenced 23 genomes from ancient individuals dating between ca. 0.2-6 KYA from North and South America, with an average depth ranging between 0.003X and 1.7X, including specimens affiliated to putative relict Paleoamerican groups such as the Pericúes from Mexico and Fuego-Patagonians from the southernmost tip of South America (*23*, *26*–*28*) (table S5). Finally, we generated SNP chip genotype data from 79 present-day individuals belonging to 28 populations from the Americas and Siberia (*28*) (table S4). All the aforementioned datasets were analyzed together with previously published genomes and SNP chip genotype data (Tables S1, S3, and S4), masking the data for recent European admixture in some present-day Native American populations (*28*).

The structure of Native American populations and the timing of their initial divergence

We explored the genetic structure of Native American populations in the context of worldwide populations using *ADMIXTURE* (*36*), employing a reference panel consisting of 3,053 individuals from 169 populations (table S3) (*28*). The panel included SNP chip genotype data from present-day individuals generated in this study and previously published studies, as well as the 4,000 year-old Saqqaq individual from Greenland (*29*) and the 12,600 year-old Anzick-1 (Clovis culture) individual from Montana (*5*) (table S3). When assuming four ancestral populations (K=4), we found a Native American-specific genetic component, indicating a shared genetic ancestry for all Native Americans including Amerindians and Athabascans (fig. S4). Assuming K=15, there is structure within the Native Americans. Athabascans and northern Amerindians (primarily from Canada) differ from the rest of the Native Americans in sharing their own genetic component (fig. S4). As reported previously, Anzick-1 falls within the genetic variation of southern Native Americans (*5*), while the Saqqaq individual shares genetic components with Siberian populations (fig. S4) (*29*).

To ascertain the population history of present-day American populations in relation to worldwide populations, we generated admixture graphs with *TreeMix* (*28*, *37*). All the modern Siberian and Native American genomes sequenced in this study, except for the North American Tsimshian genome that showed evidence of recent western Eurasian admixture (*28*), were used for this analysis, together with previously published genomes from Africa (Yoruba) (*38*), Europe (Sardinian, French) (*38*), East Asia (Dai, Han) (*38*), Siberia (Nivkh) (*39*) and the Americas (Karitiana, Athabascan, Greenlandic Inuit) (*5*, *38*, *39*) (table S1). The ancient individuals included in the analysis were Saqqaq, Anzick-1 and the 24,000 year-old Mal’ta child from south-central Siberia (*4*). *TreeMix* affirms that all Native Americans form a monophyletic group across all ten migration parameter values, with further diversification into two branches, one representing Amerindians (represented in this analysis by Amerindians from southern North America and Central and South America) and the other Athabascans (Fig. 1B and fig.

S5). Paleo-Eskimos and Inuit were supported as a separate clade relative to the Native Americans, as reported previously (Fig. 1B and fig. S5) (*29*, *39*). Our results show that the Siberian Yupik and Koryak are the closest Eurasian populations to the Americas, with the Yupik likely representing back-migration of the Inuit into Siberia (Fig. 1B and fig. S5).

To assess the pattern of the earliest human dispersal into the Americas, we estimated the timing of the divergence of ancestral Native Americans from East Asians (hereafter, including Siberians) using multiple methods. There is still some debate regarding mutation rates in the human genome (*40*), and this uncertainty could affect our estimates and results.

We applied *diCal2.0* (*28*) (Method 1), a new version of *diCal* (*41*) extended to handle complex demographic models involving multiple populations with migration (*42*), and an identity-by-state (IBS) tract method (*43*) (Method 2) to the modern genome dataset (*28*). With these, we first estimated divergence times between Native Americans and the Koryak of Siberia, one of the genetically closest sampled East Asian populations to Native Americans (fig. S5), using demographic models that reflect a clean split between the populations (*28*). With both *diCal2.0* and IBS tract method, the split of Native Americans (including Amerindians and Athabascans) from the Koryak dates to ca. 20 KYA (*28*) (tables S11A and S12 and fig. S15).

We further applied *diCal2.0* to models with gene flow post-dating the split between Native Americans and Koryak (Fig. 2A) and found that they provided a better fit to the data than the models without gene flow (*28*). Overall, simulated databased on the models inferred using *diCal2.0* and real data show very similar IBS tract length distributions (Fig. 2B) and relative cross coalescence rates (CCR) between pairs of individuals estimated using the Multiple Sequentially Markovian Coalescent (MSMC) method (Method 3) (*28*, *44*) (Figs. 2, C and D). This serves as a confirmation for the model estimates from *diCal2.0*. We evaluated all the three methods using simulations under complex demographic models, and additionally investigated the effects of switch-errors in haplotype phasing on the estimates (*28*).

We then applied the *diCal2.0* model that allows for gene flow between populations after their split to estimate divergence times for Native Americans from more geographically and genetically distant East Asian groups, including the Siberian Nivkh and Han Chinese. As before, the divergence estimates for Amerindians and Athabascans were very similar to one another, ca. 23 KYA (table S11B and figs. S18 and S21).

Hence, our results suggest that Amerindians and Athabascans were, by three different methods, consistently equidistant in time to populations that were sampled from different regions of East Asia, including some proximate to Beringia, and with varied population histories. This suggests that these two major Native American sub-groups are descendants of the same source population that split off from ancestral East Asians during the LGM. It is conceivable that harsh climatic conditions during the LGM may have contributed to the isolation of ancestral Native Americans, ultimately leading to their genetic divergence from their East Asian ancestors.

We also modeled the peopling of the Americas using a climate-informed spatial genetic model (CISGeM), in which the genetic history and local demography is informed by paleoclimatic and paleovegetation reconstructions (*28*, *45*), and found the results to be in accordance with the conclusion of a single migration source for all Native Americans. Using present-day and ancient high coverage genomes, we found that Athabascans and Anzick-1, but not Greenlandic Inuit and Saqqaq (*29*, *39*), belong to the same initial migration wave that also gave rise to present-day Amerindians from southern North America and Central and South America (Fig. 3), and that this migration likely followed a coastal route, given our current understanding of the glacial geological and paleoenvironmental parameters of the Late Pleistocene (fig. S31).

In all cases, the best fit of the demographic models to the IBS tract distribution and relative CCR by MSMC required gene flow between Siberian and Native American populations after their initial split (Figs. 2, B to D). We also found strong evidence for gene flow between Athabascans and the Inuit (table S11B) supported by results from *ADMIXTURE* (fig. S4), *TreeMix* (fig. S5), *D*-statistics employing both whole genome and SNP chip genotype data (*28*, *46*, *47*) (figs. S6 and S8A), and outgroup f_3 statistics using whole genome data (*28*, *47*) (Fig. S12). We attempted to estimate the divergence times between Inuit and Siberians as well as Inuit and Native Americans (table S11 and figs. S19 and S25 to S27), but our analyses were complicated by gene flow between Inuit and Athabascans as well as complex admixture patterns among Arctic groups (fig. S5).

We tested the duration and magnitude of post-split gene flow between Native Americans and Siberians using *diCal2.0* by introducing stopping time of gene flow as a free parameter (*28*). We still obtained the highest likelihood for a divergence time of 22 KYA between Amerindians and Siberians as well as Athabascans and Siberians, although estimates for gene flow rate and end of the gene flow differ (table S11C and fig. S22). Significant gene flow between Athabascans and Siberians seems to have stopped ca. 12 KYA (Table S11C), suggesting a link to the breaching of the Beringian Land Bridge by rising sea levels (*48*).

Overall, our results support a common Siberian origin for all Native Americans, contradicting claims for an early migration to the Americas from Europe (*49*), with their initial isolation and entrance into the Americas occurring no earlier than 23 KYA, but with subsequent admixture with East Asian populations. This additionally suggests that the Mal'ta-related admixture into the early Americans (*4*), representing ancestors of both Amerindians and Athabascans (Fig. 1 and fig. S5), occurred sometime after 23 KYA, following the Native American split from East Asians.

Subsequent in situ diversification of Native American groups

That Amerindian and Athabascan groups were part of the same migration implies that present-day genetic differences observed between them must have arisen later, after ca. 23 KYA. Using the clean-split model in *diCal2.0* on the modern genomes dataset, we estimated that Athabascans and Karitiana diverged ca. 13 KYA (95% confidence interval of ca. 11.5-14.5 KYA, estimated from parametric bootstrap results) (table S11A, fig. S16), which is consistent with results from MSMC (fig. S27) (*28*).

Where the divergence between Karitiana and Athabascans occurred is not known. However, several independent lines of evidence suggest that it is more likely to have occurred in lower latitude North America instead of eastern Beringia (Alaska). These include the equidistant split times of Amerindians and Athabascans to Asian populations, the relatively brief interval between their estimated divergence date range and the age of Anzick-1 (12.6 KYA) (*5*), and lastly, the geographic location of Anzick-1 to the south of the North American ice sheets and its clear affiliation with the 'southern branch' of Native Americans (taken broadly to include Amerindians from southern North America and Central and South America) (*5*), as determined with outgroup f_3 statistics using SNP chip genotype data from present-day worldwide populations (*47*) (Fig. 4 and figs. S13 and S14). Divergence in North America would also be consistent with the known pre-Clovis age sites in the Americas, such as Monte Verde (14.6 KYA) (*50*). The most parsimonious model would be that both Amerindians and Athabascans are descendants of the same ancestral Native American population that entered the Americas then subsequently diversified. However, we cannot discount alternative and more complex scenarios, which could be tested with additional ancient samples.

By the Clovis period (ca. 12.6 KYA), the ancestral Native American population had already diversified into 'northern' and 'southern' branches, with the former including ancestors of present-day Athabascans and northern Amerindian groups such as Chipewyan, Cree and Ojibwa and the latter including Amerindians from southern North America and Central and South America (Fig. 4 and fig. S14). We tested whether later gene flow from East Asian sources, such as the Inuit, might explain the genetic differences between these two branches. Using *D*-statistics on SNP chip genotype data (*47*) masked for non-Native ancestry, we observed a signal of gene flow between the Inuit and northwest Pacific Coast Amerindians such as Coastal Tsimshian and Nisga'a, residing in the same region as the northern Athabascans (*28*) (fig. S8B). However, this signal of admixture with the Inuit, also detected in Athabascans (figs. S6 and S8A), was not evident among northern Amerindian populations located further east such as Cree, Ojibwa and Chipewyan (*28*) (fig. S8C). This suggests that the observed difference between the 'northern' and 'southern' branches is not a consequence of post-split East Asian gene flow into the 'northern branch', and also provides a possible explanation as to why the 'southern branch' Amerindians such as Karitiana are genetically closer to the northern Amerindians located further east than to northwest coast Amerindians and Athabascans (fig. S9).

In contrast to Anzick-1, several of the Holocene individuals from the Americas, including those sequenced in this study as well as the 8,500 year old Kennewick Man (*51*), are closely related to present-day Native American populations from the same geographical regions (Fig. 4 and figs. S13 and S14). This implies genetic continuity of ancient and modern populations in some parts of the Americas over at least the last 8.5 KYA, which is in agreement with recent results from Kennewick Man (*51*).

Evidence of more distant Old World gene flow into some Native Americans

When testing for gene flow between Athabascans and Inuit with masked SNP chip genotype data-based *D*-statistics (*47*) (fig. S8), we observed a weak tendency for the Inuit to be much closer to the Athabascans than to certain Amerindians like the North American Algonquin and Cree, and the Yaqui and Arhuaco of Central and South America (respectively), as compared to other Amerindians such as the Palikur and Surui of Brazil (fig. S8).

To further investigate this trend, we tested for additional gene flow from Eurasian populations into the Americas with *D*-statistics using the masked SNP chip genotype dataset (*47*). We found that some American populations, including the Aleutian Islanders, Surui, and Athabascans are closer to Australo-Melanesians compared to other Native Americans, such as North American Ojibwa, Cree and Algonquin, and the South American Purepecha, Arhuaco and Wayuu (fig. S10). The Surui are, in fact, one of closest Native American populations to East Asians and Australo-Melanesians, the latter including Papuans, non-Papuan Melanesians, Solomon Islanders, and South East Asian hunter-gatherers such as Aeta (fig. S10). We acknowledge that this observation is based on the analysis of a small fraction of the whole genome and SNP chip genotype datasets, especially for the Aleutian Islander data that is heavily masked due to recent admixture with Europeans (*28*), and that the trends in the data are weak.

Nonetheless, if it proves correct, these results suggest there may be a distant Old World signal related to Australo-Melanesians and East Asians in some Native Americans. The widely scattered and differential affinity of Native Americans to the Australo-Melanesians, ranging from a strong signal in the Surui to much weaker signal in northern Amerindians such as Ojibwa, points to this gene flow occurring after the initial peopling by Native American ancestors.

However, how this signal may have ultimately reached South America remains unclear. One possible means is along a northern route via the Aleutian Islanders, previously found to be closely related to the Inuit (*39*), who have a relatively greater affinity to East Asians, Oceanians and Denisovan than Native Americans in both whole genome and SNP chip genotype data-based *D*-tests (table S10 and figs. S10 and S11). On the basis of archaeological evidence and mtDNA data from ancient and modern samples, the Aleutian Islands are hypothesized to have been peopled as early as ca. 9 KYA by 'Paleo-Aleuts' who were succeeded by the 'Neo-Aleuts', with present-day Aleutian Islanders potentially resulting from admixture between these two populations (*52*, *53*). Perhaps their complex genetic history included input from a population related to Australo-Melanesians through an East Asian continental route, and this genomic signal might have been subsequently transferred to parts of the Americas, including South America, through past gene flow events (Fig. 1). Evidence for this gene flow is supported by *diCal2.0* and MSMC analyses showing a weak but recent gene flow into South Americans from populations related to present-day Northeast Asians (Koryak) (Fig. 2C and table S11C), who might be considered a proxy for the related Aleutian Islanders.

Testing the Paleoamerican model

The detection of an Australo-Melanesian genetic signal in the Americas, however subtle, returns the discussion to the Paleoamerican model, which hypothesizes, on the basis of cranial morphology, that two temporally and source-distinct populations colonized the Americas. The earlier population reportedly originated in Asia in the Late Pleistocene and gave rise to both Paleoamericans and present-day Australo-Melanesians, whose shared cranial morphological attributes are presumed to indicate their common ancestry (*23*). The Paleoamericans were, in turn, thought to have been largely replaced by ancestors of present-day Amerindians, whose crania resemble modern East Asians and who are argued to be descendants of later arriving Mongoloid populations (*14*, *23*, *26*, *54*). The presence of Paleoamericans is inferred primarily from ancient archaeological specimens in North and South America, and a few relict populations of more recent age, which include the extinct Pericúes and Fuego-Patagonians (*24*, *25*, *55*).

The Paleoamerican hypothesis predicts that these groups should be genetically closer to Australo-Melanesians than other Amerindians. Previous studies of mtDNA and Y chromosome data obtained from Fuego-Patagonian and Paleoamerican skeletons have identified haplogroups similar to those of modern Native Americans (*55*–*57*). Although these results indicate some shared maternal and paternal ancestry with contemporary Native Americans, uniparental markers can be misleading when drawing conclusions about the demographic history of populations. To conclusively identify the broader population of ancestors who may have contributed to the Paleoamerican gene pool, autosomal genomic data are required.

We, therefore, sequenced 17 ancient individuals affiliated to the now-extinct Pericúes from Mexico and Fuego-Patagonians from Chile and Argentina (*28*), who, on the basis of their distinctive skull morphologies, are claimed to be relicts of Paleoamericans (*23*, *27*, *58*, *59*). Additionally, we sequenced two pre-Columbian mummies from northern Mexico (Sierra Tarahumara) to serve as morphological controls, since they are expected to fall within the range of Native American morphological cranial variation (*28*). We found that the ancient samples cluster with other Native American groups and are outside the range of Oceanian genetic variation (*28*) (Fig. 5 and figs. S32, S33, and S34). Similarly, outgroup f_3 statistics (*47*) reveal low shared genetic ancestry between the ancient samples and Oceanians (*28*) (Figs. S36, S37), and genome-based and masked SNP chip genotype data-based *D*-statistics (*46*, *47*) show no evidence for gene flow from Oceanians into the Pericúes or Fuego-Patagonians (*28*) (fig. S39).

As the Paleoamerican model is based on cranial morphology (*23*, *27*, *58*, *59*), we also measured craniometric data for the ancient samples and assessed their phenotypic affinities to supposed Paleoamericans, Amerindians and worldwide populations (*28*). The results revealed that the analyzed Fuego-Patagonians showed closest craniometric affinity to Arctic populations and the Paleoamericans, while the analyzed female Pericúes showed closest craniometric affinities to populations from North America, the Arctic region and Northern Japan (table S15). More importantly, our analyses demonstrated that the presumed ancestral ancient Paleoamerican reference sample from Lagoa Santa, Brazil (*24*) had closest affinities to Arctic and East Asian populations (table S15). Consequently, for the Fuego-Patagonians, the female Pericúes and the Lagoa Santa Paleoamerican sample, we were not able to replicate previous results (*24*) that report close similarity of Paleoamerican and Australo-Melanesian cranial morphologies. We note that male Pericúes samples displayed more craniometric affinities with populations from Africa and Australia relative to the female individuals of their population (fig. S41). The results of analyses based on craniometric data are, thus, highly sensitive to sample structure and the statistical approach and data filtering used (*51*). Our morphometric analyses suggest that these ancient samples are not true relicts of a distinct migration, as claimed, and hence do not support the Paleoamerican model. Similarly, our genomic data also provide no support for an early migration of populations directly related to Australo-Melanesians into the Americas.

Discussion

That Native Americans diverged from their East Asian ancestors during the LGM and no earlier than 23 KYA provides an upper bound, and perhaps the climatic and environmental context, for the initial isolation of their ancestral population, and a maximum estimate for the entrance and subsequent spread into the Americas. This result is consistent with the model that people entered the Americas prior to the development of the Clovis complex and had reached as far as southern South America by 14.6 KYA. As archaeological evidence provides only a minimum age for human presence in the Americas, we can anticipate the possible discovery of sites that approach the time of the divergence of East Asians and Native Americans. However, our estimate for the initial divergence and entry of Native American ancestors does not support archaeological claims for an initial peopling significantly earlier than the LGM (*8*–*10*).

While our data cannot provide the precise geographical context for the initial peopling process, it has allowed us to more accurately estimate its temporal dynamics. This, in turn, has enabled us to re-assess the Beringian Incubation Model, which, based on mtDNA data and the timing and geographical distribution of archaeological sites, hypothesized a ca. 15,000 year-long period of isolation of ancestral Native Americans in Beringia during the LGM (*19*–*21*). Our results, along with recent findings of mtDNA haplogroup C1 in Iceland and ancient northwest Russia (*60*), do not fit with the proposed 15,000-year span of the Beringian Incubation Model (*19*–*21*). It is possible that a shorter period of isolation occurred (ca. 8 KYA), but whether it occurred in Siberia or Beringia will have to be determined by future ancient DNA and archaeological findings. Given the genetic continuity between Native Americans and some East Asian populations (figs. S4 and S5), other demographic factors, such as surfing during population expansions into unoccupied regions (*61*), may ultimately need to be taken into account to better understand the presence of a large number of high frequency private variants in the indigenous populations of the Americas.

The data presented here are consistent with a single initial migration of all Native Americans and with later gene flow from sources related to East Asians and, more distantly, Australo-Melanesians. From that single migration, there was a diversification of ancestral Native Americans leading to the formation of 'northern' and 'southern' branches, which appears to have taken place ca. 13 KYA within the Americas. This split is consistent with the patterns of uniparental genomic regions of mtDNA haplogroup X and some Y chromosome C haplotypes being present in northern, but not southern, populations in the Americas (*18*, *62*). This diversification event coincides roughly with the opening of habitable routes along the coastal and the interior corridors into unglaciated North America some 16 KYA and 14 KYA, respectively (*63*, *64*), suggesting a possible role of one or both these routes in the isolation and subsequent dispersal of Native Americans across the continent.

Methods

DNA was extracted from 31 present-day individuals from the Americas, Siberia and Oceania and 23 ancient samples from the Americas, and converted to Illumina libraries and shotgun-sequenced (*28*). Three of the ancient samples were radiocarbon dated, of which two were corrected for marine reservoir offset (*28*). SNP chip genotype data was generated from 79 present-day Siberians and Native Americans affiliated to 28 populations (*28*). Raw data from SNP chip and shotgun sequencing were processed using standard computational procedures (*28*). Error rate analysis, DNA damage analysis, contamination estimation, sex determination, mtDNA and Y chromosome haplogroup assignment, ADMIXTURE analysis, ancestry painting and admixture masking, Principal Component Analysis using SNP chip genotype data, *TreeMix* analysis on genomic sequence data, *D*-statistic and outgroup f_3-statistic tests on SNP chip genotype and genomic sequence data, divergence time estimation using *diCal2.0*, an IBS tract method and MSMC, Climate-Informed Spatial Genetic Model analysis, and, craniometric analysis were performed as described (*28*).

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/cgi/content/full/science.aab3884/DC1
Materials and Methods
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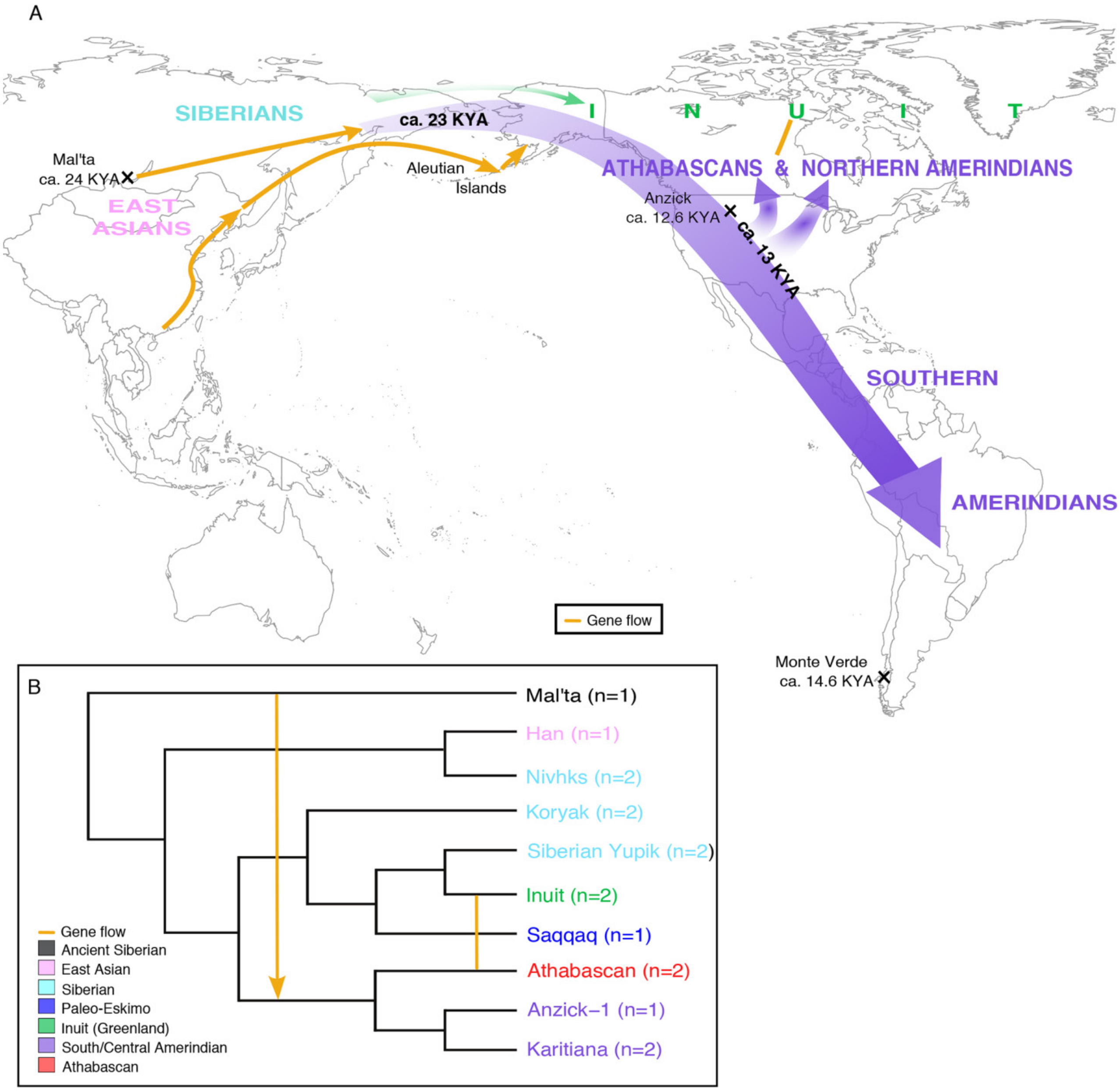
Fig. 1. Origins and population history of Native Americans. (A) Our results show that the ancestors of all present-day Native Americans, including Amerindians and Athabascans, derived from a single migration wave into the Americas (purple), separate from the Inuit (green). This migration from East Asia occurred no later than 23 KYA and is in agreement with archaeological evidence from sites such as Monte Verde (*50*). A split between the northern and southern branches of Native Americans occurred ca. 13 KYA, with the former comprising Athabascans and northern Amerindians and the latter consisting of Amerindians in northern North America and Central and South America including the Anzick-1 individual (*5*). There is an admixture signal between Inuit and Athabascans and some northern Amerindians (yellow line); however, the gene flow direction is unresolved due to the complexity of the admixture events (*28*). Additionally, we see a weak signal related to Australo-Melanesians in some Native Americans, which may have been mediated through East Asians and Aleutian Islanders (yellow arrows). Also shown is the Mal'ta gene flow into Native American ancestors some 23 KYA (yellow arrow) (*4*). It is currently not possible for us to ascertain the exact geographical locations of the depicted events; hence, the positioning of the arrows should not be considered a reflection of these. B. Admixture plot created on the basis of *TreeMix* results (fig. S5) shows that all Native Americans form a clade, separate from the Inuit, with gene flow between some Native Americans and the North American Arctic. The number of genome-sequenced individuals included in the analysis is shown in brackets.



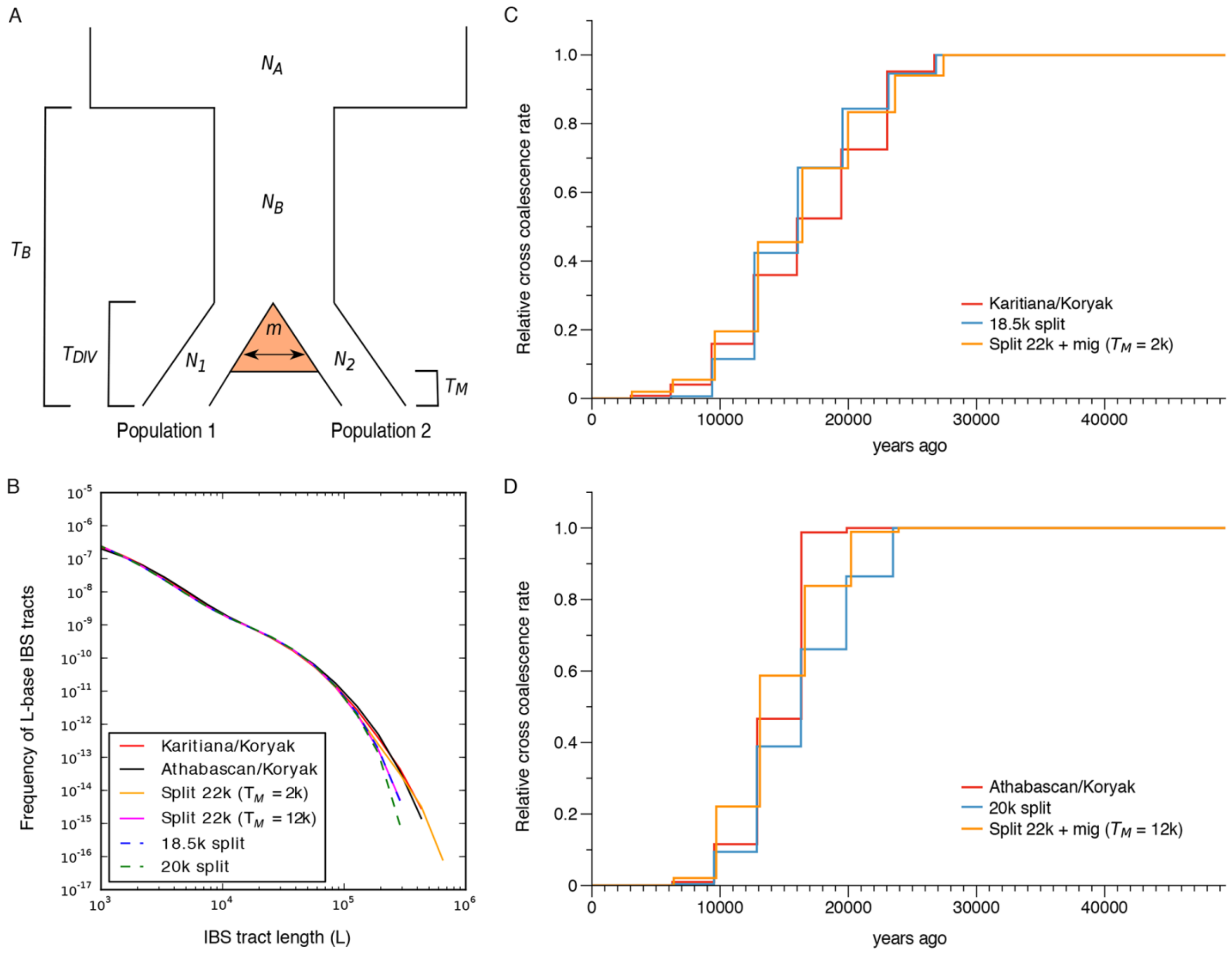


Fig. 2. Divergence estimates between Native Americans and Siberian Koryak. (**A**) The demographic model used allows for continuous gene flow between populations 1 and 2, starting from the time T_{DIV} of divergence and ending at T_M. The backward probability of migration per individual per generation is denoted by *m*. The bottleneck at T_B captures the out-of-Africa event. (**B**) The red and black solid curves depict empirical distributions of IBS tracts shared between Karitiana-Koryak and Athabascan-Koryak, respectively. The orange, pink, dashed blue and dashed green curves depict IBS tracts shared between the two population pairs, simulated under two demographic models based on results from *diCal2.0*. Overall, for Karitiana-Koryak and Athabascan-Koryak, the migration scenarios (orange and pink, respectively) match the empirical curves (red and black, respectively) better than the clean split scenarios (dashed blue and dashed green, respectively), with more long IBS tracts showing evidence of recent common ancestry between Koryaks and Native Americans. (**C** and **D**) Relative cross coalescence rates (CCR) for the Karitiana-Koryak and Athabascan-Koryak divergence (red), respectively, including data simulated under the two demographic models in panel B. In both cases, the model with gene flow (orange) fits the data (red) better than the clean split model (blue). The migration model explains a broader CCR tail in the case of Karitiana-Koryak and the relatively late onset of the CCR decay for Athabascan-Koryak.

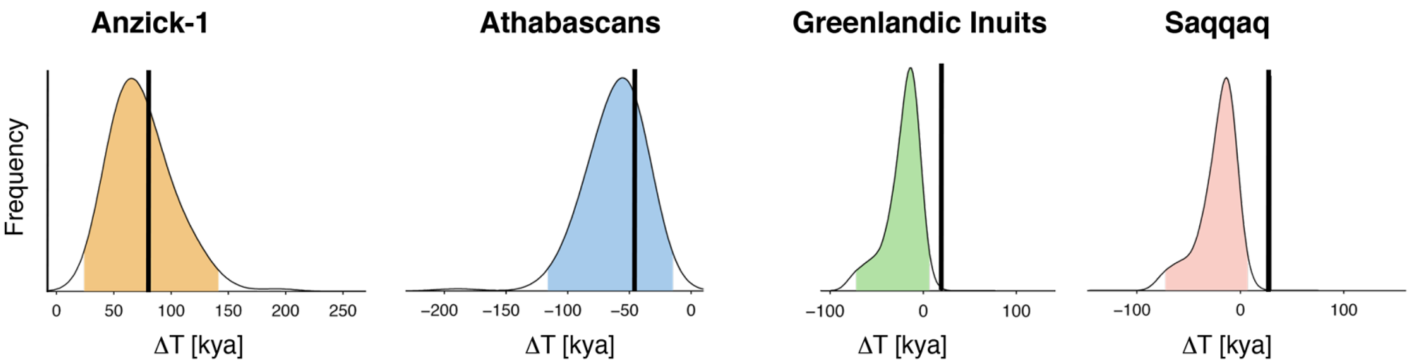


Fig. 3. Testing migrations into the Americas using a climate-informed model. Estimates of difference in genetic divergence between Amerindians (from southern North America and Central and South America) or Koryak versus Athabascan and Greenlandic Inuit and the ancient Saqqaq and Anzick-1 genomes (black vertical lines), compared to posterior probability distribution predicted from a climate-informed spatial genetic model reconstructing a single wave into the Americas (curves, the colored part represents the 95% credibility interval). ΔT for population X is defined as T(X,Koryak)-T(X,Central and South Amerindians) (*28*). Both Anzick-1 and the Athabascans were part of the same wave into the Americas to which other Amerindian populations from southern North America and Central and South America belonged, while the Inuit and Saqqaq are the descendants of different waves (observed values outside the 95% credibility interval).

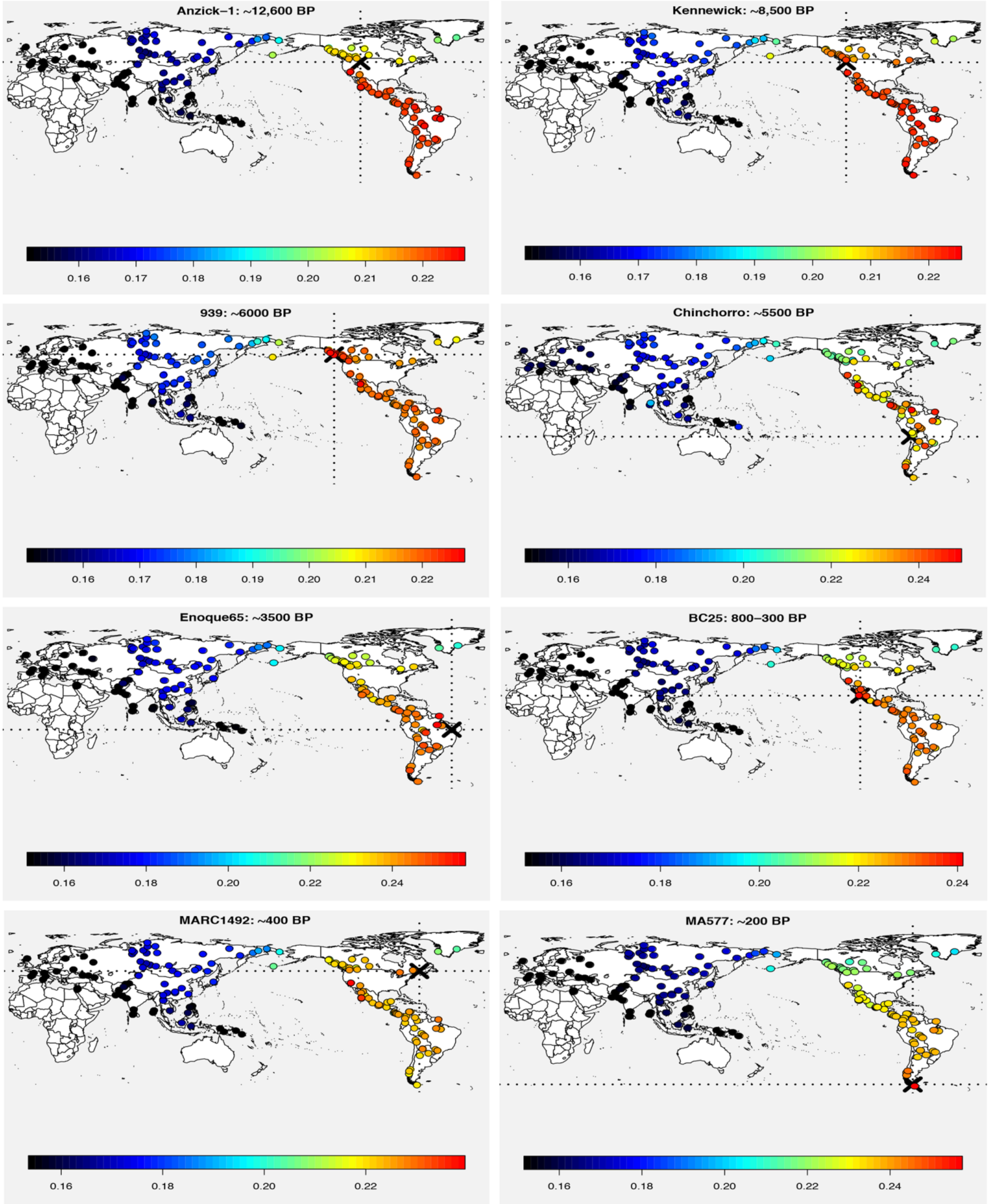

Anzick–1: ~12,600 BP
0.16 0.17 0.18 0.19 0.20 0.21 0.22
Kennewick: ~8,500 BP
0.16 0.17 0.18 0.19 0.20 0.21 0.22
939: ~6000 BP
0.16 0.17 0.18 0.19 0.20 0.21 0.22
Chinchorro: ~5500 BP
0.16 0.18 0.20 0.22 0.24
Enoque65: ~3500 BP
0.16 0.18 0.20 0.22 0.24
BC25: 800–300 BP
0.16 0.18 0.20 0.22 0.24
MARC1492: ~400 BP
0.16 0.18 0.20 0.22
MA577: ~200 BP
0.16 0.18 0.20 0.22 0.24

Fig. 4. Diversification within the Americas. SNP chip genotype data-based outgroup f_3 statistics (*47*) of the form f_3(X, Ancient; Yoruba) were used to estimate the shared ancestry between ancient samples from the Americas and a large panel of worldwide present-day populations (X), including Athabascan and Amerindian groups from North America (table S3), some of which were masked for non-Native ancestry prior to the analysis (*28*). The outgroup f_3 statistics are depicted as heat maps with the sampling location of the ancient sample marked by the dotted lines, and corresponding ranked plots with error bars are shown in fig. S14. BP refers to time before present. We find the Anzick-1 sample to share most ancestry with the 'southern' branch of Native Americans when using multiple northern Native Americans sequenced in this study, consistent with (*5*). The seven Holocene aged samples share most ancestry with Native Americans, with a general tendency to be genetically closer to present-day Native American populations from the same geographical region.

Fig. 5. The Paleoamerican model. (**A**) Principal Component Analysis plot of 19 ancient samples combined with a worldwide reference panel, including 1,823 individuals from (*6*). Our samples plot exclusively with American samples. For plots with other reference panels consisting of Native American populations, see fig. S32. (**B**) Population structure in the ancient Pericú, Mexican mummy and Fuego-Patagonian individuals from this study. Ancestry proportions are shown when assuming six ancestral populations (*K* = 6). The top bar shows the ancestry proportions of the 19 ancient individuals, Anzick-1 (*5*), and two present-day Native American genomes from this study (Huichol and Aymara). The plot at the bottom illustrates the ancestry proportions for 1,823 individuals from (*6*). Our samples show primarily Native American (ivory, >92%) and Siberian (red, ca. 5%) ancestry. For the plot with *K*=13, see fig. S33.