RESEARCH ARTICLE

PHYLOGEOGRAPHY

Early dispersal of domestic horses into the Great Plains and northern Rockies

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The horse is central to many Indigenous cultures across the American Southwest and the Great Plains. However, when and how horses were first integrated into Indigenous lifeways remain contentious, with extant models derived largely from colonial records. We conducted an interdisciplinary study of an assemblage of historic archaeological horse remains, integrating genomic, isotopic, radiocarbon, and paleopathological evidence. Archaeological and modern North American horses show strong Iberian genetic affinities, with later influx from British sources, but no Viking proximity. Horses rapidly spread from the south into the northern Rockies and central plains by the first half of the 17th century CE, likely through Indigenous exchange networks. They were deeply integrated into Indigenous societies before the arrival of 18th-century European observers, as reflected in herd management, ceremonial practices, and culture.

The spread of domestic horses and their integration into Indigenous societies contributed to profound social and ecological transformations across western North America. However, the mechanisms and timing of this transition are poorly understood. Horses and other members of the genus *Equus* originated in North America (*1*, *2*). Horses and equids formed an important component of human lifeways across the continent during the final Pleistocene (*3*–*5*), which is still encoded in some Indigenous oral traditions, including those of the Lakota (*6*). Although Western scholars commonly consider horses to have disappeared at lower latitudes by the early Holocene, environmental DNA suggests their presence in arctic zones as late as 5000 to 6000 years before the present (*7*, *8*). Few archaeozoological studies have carefully addressed their possible persistence at lower latitudes during the Holocene.

Viking colonizers brought horses as far as Greenland during the 10th to 14th centuries CE (*9*) and settled along areas of the Newfoundland coast during the 11th century CE (*10*). There is, however, no direct evidence that Viking horses reached settlements on the mainland (*11*). Instead, most western scholars accept that horses were first reintroduced into the Americas by Spanish settlers in the late 15th century CE, reaching the mainland in the early 16th century CE with the Spanish colonization of Mexico (*12*). During the 17th to 19th centuries CE, colonizing European powers, including the British, Spanish, and French (*13*, *14*), and possibly Russian and Chinese merchants (*15*) imported considerable numbers of horses into western North America.

Whereas horses would generally be categorized as domestic commodities, Indigenous peoples often maintain different relationships with them. Lakota peoples attribute to horses a nationhood status equal to their own. The Lakota–horse relationship is thus one of great reverence, deeply embedded in their identity, spirituality, science, and cosmogony. Lakota peoples do not have concepts for "wild" and "domesticated." In fact, *Šungwakaŋ*—"the Horse Nation"—was neither controlled behind fences nor forced into breeding. Rather, the Lakota peoples strove to cultivate their environment and adapt their lifeways to ensure that *Šungwakaŋ* could live aligned with its natural systems. Within this nation-to-nation alliance, the horse enhanced the abilities of the Lakota with regard to hunting, mobility, healing, and more (*16*). Therefore, for the Lakota peoples, saying "our horse" never reflects ownership but rather responsibility for a sacred relative.

European colonization entirely altered Indigenous social dynamics, hierarchy, and lifeways, introducing profound changes to subsistence modes, movement, and warfare (*17*). Many Indigenous peoples within the Great Plains and American Southwest developed horse-based pastoral or hunting economies and expanded transcontinental networks of raiding and exchange. Some became militarily dominant polities that maintained autonomy and sovereignty into the end of the 19th century CE, with many maintaining this sovereignty today (*18*, *19*).

Historical models for the post-Columbian North American dispersal of horses and their integration into Indigenous cultures are almost exclusively derived from textual sources written by European observers dating largely to the 18th and 19th centuries CE [e.g., (*20*, *21*)]. These sources depict horses first spreading in appreciable numbers north from what is today the American Southwest after the Pueblo Revolt of 1680 CE, when Spanish settlers were temporarily expelled from much of New Mexico (*22*). Given that most of the continent north of New Mexico was terra incognita to European chroniclers, natural and cultural landscapes remained largely uncharacterized until the early 19th century CE (*23*). Furthermore, these Euro-American historic records are often rife with inaccuracies and strong anti-Indigenous biases, depreciating the fundamental relationship between Indigenous peoples and horses (*24*).

Despite representing a major source for understanding the timing and ways in which horses were managed, ridden, and integrated into early societies, archaeological remains of domestic horses from Indigenous contexts are also overlooked (*24*). In this study, we extensively surveyed existing archaeological collections to identify early historic horse specimens with potential for reconstructing early human–horse relationships across the American Southwest and Great Plains (Fig. 1). Together, DNA, archaeozoological, and stable isotope data support the introduction of

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Spanish-sourced domestic horses into Indigenous societies across the plains before the first half of the 17th century CE.

Results

Indigenous societies incorporated horses before the Pueblo Revolt

Of 33 early American equid specimens, we successfully radiocarbon dated 29 and characterized a total of 27 genetically, along with six new specimens from Eurasia (producing nine ancient genomes with an average depth-of-coverage of 2.06× to 12.24×, with substantial genome-wide sequence data for seven additional horse specimens, 0.06× to 0.96×, plus one donkey genome, 1.32×) (Fig. 1). Zonkey software analyses (*25*) confirmed all specimens as horses, except NW36 from Chupaderos, Mexico, which is a donkey jennet (table S1). Although a plateau in the radiocarbon calibration curve prevents easy discrimination between horses dating between 1670 CE and the early 20th century CE, we identified three horses from North American Indigenous contexts conclusively predating the Pueblo Revolt. Near-infrared (NIR) spectrum analysis failed to detect any external contaminants that could have affected radiocarbon dating (materials and methods section 3). The three specimens include a juvenile horse burial from the site of Blacks Fork in southwestern Wyoming, an adult horse cranium from Kaw River, Kansas, and isolated skeletal elements from the site of Paa'ko, New Mexico, along with new analysis of a previously dated specimen from American Falls Reservoir, Idaho, dated to between 1597 and 1657 CE (*26*), which we also assessed with NIR spectroscopy (materials and methods section 3). Assuming that the historic reintegration of horses was bounded temporally by the first presence of European horses on the North American mainland (1519 CE), Bayesian radiocarbon modeling suggests a date of between 1516 and 1599 CE (2σ modeled range) for the initial adoption of horses by Indigenous societies in western North America, with a median boundary date of ~1544 CE (Fig. 1D and materials and methods section 2). Various models provided good measures of agreement (A_{model} and $A_{overall}$ > 80 in all cases), and excluding anomalous values did not meaningfully affect date estimates (materials and methods section 2).

Historic North American horses descend primarily from Spanish genetic sources

Molecular phylogeny revealed that historic and modern North American male horses carried Y-chromosomal haplotypes belonging to the "Crown group" (Fig. 2A), which became dominant within the past ~1500 years, following the increasing popularity of oriental stallions at the origin of most non-Asian domestic bloodlines today, including Arabians, Barbs, and Thoroughbreds (*27*). Mitochondrial phylogenetic inference also rejected maternal continuity from Late Pleistocene horses excavated both north and south of the North American ice sheets (Fig. 2B). Furthermore, BIONJ phylogenetic reconstruction based on autosomal variation at ~7.5 million nucleotide transversions supported a deep divergence between Late Pleistocene North American horses and all present and past lineages identified in Eurasia. This analysis placed both historic and modern North American horses within the genomic variation of modern domestic horses (Fig. 2C). Combined, these phylogenetic reconstructions portray historic and modern North American horses as mainly descending from domestic bloodlines that started spreading outside their native area of the Don-Volga region no earlier than 4200 years ago (*28*).

Admixture graph modeling did not show evidence of gene flow from Late Pleistocene into historic or modern North American horses (fig. S6.2). The individual ancestry profiles of North American horses were consistent with those found in recent domestic Eurasian bloodlines, sporadically including a minor possible contribution from Late Pleistocene North American horses or related lineages (<0.73%) (Fig. 2C). This ancestry was, however, not exclusive to historic or modern North American horses but instead shared across most Eurasian lineages, including a ~4000-year-old horse from Iberia, a ~5100-year-old horse from western Beringia, and several ancient domestic specimens such as a 1447 to 1621 CE sample from Iran (Belgheis). Therefore, the minor ancestry component detected likely reflects multiple ancient contacts between Eurasia and North America through the Beringian land bridge during the past 830,000 years, in line with previously reported studies (*26*) and also apparent in mitochondrial phylogenies (Fig. 2B).

To further characterize the main genetic sources of North American horses, we implemented the qpAdm modeling rotation scheme (*29*), considering either single or two-donor sources among 37 populations. These included

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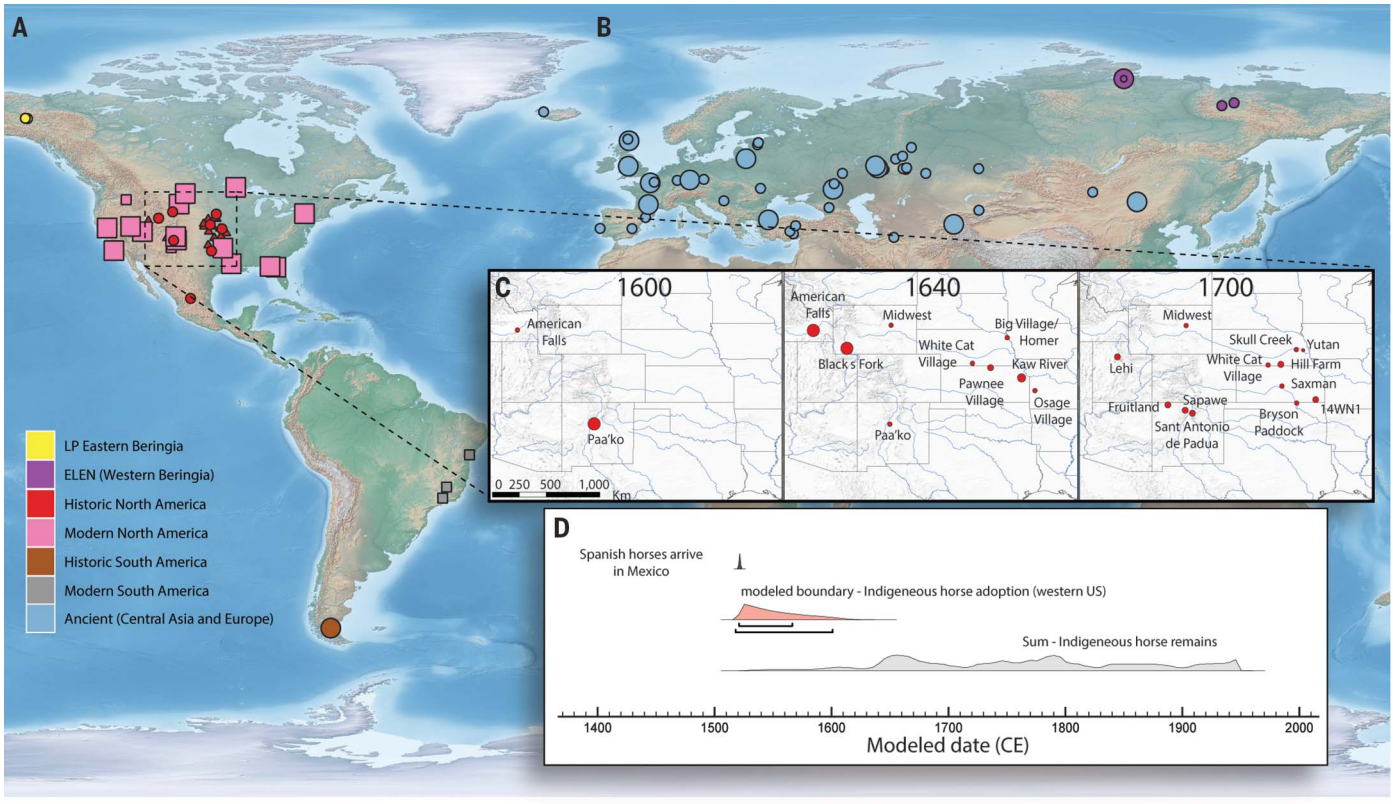


Fig. 1. Sample spatial and chronological distribution. (**A**) American samples. Processed archaeological and/or museum specimens are shown as red triangles, with those successfully sequenced shown as a plain circle; modern specimens are indicated with squares. LP, Late Pleistocene [data from Vershinina *et al.* (*26*)]; ELEN, *Equus lenensis* (Siberia). (**B**) Ancient Eurasian samples in the comparative panel (table S1). Horses from western Beringia are colored in purple, the remaining in blue. Modern genomes are not projected on the map but are provided in table S1. (**C**) Geographic visualization of Bayesian radiocarbon dates for early horse dispersals. Produced in OxCal assuming a uniform prior, with results transferred and visualized in ArcGIS. For each specimen, point diameter corresponds to the portion of total probability distribution within each time slice. Note that presence or absence of a dot does not necessarily indicate occupation during a given time slice (see materials and methods section 2 for detailed chronological modeling of sites thought to predate 1680 CE). (**D**) Modeled radiocarbon boundary for introduction of Spanish-sourced domestic horses into Indigenous societies in the western United States, based on analyzed radiocarbon dates.

Late Pleistocene North American horses as well as a representative panel of both modern and ancient domestic horses from around the globe. This analysis rejected Late Pleistocene North American horses as a possible source for both historic and modern North American horses but supported domestic bloodlines with almost exclusively European origins. Moreover, historic North American horses showed strong genetic affinities to three ancient domestic horses from Spain (Jal5885), Iran (Belgheis), and France (Inva22), dated to between the 15th and 18th centuries CE. This was true for all specimens except the one from Fort Boonesborough (Boones1/Kentucky, 1778 CE), which showed greater genetic affinity to British horses from the 18th century CE (Witter Place) (Fig. 3A). Notably, the influence of British bloodlines is also apparent among modern North American horses, which are commonly modeled as mixtures between Spanish-like (Galiceño and Cartujano) and British-like sources (Thoroughbreds and Welsh, Shetland, and Dartmoor Hill ponies) (table S3 and Fig. 3B). This indicates a temporal shift in the genetic composition of North American horses tracing new inputs from growing British and, later, American presence in eastern North America, and the integration of these horses into Indigenous spheres of interaction. Historic North American horses show greater relatedness to the historic Iberian specimen (Jal5885) than to modern Welsh bloodlines, but modern North American horses show increased Welsh relatedness (Fig. 3, B, C, and E). This is true for all except for feral horses isolated in the Santa Cruz Islands (STCZ3322 and STCZ3327), consistent with their alleged Spanish historical origins. Finally, both historic and most modern North American groups remain closer genetically to Jal5885 than to Icelandic horses (Fig. 3D), and qpAdm modeling revealed ancestry profiles incompatible with genetic contribution from a Viking specimen dating to between the 9th and 11th centuries CE (VHR102) (supplementary materials section 6).

The genomic analyses described above focus on the minute fraction of the genome that is different across all horse lineages investigated. However, the Lakota find key instruction in the >99% of the genome fraction that appears common to all.

Pre–Pueblo Revolt contribution of horses to Indigenous beliefs, trade, and transport networks

Archaeological specimens dated to the early 17th century CE show pathological and osteological evidence of care, management, and use in transport. A horse phalanx from an Indigenous-affiliated context at Paa'ko Pueblo, New Mexico, and a metacarpal from American Falls Reservoir, Idaho, demonstrate the presence of horses among Native communities as far north as Idaho by the first half of the 17th century CE. Furthermore, a foal from Blacks Fork, Wyoming, exhibits entheseal ossification of the nuchal ligament attachment at the rear of the skull at levels typically and exclusively found in horses used for transport or kept in confinement (*30*, *31*). It also features a severe, healed cranial fracture that may have resulted from a kick caused by confinement in close

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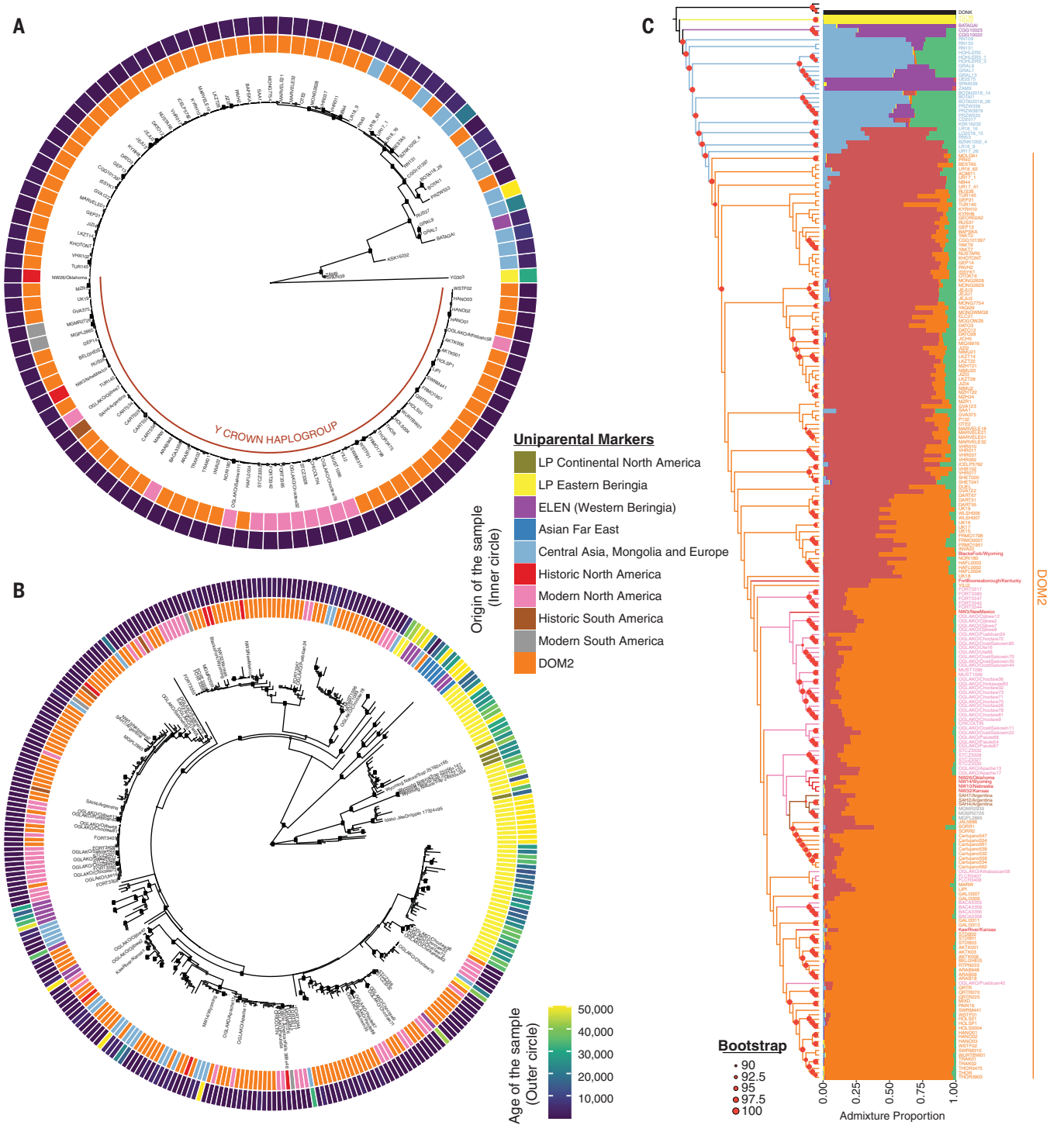


Fig. 2. Phylogenetic affinities. (**A**) Y-chromosomal maximum-likelihood tree (N = 110; 5244 nucleotide transversions). (**B**) Mitochondrial maximum-likelihood tree (N = 340; 16,406 base pairs). (**C**) Neighbor-joining tree based on ~7.5 million nucleotide transversions (N = 241; left), and the corresponding genetic ancestry profiles (right). The ancestry proportions for K = 7 genetic components were estimated using Struct-f4 (*28*). Sample names written as "OGLAKO/Apache" represent modern North American horses culturally associated with Apache communities. LP, Late Pleistocene; ELEN, *Equus lenensis* (Siberia); DOM2, modern domestic lineage descending from a lower Don-Volga genetic source expanding to Eurasia after 4200 years ago.

proximity to other horses (materials and methods section 4). Moreover, this foal was recovered in ritual features alongside coyotes (*32*), indicating that horses were already integrated into existing social and ceremonial traditions by the first half of the 17th century CE. Nuchal ossification along with characteristic damage linked to the use of a metal bit, including erosion of the anterior cementum and enamel of the lower second premolar, were also found in the horse from Kaw River, Kansas, dating to the same period (Fig. 4) (*33*). Several other pathological features reflect the use of a metal curb bit of the type used by early Spanish colonists and later Mexican and

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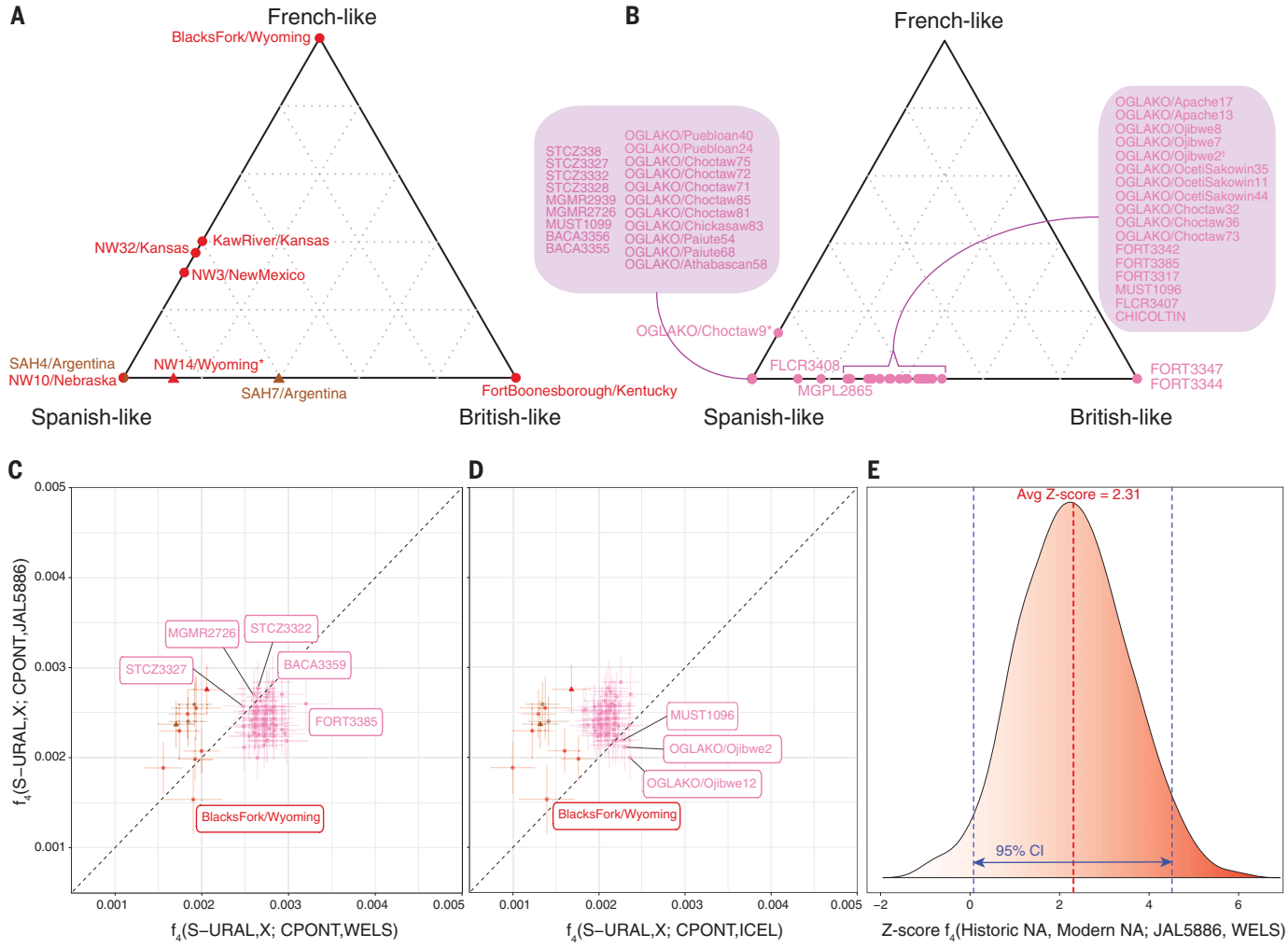


Fig. 3. Temporal changes in the genomic makeup of American horses. (**A**) Ternary plots showing ancestry combinations of the historic horse genomes from North America. (**B**) Ternary plots showing ancestry combinations of the modern horse genomes from North America. Ancestry proportions were estimated using qpAdm modeling and rotating 37 possible donor sources. Models with highest *P* values are shown where multiple models could not be rejected. Asterisks depict two samples for which the ancestry profiles presented correspond to the second best qpAdm model (table S3), while the cross accompanying OGLAKO/Ojiwbe2 indicates that its best qpAdm model involves Galiceño and Icelandic horses as donor populations, instead of British sources (supplementary materials section 6). (**C**) Relative genetic affinities of historic and modern North American horses to Jal5885 versus Welsh horses. Genetic affinities are estimated using f_4-statistics in the form of (S-URAL, X; C-PONT, Jal5885 or Welsh), where X represents historic and/or modern horses from North America, and C-PONT horses from the third millennium CE showing the closest genomic affinities to modern DOM2 domesticates. Triangles show the two historic samples that returned modern radiocarbon dates (NW14/Wyoming and SAH7/Argentina). (**D**) Relative genetic affinities of historic and modern North American horses to Jal5885 versus Icelandic horses. The calculations are the same as in (C), except that modern Welsh horse genomes were replaced by genomes from modern Icelandic horses and the VHR102 Viking sample (850 CE to 1050 CE). An additional qpAdm analysis considering modern Icelandic horses and the sample VHR102 as separate donors of genetic ancestry confirmed that the specimen OGLAKO/Ojibwe2 received introgression from modern Icelandic horses, ruling out genetic contribution from relict populations of Viking horses (supplementary materials section 6). Error bars correspond to twice the standard error estimated from jackknifing. (**E**) Distribution of Z-scores for f_4-statistics of the form (Historic North American Horse, Modern North American Horse; Jal5885, Welsh).

Navajo craftsmen, such as the fracturing of the upper palate caused by the curb (*34*) and arthritis of the temporomandibular joint. Combined, these analyses indicate that early plains horses were already used for mounted riding.

Strontium isotope values for Blacks Fork, reflecting prenatal (dP4, $^{87}Sr/^{86}Sr = 0.70970$) and postnatal (M1, $^{87}Sr/^{86}Sr = 0.70969$) values for the foal, are directly in line with published values for modern fauna from the Green River Basin, where the specimen was found (0.70950 to 0.71000) (*35*, *36*). Although similar values characterize some stretches of the Colorado River tributary system farther to the south (*37*), the Blacks Fork values rule out most of Wyoming, including the border with Utah (*38*). Additionally, strontium isotope results from the Kaw horse, Kansas, are consistent with available values from northeastern Kansas (*39*) but indicate some mobility during the recorded sequence ($^{87}Sr/^{86}Sr = 0.70905$ near the crown, versus $^{87}Sr/^{86}Sr = 0.70930$ near the root), which spans a 12- to 14-month period across the horse's fourth and fifth year of life, according to mineralization schedules (*40*). When considered alongside stable isotopes of oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$), strontium isotope values suggest that the Kaw horse spent part of its life farther north, indicating gradual movement from an area matching reference data from South Dakota, Nebraska, and Iowa (Fig. 4 and materials and methods section 5). Therefore, isotope values from both early horses with complete dentition suggest that the animals were either raised and managed

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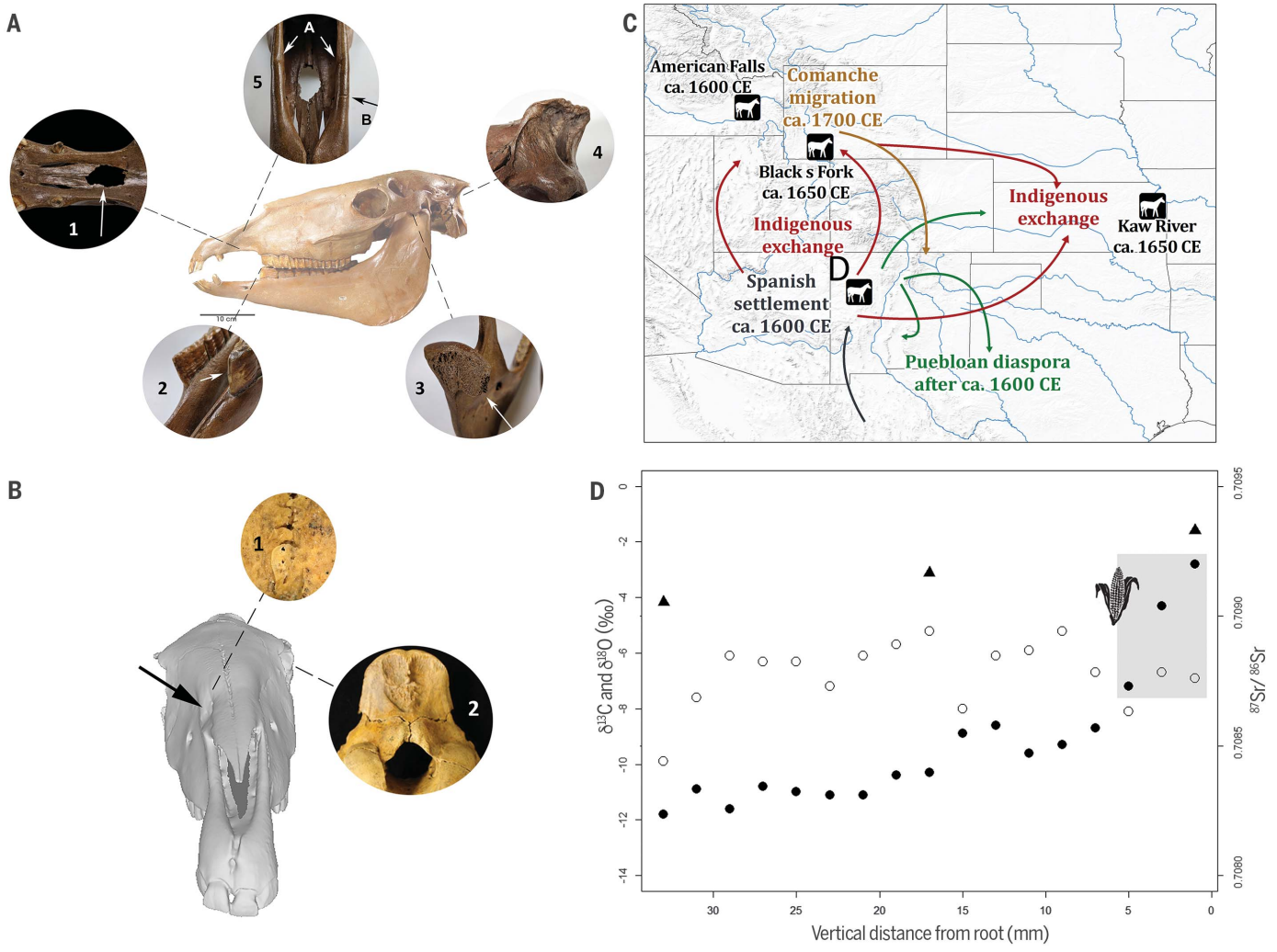


Fig. 4. Horse herding in the 17th century CE. (**A**) Osteological indicators of bridling and riding: (1) palatal damage from curb bit; (2) bit damage to anterior margin of lower second premolar; (3) osteoarthritis at the temporomandibular joint; (4) entheseal changes to the nuchal ligament attachment site; and (5) remodeling of the premaxilla. (**B**) Osteological indicators of human activity: (1) Healed kick fracture in young foal, suggesting health care. The inset shows healing at 50× magnification. (2) Ossification of the nuchal ligament, indicating use in transport or confinement and/or tethering. (**C**) Modeled northward dispersal of horses. Model based on archaeological discoveries and consideration of historically documented cultural developments and migrations. (**D**) Isotopic evidence for foddering. Stable carbon and oxygen and strontium isotope sampling locations for the Kaw River horse, as measured in millimeters from the root (lower-right third molar). Sampling locations are represented on the *x* axis as the midpoint of a 2-mm section (e.g., the section from 0 to 2 mm is shown as "1" on the graph). Filled triangles show strontium isotope values, with stable carbon values represented by filled circles, and stable oxygen values as open circles. [Kaw horse image credit: E. Scott]

locally (Blacks Fork) or within a territory extending even farther away from the European colonial sphere (Kaw).

A $\delta^{13}C$ spike toward the end of the sampled section of the Kaw molar shows a strong input of C_4-pathway plants, potentially reflecting winter foddering with the Indigenous domestic crop maize (materials and methods section 5), a traditional practice among Plains groups, including the Pawnee. Other situations, such as herd movement south and west to rangeland higher in C_4 grasses or during events such as seasonal bison hunts, could account for the enriched value but are not consistent with strontium and oxygen isotope data. Pawnee (*Chaticks si Chaticks*) villages typically relied on stores of maize to subsist through the winter (*41*), and the practice of winter foddering horses with maize in the northern Missouri River region is documented ethnographically during the 18th and 19th centuries CE, including among the Pawnee (*42*, *43*). Regardless of whether the Kaw specimen was affiliated with ancestral Pawnee or another Central Plains nation, our results indicate the presence of horses in Indigenous cultural and economic systems of the Missouri River drainage during the first half of the 17th century CE.

Discussion

Our archaeological analyses show the dispersal of domestic horses from Spanish settlements in the American Southwest to the northern Rockies and central Great Plains by the first half of the 17th century CE at the latest. They provide evidence of local raising and veterinary care of horses, likely foddering with domestic maize, and use of horses in transport by Indigenous peoples by this time. A directly dated radiocarbon specimen from Paa'ko Pueblo in northern New Mexico shows that horses reached the region via Indigenous groups before Spanish colonization of the American Southwest, as previously hypothesized (*44*, *45*). Moreover, our new temporal framework shows that horses were present across the plains long before any documented European presence in the Rockies or the central plains. Despite their

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Iberian genetic makeup and earlier arguments attributing one of these horses to Spanish exploration (*46*), strontium, carbon, and oxygen isotope results suggest that these animals were raised and died locally. Osteological analyses also provide some indication that horse dispersal was tied to broader economic links; the Kaw River horse was indeed controlled with a European-style metal curb bit, and the Blacks Fork horse body was cut with metal tools (*32*). Therefore, a possible mechanism of horse dispersal was exchange across Indigenous networks at the margins of New Mexico and the American Southwest (*47*). Once acquired, horses could have moved via ancient trade routes based on kinship ties and social networks established throughout the Great Plains and Rockies millennia before European contact (*48*). The dispersal of Puebloan groups toward the northeast, from Spanish New Mexico into western Kansas, provides another mechanism for the transmission of domestic horses into the Central Plains.

Our findings have deep ramifications for our understanding of social dynamics in the Great Plains during a period of disruptive social changes for Indigenous peoples. The area of southwestern Wyoming including Blacks Fork is considered to be a homeland for the Shoshonean-speaking ancestral Comanche (Nʉmʉnʉʉ), who migrated to the southern plains of Texas, New Mexico, Colorado, and Oklahoma before the early 18th century CE (*49*, *50*). The drive to acquire horses from Spanish New Mexico is often cited as a likely mechanism for this transcontinental movement (*50*). However, our new data—which align with some Comanche and Shoshone oral accounts (*51*) (materials and methods section 7)—suggest that ancestral Comanche had already integrated horse raising, ritual practices, and transport into their lifeways at least a full half century before their southward migration, effectively moving to the southern plains as horse herders. Once in the southern plains, the Comanche were able to marshal these advantages, along with their herding and equestrian skills, to build an empire on horse and bison trade by the middle of the 18th century CE (*19*). By the time Europeans arrived in southwestern Wyoming, the area was already a critical "secondary diffusion center" for horse transmission to Northern Plains groups (*17*, *52*). Considering the small body of archaeological data available, our findings raise the possibility of rapid, non-European transmission of horses farther northward, including the Columbia Plateau, the Canadian Rockies, and the middle and upper Missouri regions.

DNA data from horses currently caretaken and historically protected by the Oglala Lakota were included in this study. All protocols for the transmission of sacred and traditional knowledge were followed, as outlined by our Lakota Elder Knowledge Keeper Internal Review Board. They provide further context of the findings, which clarifies the Lakota culture and their relationship with the horse. Chief Joe American Horse states: "Horses have been part of us since long before other cultures came to our lands, and we are a part of them. The Horse Nation is our relative. We always protect our relatives and the next seven generations. We stand with the horse and we will always do so however it has evolved through its journey. That is what being Lakota is" (original quote, in Lakota, provided in materials and methods section 7). This study established that Indigenous peoples were living and interacting with the horse before the Pueblo Revolt of 1680 CE, which was the earliest date accepted by Western science. However, current genetic evidence shows that the horses caretaken by Indigenous peoples from as early as the first half of the 17th century CE do not share an excess of genetic ancestry with Late Pleistocene North American horses. Given that the Horse Nation is foundational to Lakota lifeways (*16*), one possible implication of this finding is that relationships of the kind developed by Lakota peoples could have already been in place by the Late Pleistocene. Such life management practices may even have extended to other members of the horse family at that time. Testing these implications requires further paleontological, archaeological, genetic, and ethnographic research. Dr. Antonia Loretta Afraid of Bear-Cook adds: "The Horse Nation always chose their own mates. Bringing in new blood is a replenishment and renewal process of life that we celebrate. It strengthens our *wé* (the life force from our blood). No matter how our horses may have transformed, or where they are around the world, we will always call to them. Together we are home" (original quote, in Lakota, provided in materials and methods section 7). This study demonstrates that colonization did not just drastically affect Indigenous peoples but also their horses, whose genetics captures an ancestry shift from Spanish to British bloodlines. Dr. Antonia Loretta Afraid of Bear-Cook thus reminds us that the current genetic makeup of the horse does not change the Lakota responsibility toward *Šungwakaŋ*. In fact, for the Lakota and other Indigenous peoples with deep ancestral relationships with the horse, their evolution was not to be feared or controlled, but rather something to be respected. Protecting horses now, regardless of their origins, is in fact protecting the Lakota and other Indigenous lifeways. A commitment to protecting these is a commitment to protect all life.

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Early dispersal of domestic horses into the Great Plains and northern Rockies

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Making a horse culture

Horses evolved in North America and dispersed to Eurasia across the Bering Land Bridge. They continued to evolve and were domesticated in Eurasia, but, as far as we know, they became extinct in North America by the late Pleistocene and were then reintroduced by European colonizers. Taylor *et al*. looked at the genetics of horses across the Old and New Worlds and studied archaeological samples. They found no evidence for direct Pleistocene ancestry of North American horses, but they did find that horses of European descent had been integrated into indigenous cultures across western North America long before the arrival of Europeans in that region. —SNV

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