

# Genomic Diversity and Admixture Differs for Stone-Age Scandinavian Foragers and Farmers

Pontus Skoglund,<sup>1\*</sup> Helena Malmström,<sup>1\*</sup> Ayça Omrak,<sup>2</sup> Maanasa Raghavan,<sup>3</sup> Cristina Valdiosera,<sup>4</sup> Torsten Günther,<sup>1</sup> Per Hall,<sup>5</sup> Kristiina Tambets,<sup>6</sup> Jüri Parik,<sup>6</sup> Karl-Göran Sjögren,<sup>7</sup> Jan Apel,<sup>8</sup> Eske Willerslev,<sup>3</sup> Jan Storå,<sup>2</sup> Anders Götherström,<sup>2,†</sup> Mattias Jakobsson<sup>1,9,‡</sup>

Prehistoric population structure associated with the transition to an agricultural lifestyle in Europe remains a contentious idea. Population-genomic data from 11 Scandinavian Stone Age human remains suggest that hunter-gatherers had lower genetic diversity than that of farmers. Despite their close geographical proximity, the genetic differentiation between the two Stone Age groups was greater than that observed among extant European populations. Additionally, the Scandinavian Neolithic farmers exhibited a greater degree of hunter-gatherer-related admixture than that of the Tyrolean Iceman, who also originated from a farming context. In contrast, Scandinavian hunter-gatherers displayed no significant evidence of introgression from farmers. Our findings suggest that Stone Age foraging groups were historically in low numbers, likely owing to oscillating living conditions or restricted carrying capacity, and that they were partially incorporated into expanding farming groups.

The impact of the adoption of agriculture in Europe—the Neolithic transition—has long been debated in archaeology (1) and was one of the first historical questions to be addressed by population geneticists (2). There are contrary schools of thought of the relative importance of migration versus cultural diffusion as the Neolithic lifestyle dispersed across Europe. Farming appeared in the Near East at least 10,000 years before present (B.P.) and spread into Europe via the Balkan and Mediterranean regions, arriving in Scandinavia ~6000 years B.P. (3). Analyses of mitochondrial DNA (4–6) and genomic sequences (7–9) from Stone Age human remains provide evidence that farming and foraging groups were genetically distinct and that admixture between these groups played a role in forming the genetic landscape of modern-day Europe. However, most studies so far have focused on the comparison of ancient individuals to recent groups, and the degree of direct genetic relatedness between ancient groups, gene flow, and within-group genomic variation remains unaddressed.

We generated between 0.01- and 2.2-fold genome-wide coverage for six Neolithic hunter-gatherers from the Pitted Ware Culture context (PWC), four Neolithic farmers from the Funnel Beaker culture context (TRB), and one late Mesolithic hunter-gatherer (Table 1). All of the Neolithic individuals were excavated in Sweden and were dated either directly or contextually to ~5000 years B.P. The late Mesolithic hunter-gatherer individual, directly dated to ~7500 years B.P., was excavated in Sweden in close proximity to the Neolithic hunter-gatherers. All generated sequence data showed evidence of nucleotide misincorporations (figs. S1 to S3) characteristic of postmortem degradation.

The mitochondrial genome was covered to an average depth of at least 23-fold for seven of the individuals, and estimates of contamination were low (Table 1). All six Neolithic hunter-gatherers and the late Mesolithic hunter-gatherer were assigned to haplogroups U or V (Table 1), similar to other Mesolithic and Paleolithic hunter-gatherers (4, 8, 10). The four TRB individuals were assigned to haplogroups H and K, similar to previous results (5) and as observed in other Neolithic farmers in Europe

(6). The Y chromosome of the Ajvide58 individual (Neolithic hunter-gatherer) was assigned to haplogroup I2a1 (table S5), a specific subhaplogroup uncommon in current-day Scandinavia (11). Recent studies suggest that variants associated with phenotypes and immune system genes differ between Stone Age hunter-gatherers and farmers, often from ancestral to derived variants (8, 9). However, we found little evidence of differentiation for these variants (tables S6 to S10) between Neolithic Scandinavian hunter-gatherers and farmers, except for the SLC24A5 locus involved in pigmentation. Ajvide58, like the Mesolithic Iberian LaBranca1 (8), carried the ancestral allele, and both the Tyrolean Iceman (9) and Gökhem2 carried the derived allele (table S8), which is associated with light pigmentation and nearly fixed in current-day Europe and common in current-day South Asia (12).

To investigate the ancient individuals' relationship to the modern-day genetic landscape, we used principal component (PC) analysis with a set of 57 Western Eurasian populations (table S11), including individuals across modern-day Sweden, and projected the 11 Scandinavian Stone Age individuals together with the Mesolithic Iberian LaBranca1 (8), the Paleolithic Siberian MA1 (13), and the Chalcolithic (~5300 years B.P.) Tyrolean Iceman (Fig. 1A) (9). All six Neolithic hunter-gatherers clustered outside the variation

<sup>1</sup>Department of Evolutionary Biology, Uppsala University, Uppsala 752 36, Sweden. <sup>2</sup>Department of Archaeology and Classical studies, Stockholm University, Stockholm 106 91, Sweden. <sup>3</sup>Centre for GeoGenetics, Natural History Museum of Denmark, University of Copenhagen, Copenhagen 1350, Denmark. <sup>4</sup>Department of Archaeology, Environment and Community Planning, La Trobe University, Melbourne VIC 3086, Australia. <sup>5</sup>Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm 171 77, Sweden. <sup>6</sup>Evolutionary Biology Group, Estonian Biocentre and University of Tartu, Tartu 51010, Estonia. <sup>7</sup>Department of Historical Studies, University of Gothenburg, Gothenburg, 405 30, Sweden. <sup>8</sup>Department of Archaeology and Ancient History, Lund University, Lund, 221 00, Sweden. <sup>9</sup>Science for Life Laboratory, Uppsala University, Uppsala 752 36, Sweden.

\*These authors contributed equally to this work.

†Present address: Department of Genetics, Harvard Medical School, Boston, MA 02115, USA.

‡Corresponding author. E-mail: tsarapkin@googlemail.com (A.G.); mattias.jakobsson@ebc.uu.se (M.J.)

**Table 1. Ancient genomic sequence data.** Only sequences with mapping quality of at least 30 were used. mtDNA, mitochondrial DNA; hg, haplogroup; Contam., Contamination estimate; CI, confidence interval; cal years BP, calibrated years BP. Dashes indicate no reliable estimate.

Sample	Context	Genome coverage	mtDNA coverage	mtDNA hg	Contam. (95% CI)	Source	Age (cal years B.P.)*	Genetic sex
StoraFörvar11	Mesolithic	0.09	25.6	U5a1	0 to 22.2%	This study	7500 to 7250	Male
Ajvide52	PWC	0.09	49.4	V	0 to 3.7%	This study and (7)	4900 to 4600	Male
Ajvide53	PWC	0.03	2.5	U4d	—	This study	4900 to 4600	Female
Ajvide58	PWC	2.22	161.7	U4d	0 to 0.6%	This study	4900 to 4600	Male
Ajvide59	PWC	0.01	1.3	U	—	This study	4900 to 4600	Male
Ajvide70	PWC	0.16	52.5	U4d	1.5 to 7.7%	This study and (7)	4900 to 4600	Male
Ire8	PWC	0.04	43.2	U4d	1.6 to 9.6%	This study and (7)	5100 to 4150	Male
Gökhem2	TRB	1.33	91.9	H1c	0 to 2.7%	This study	5050 to 4750	Female
Gökhem4	TRB	0.04	6.5	H	0 to 25.9%	(7)	5280 to 4890	Male
Gökhem5	TRB	0.02	26.2	K1e	0 to 4%	This study	5050 to 4750	Female
Gökhem7	TRB	0.01	32.8	H24	0 to 7.6%	This study	5050 to 4750	Female

\*Details and references for the radiocarbon dating can be found in (17).

of modern populations, which is consistent with a previous study (7). The Mesolithic Scandinavian and the Mesolithic Iberian sample also clustered together in this PC space, which is consistent with population continuity from late Mesolithic groups to Neolithic Scandinavian hunter-gatherers. The Mesolithic and the Scandinavian Neolithic hunter-gatherers do not cluster particularly close to any individuals self-identifying as Swedish Saami (14) or indigenous populations from central Russia. All Scandinavian farmer individuals clustered among southern and central European populations.

To test whether the North-South difference between farmers and hunter-gatherers was consistent for different individuals from each cultural context, we examined which modern-day population had the greatest genetic affinity to particular ancient individuals by identifying the modern-day population with the greatest shared genetic drift with each ancient individual using an outgroup  $f_3$ -statistic (13, 15). The greatest shared genetic drift with Ajvide58 was observed for Lithuanians, whereas the greatest shared genetic drift with Gökhem2 was

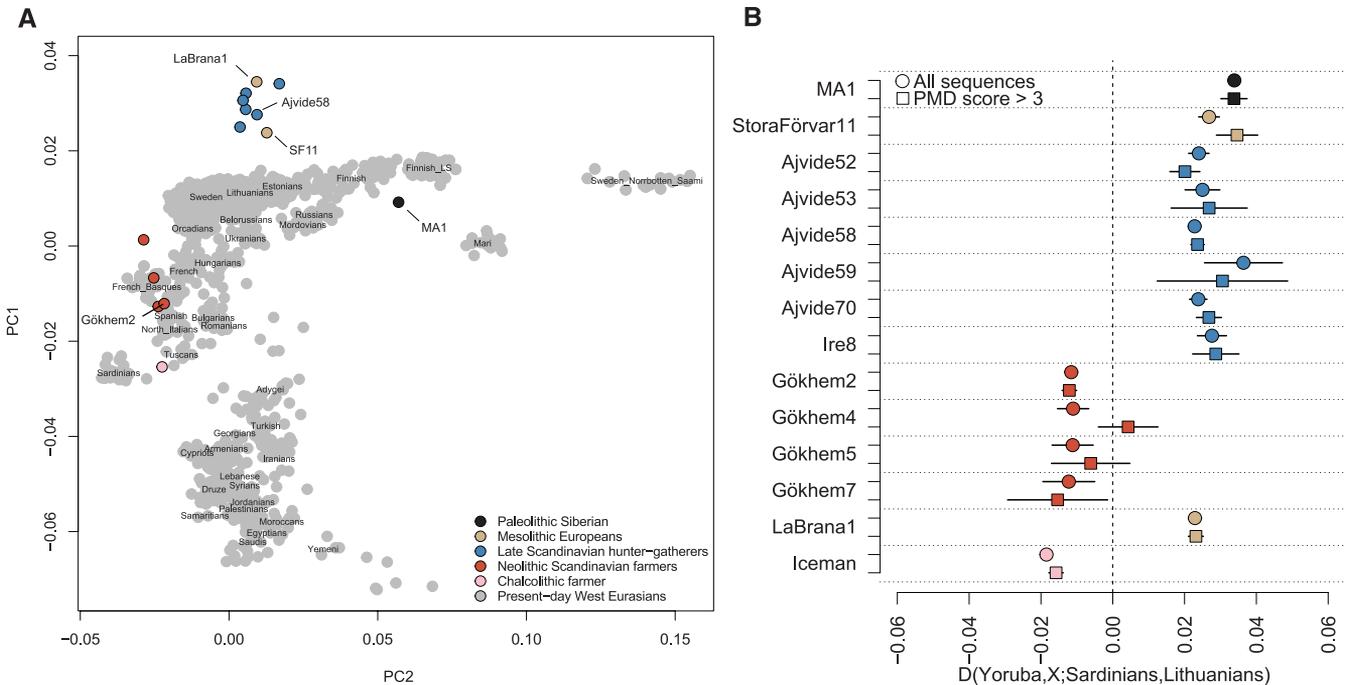
observed for Sardinians (Fig. 1, C and D). Both of these higher-coverage Neolithic individuals show negligible levels of contamination (Table 1).

We also computed  $D$ -statistics (15) to test whether each single Stone Age individual was closer to Lithuanians or Sardinians and found statistically significant segregation between all Stone Age farmers and hunter-gatherers (Fig. 1B); we found the same results when we restricted the analyses to sequences that displayed clear evidence of postmortem damage (16). Focusing on modern-day Swedish groups, which are intermediate to the two Scandinavian Neolithic groups (7), direct tests indicate that modern-day Swedish populations are closer to Ajvide58 (table S14). In addition to Sardinians, many current-day groups from the Near East and southern Europe are significantly closer to Gökhem2 than to Ajvide58 (17).

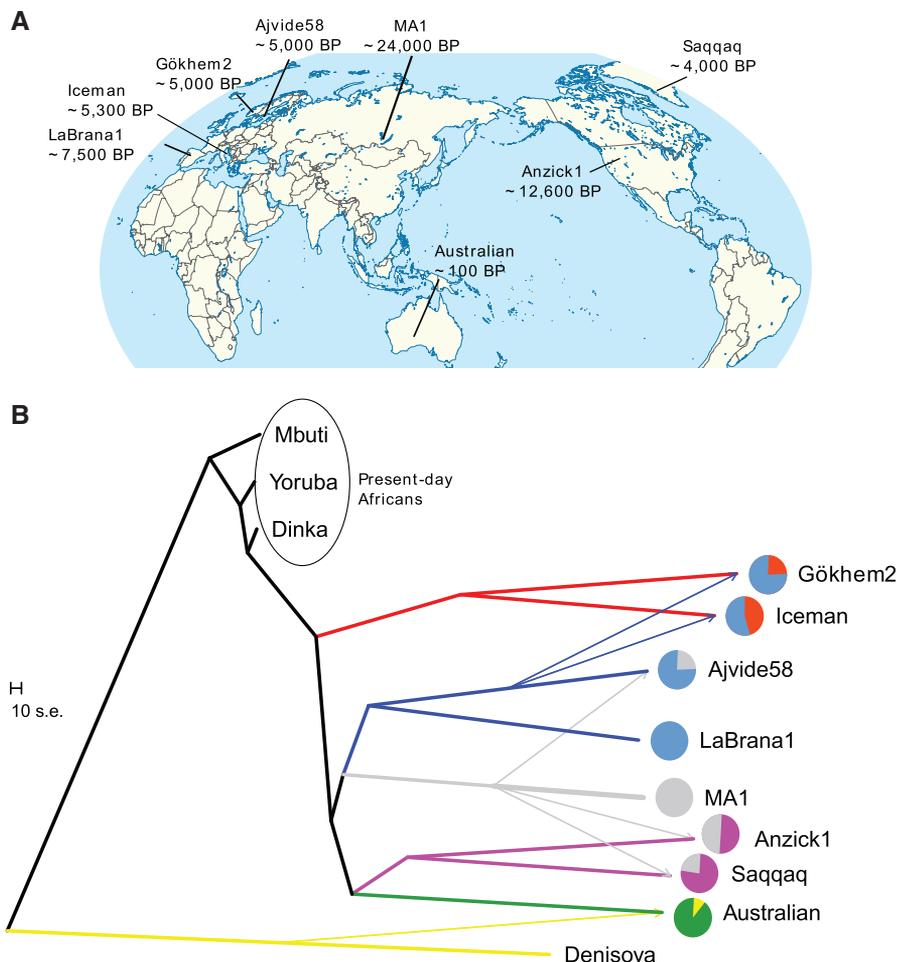
Because both Stone Age farmers and hunter-gatherers contributed genetic material to modern-day European groups (7), we investigated whether this putative admixture between ancestral populations had already begun in the Neolithic. We

tested symmetry between ancient genomes (table S13) and found that although the Tyrolean Iceman is consistent with forming a group with modern-day Sardinians to the exclusion of Stone Age hunter-gatherers ( $D$ -statistics,  $|Z| < 2$ ), the Scandinavian early farmer Gökhem2 is significantly closer to hunter-gatherers ( $2 < |Z| < 8$  for all comparisons with  $>100,000$  loci). In contrast, the Scandinavian hunter-gatherer Ajvide58, which postdates the arrival of agriculture in Scandinavia, shows no significant evidence of admixture ( $|Z| < 2$ ) from early farmers when contrasted with an Iberian Mesolithic individual [LaBrana1, which predates agriculture in Iberia (table S13)]. This suggests that the ancestors of the group represented by Gökhem2 admixed with individuals from hunter-gatherer groups during the northward expansion, whereas the Scandinavian Neolithic hunter-gatherers show no meaningful evidence of admixture with incoming farmers despite at least 40 generations of coexistence in Scandinavia.

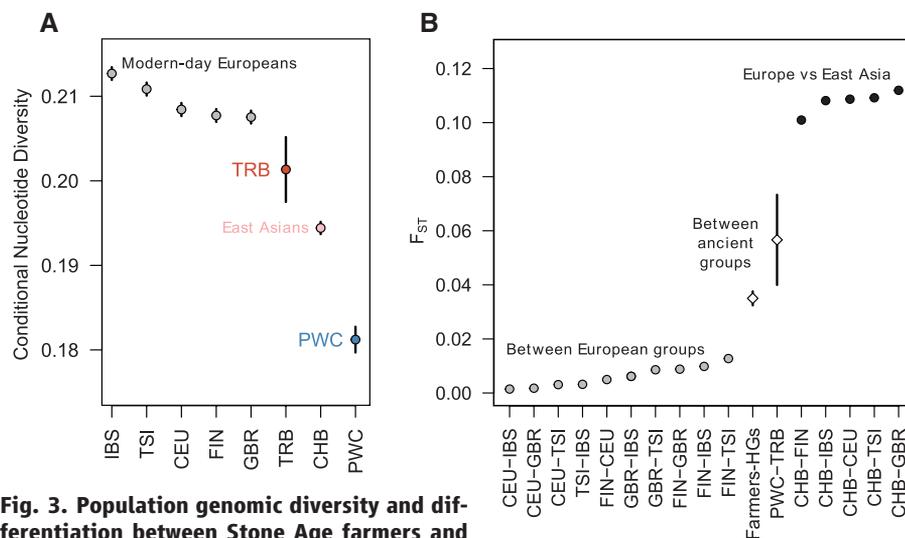
We fitted an admixture graph population model (17) to all publicly available ancient



**Fig. 1. Population structure and genetic affinities of ancient Eurasians.** (A) Ancient individuals were projected on PCs computed on 57 modern-day Western Eurasian groups. (B)  $D$ -statistics assessing affinity to either Lithuanians or Sardinians show stratification between all sequenced ancient Eurasian individuals (circles), which is robust for when only sequences with clear evidence of degradation are used (squares). Error bars represent 1 SE on each side (total 2 SEs). (C) Shared genetic drift between Western Eurasian populations and Ajvide58, a Neolithic hunter-gatherer from Scandinavia. (D) Shared genetic drift between Western Eurasian populations and Gökhem2, an early farmer from Scandinavia.



**Fig. 2. Sample locations and population history model.** (A) Sample locations of ancient human remains that are included in the population history model. (B) Admixture graph of population history fitted to ancient genomes, showing more hunter-gatherer admixture in Neolithic Scandinavian farmers than in central European farmers (table S15).



**Fig. 3. Population genomic diversity and differentiation between Stone Age farmers and hunter-gatherers contrasted with modern-day groups.** (A) Nucleotide diversity estimated as the average pairwise difference at transversion single-nucleotide polymorphisms (SNPs) identified in an African Yoruba individual. (B) Wright's  $F_{ST}$  estimated at transversion SNPs identified in African Yoruba and Mbuti individuals. Error bars represent 1 SE on each side (total 2 SEs), estimated by using a block jackknife procedure across the genome, with 5 Mb in each block. IBS, Spanish; TSI, Tuscan; CEU, Northern and Western European ancestry; FIN, Finnish; GBR, British; CHB, Chinese.

genomes of at least onefold coverage [as well as a version including modern-day individuals from Sardinia and France (17)] and incorporated the gene-flow events identified in the  $D$ -tests above as well as in previous studies (Fig. 2A). Ancestry related to the Upper Paleolithic Siberian MA1 is estimated to  $\sim 15\%$  in Ajvide58 (table S15), which is not found in the more southerly LaBran1, suggesting gene-flow or shared ancestry among Northern Eurasian hunter-gatherer populations. Gökhem2 and the Tyrolean Iceman had ancestry from a basal group separated from all other ancient genomes (Fig. 2B) (17, 18). However, the early farmers also have a substantial amount of ancestry related to European hunter-gatherers, which is significantly higher in Gökhem2 ( $77.2 \pm 6.1\%$ ) as compared with the Tyrolean Iceman ( $56.0 \pm 3.0\%$ ), which is consistent with the  $D$ -statistics results above.

A possible contact phase in Northern Europe between expanding farming populations and hunter-gatherers that may explain the admixture in Gökhem2 is the period between  $\sim 7500$  and  $6000$  years B.P., when the hunter-gatherer Ertebølle culture coexisted for more than a millennium with the early farming Linearbandkeramik (LBK) complex (19, 20). Hunter-gatherers and farmers also coexisted during the Early Neolithic expansion of agriculture into Scandinavia, which may have involved admixture between groups, but little is known about the populations from this period because skeletal remains are scarce.

Comparison of relative levels of genetic diversity in populations can provide information on effective population sizes because smaller populations often have reduced levels of diversity. We computed “conditional nucleotide diversity” (a relative measure of genetic diversity) for the Neolithic Scandinavian groups based on positions that are variable in single African individuals sequenced to high coverage (21) in order to avoid effects of post mortem degradation and sequence errors (17). To avoid effects of potential inbreeding, we always compared variants from separate individuals (17). The Scandinavian Neolithic hunter-gatherer group had significantly lower conditional nucleotide diversity ( $0.181 \pm 0.0015$ ) as compared with that of the Scandinavian Neolithic farmer group ( $0.201 \pm 0.0038$ ) (Fig. 3A and fig. S9). Although the specific properties of ancient DNA may still affect comparisons with sequence data from modern-day individuals, the conditional nucleotide diversity in the hunter-gatherers was also lower than in any modern-day European and a Chinese population (22) analyzed by using the same approach as for the ancient groups. In contrast, the diversity of the TRB is more similar to the level observed in modern-day populations (Fig. 3A).

The conditional approach also allowed us to estimate population genetic differentiation, Wright's  $F_{ST}$ , to  $0.057 \pm 0.017$  between TRB and PWC, and to  $0.035 \pm 0.0026$  between pan-European hunter-gatherers (Ajvide52 and LaBran1) and farmers (Gökhem2 and Iceman). Both of these values are larger than the maximum

observed pairwise  $F_{ST}$  between European populations in the 1000 Genomes project, which was  $0.013 \pm 0.00059$  between Finnish and Italian individuals (Fig. 3B). These estimates suggest greater genetic stratification among Stone Age European groups as compared with current-day groups of European ancestry (7) but that this stratification in Stone Age Europe was correlated with the mode of subsistence instead of geography, as in current-day Europe (23).

The distinct features of the two Neolithic Scandinavian groups—nonsymmetric gene-flow into farmers, low level of diversity among hunter-gatherers, and strong differentiation between groups—have important implications for our understanding of the demographic histories of these groups. The greater diversity in the farmer population may have been influenced by gene flow from hunter-gatherers. However, the low level of genetic diversity in Neolithic hunter-gatherers likely has a demographic explanation, similar to that of the Iberian Mesolithic individual (8). Although we cannot exclude that this low diversity is a feature restricted to the Gotland island hunter-gatherer population, the low diversity may be due to the fact that hunter-gatherer ancestors resided in ice-free refugia in Europe during the Last Glacial Maximum (LGM), potentially causing population bottlenecks. Climatic changes and occasional population crashes also likely affected the population sizes of hunter-gatherers (24, 25). Furthermore, mobility may have decreased among late hunter-gatherer groups, especially when settling in coastal areas (20). Meanwhile, the population ancestral to the Neolithic farmers, that later were to expand across Europe, resided in warmer areas that could sustain larger population sizes during the LGM. Although it is possible that climate also affected populations in southern Eurasia, it may have been in a different manner (26), and farming economies are associated with greater carrying capacity than those of hunter-gatherer economies. It is likely that several factors contributed to the different levels of genetic diversity, and disentangling these processes and assessing their generality in prehistoric Europe may be possible as more genomic data from a wider geographic and temporal range becomes available.

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**Acknowledgments:** We thank L. Gattepaille, M. Metspalu, T. Naidoo, M. Rasmussen, S. Rasmussen, D. Reich, E. Salmela, and P. Wallin for technical assistance and discussions. The SNP data for the modern-day Swedish individuals is available from P. Hall at the Karolinska Institute under a materials transfer agreement. We thank the late L. Beckman for contributing the Saami samples; K.T. (ktambets@gmail.com) retains governance over the Saami and the Mari samples. This project was supported by grants from the Nilsson-Ehle

Foundation (P.S.), Helge Ax:son Foundation (P.S.), Royal Swedish Academy of Science (FOA12H-177 to P.S.), Danish National Research Foundation (E.W. and M.R.), Swedish Research Council (J.A. and J.S.), Berit Wallenberg Foundation (J.A. and J.S.), Wenner-Gren Foundations (T.G.) and European Research Council (M.J.). P.S., H.M., A.G., and M.J. conceived and designed the study. E.W., J.S., A.G., and M.J. supervised the study. H.M., A.O., M.R., and C.V. generated DNA sequence data from ancient human remains. P.S. processed and prepared the data. P.S., H.M., and T.G. analyzed the genetic data, supervised by M.J. with the following contributions: mtDNA and Y-chromosome (H.M. and P.S.); functional SNPs (T.G. and P.S.); and contamination, biological sex, and population genetic analyses (P.S.). K.-G.S., J.S., and J.A. provided archaeological information and interpretation. P.H., K.T., and J.P. contributed samples. P.S., H.M., J.S., A.G., and M.J. wrote the manuscript with input from all authors. Data are available from the European Nucleotide Archive under accession no. PRJEB6090, and data aligned to the human reference genome are available at [www.ebc.uu.se/Jakobsson](http://www.ebc.uu.se/Jakobsson). The authors declare no competing interests.

#### Supplementary Materials

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Materials and Methods  
Supplementary References  
Figs. S1 to S9  
Tables S1 to S16  
References (27–101)

17 March 2014; accepted 16 April 2014  
Published online 24 April 2014;  
10.1126/science.1253448

## Late Pleistocene Human Skeleton and mtDNA Link Paleoamericans and Modern Native Americans

James C. Chatters,<sup>1\*</sup> Douglas J. Kennett,<sup>2</sup> Yemane Asmerom,<sup>3</sup> Brian M. Kemp,<sup>4</sup> Victor Polyak,<sup>3</sup> Alberto Nava Blank,<sup>5</sup> Patricia A. Beddows,<sup>6</sup> Eduard Reinhardt,<sup>7</sup> Joaquin Arroyo-Cabrales,<sup>8</sup> Deborah A. Bolnick,<sup>9</sup> Ripan S. Malhi,<sup>10</sup> Brendan J. Culleton,<sup>2</sup> Pilar Luna Erreguerena,<sup>11</sup> Dominique Rissolo,<sup>12</sup> Shanti Morell-Hart,<sup>13</sup> Thomas W. Stafford Jr.<sup>14</sup>

Because of differences in craniofacial morphology and dentition between the earliest American skeletons and modern Native Americans, separate origins have been postulated for them, despite genetic evidence to the contrary. We describe a near-complete human skeleton with an intact cranium and preserved DNA found with extinct fauna in a submerged cave on Mexico's Yucatan Peninsula. This skeleton dates to between 13,000 and 12,000 calendar years ago and has Paleoamerican craniofacial characteristics and a Beringian-derived mitochondrial DNA (mtDNA) haplogroup (D1). Thus, the differences between Paleoamericans and Native Americans probably resulted from in situ evolution rather than separate ancestry.

Genetic studies of contemporary Native Americans and late prehistoric skeletal remains from the Americas have consistently supported the idea that Native Americans are descended from Siberian ancestors who moved into eastern Beringia between 26,000 and 18,000 years ago (26 to 18 ka), spreading southward into the Americas after 17 ka (1). A complete genome analysis of the 12.6-ka Anzick infant from Montana (2), and mitochondrial DNA (mtDNA) from the 14.1-ka coprolites from Paisley Caves in Oregon (3) and mtDNA from other early (10.5 to 10.2 ka) remains from Nevada and Alaska (4, 5) support this hypothesis. With Anzick linked to the Clovis culture and Paisley Caves to the West-

ern Stemmed tradition—North America's two widespread early archaeological complexes—the genetic evidence for a Beringian origin of the earliest inhabitants of western North America is compelling.

The ancestry of the earliest Americans is still debated, however, because the oldest skeletal remains from the Americas (>9 ka, the Paleoamericans) consistently fail to group morphometrically with modern Native Americans, Siberians, and other northeast Asians (6). Paleoamericans exhibit longer, narrower crania and smaller, shorter, more projecting faces than later Native Americans (7). In nearly all cases, they are morphologically most similar to modern peoples of Africa,



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*Science* **344**, 747 (2014);  
DOI: 10.1126/science.1253448

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