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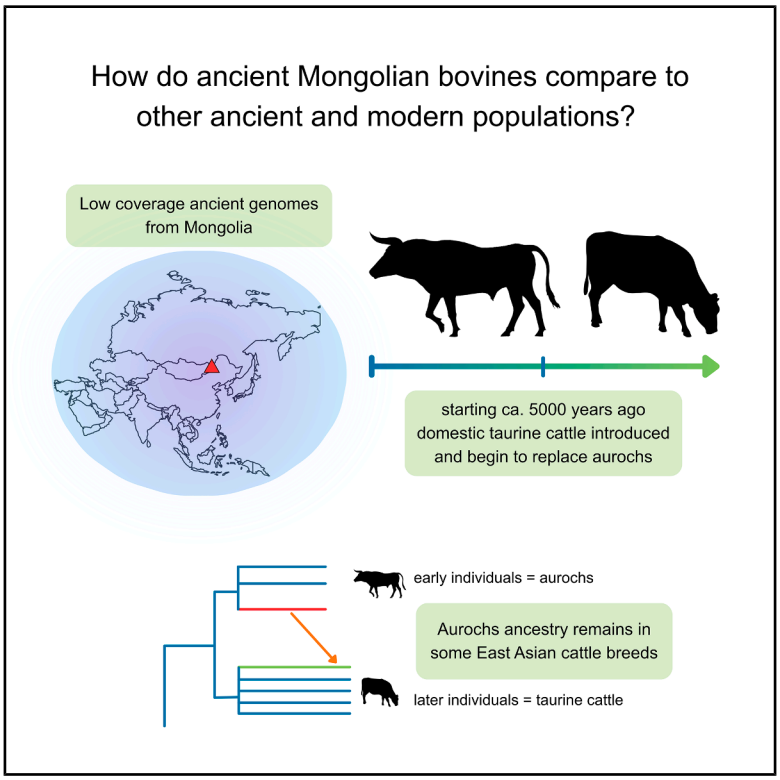
Ancient Mongolian aurochs and cattle genomes reveal population shifts associated with the expansion of herding

Graphical abstract



Highlights

- We sequence Mongolian bovine genomes from 7700 to 2000 cal BP
- Population turnover between North Asian Aurochs and taurines begins at 5000 cal BP
- Ancient taurines interbred with Mongolian aurochs
- Some modern breeds carry signatures of ancient Mongolian aurochs

Authors

Katherine Brunson, Kelsey E. Witt, Susan Monge, ..., Byambatseren Batdalai, Ganbaatar Galdan, Lisa Janz

Correspondence

lisa.janz@utoronto.ca

In brief

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Ancient Mongolian aurochs and cattle genomes reveal population shifts associated with the expansion of herding

Katherine Brunson,[1,22] Kelsey E. Witt,[2,22] Susan Monge,[3,4] Sloan Williams,[4] Robin Singleton,[2] David Peede,[5,6,7] Davaakhuu Odsuren,[8,9] Dashzeveg Bukhchuluun,[10] Asa Cameron,[10,11] Paul Szpak,[12] Chunag Amartuvshin,[13,14] Joshua Wright,[15] Sarah Pleuger,[16] Myagmar Erdene,[13] Dashtseveg Tumen,[13] Leland Rogers,[17] Dorjpurev Khatanbaatar,[18] Victoria Wilson,[14] Zoljargal Altanbayar,[13] Adiyasuren Molor,[19,20] Byambatseren Batdalai,[14] Ganbaatar Galdan,[9] and Lisa Janz[21,23,*]

[1]Archaeology Program, Wesleyan University, Middletown, CT 06459, USA
[2]Department of Genetics and Biochemistry and Institute for Human Genetics, Clemson University, Clemson, SC 29634, USA
[3]Department of World Archaeology, Leiden University, Leiden 2311 EZ, the Netherlands
[4]Department of Anthropology, University of Illinois Chicago, Chicago, IL 60607, USA
[5]Center for Computational Molecular Biology, Brown University, Providence, RI 02912, USA
[6]Department of Ecology, Evolution, and Organismal Biology, Brown University, Providence, RI 02912, USA
[7]Institute at Brown for Environment and Society, Brown University, Providence, RI 02912, USA
[8]Department of History, Mongolian National University of Education, Sukhbaatar District, Ulaanbaatar 210648, Mongolia
[9]Institute of Archaeology, Mongolian Academy of Sciences, Ulaanbaatar-51, Ulaanbaatar, Mongolia
[10]Department of Anthropology, Yale University, New Haven, CT 06511, USA
[11]Department of Anthropology, The Pennsylvania State University, University Park, PA 16802, USA
[12]Department of Anthropology, Trent University, Peterborough, ON K9J 6Y1, Canada
[13]Department of Archaeology, Anthropology, and Demography, National University of Mongolia, Ulaanbaatar 210646, Mongolia
[14]Institute of Nomadic Archaeology, National University of Mongolia, Ulaanbaatar 13343, Mongolia
[15]Department of Archaeology, University of Aberdeen, King's College, Aberdeen AB24 3FX, UK
[16]School of History, Classics and Archaeology, University of Edinburgh, Edinburgh EH8 9AG, UK
[17]Department of Anthropology, University of North Carolina Wilmington, Wilmington, NC 28403, USA
[18]Department of History, Culture and Tourism, University of Science and Technology, Ulaanbaatar 13381, Mongolia
[19]McMaster Ancient DNA Centre, McMaster University, Hamilton, ON L8S 4L9, Canada
[20]Department of Anthropology, McMaster University, Hamilton, ON L8S 4L9, Canada
[21]Department of Anthropology, University of Toronto Scarborough, Scarborough, ON M1C 1A4, Canada
[22]These authors contributed equally
[23]Lead contact
*Correspondence: lisa.janz@utoronto.ca
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SUMMARY

Humans hunted aurochs (*Bos primigenius*) for millennia in Mongolia prior to the introduction of domestic cattle sometime after ca. 5,000 years ago. Here, we present genomic data from Mongolian aurochs and domestic cattle at key points in Mongolia's prehistory to understand changes in population history associated with the adoption of domestic taurine cattle (*B. taurus*). We compare these low-coverage genomes with other cattle genomes worldwide and make comparisons about the nature of bovine populations before and after the adoption of domestic cattle. Individuals dating to before the introduction of taurine cattle have shared ancestry with North Asian aurochs, and individuals dating after the introduction of taurine cattle are related to other ancient East Asian cattle from archaeological sites such as Shimao in the Ordos region. We identify unique connections between ancient Mongolian aurochs and cattle and modern cattle breeds from Central China and Tibet.

INTRODUCTION

The extinct aurochs (*Bos primigenius*) was once widespread across Eurasia and Africa, with populations in Southwest Asia giving rise to domestic taurine cattle (*B. taurus*) by at least 10,000 years ago.[1–3] Until recently, most zooarchaeological and paleogenomic research on aurochs and domestic cattle has focused on Western Eurasia and Europe, revealing complex histories of admixture and management.[3] Paleogenetic studies have also identified a unique East Eurasian aurochs population that survived in north Asia until at least 3,700 years ago[4–7] and likely later into the Bronze Age at Chinese sites such as the

late Shang Dynasty capital at Anyang ca. 1250–1046 BCE.[8] This population of aurochs contributed some ancestry to domestic cattle in East Asia,[5,6,9] but questions remain about exactly when aurochs went extinct, whether people ever experimented with managing aurochs, and the extent of interbreeding between East Asian aurochs and ancient domestic cattle populations. Here, we begin to address these lingering questions using aurochs and cattle remains from archaeological sites on the eastern Mongolian Plateau, a region of particular interest due to long-standing evidence for intensive human-bovine interaction. We include individuals associated with specialized aurochs hunting and burial contexts dating to an early period in the adoption of pastoralism. The primary goal is to understand whether the legacy of specialized relationships with aurochs included genomic contribution to local domesticated breeds. In other words, were lineages of these important prey species incorporated into domesticated herds?

The first comprehensive study of aurochs genomes worldwide identified four main populations: one in Europe, one that included the ancestors of domestic taurine cattle, one in South Asia that gave rise to domestic indicine cattle, and one in North Asia, which included samples from Siberia and Central Asia.[6] During and after domestication, admixture between aurochs, taurine cattle, and South Asian indicine/zebu cattle (*B. indicus*) was common in Western Eurasia[3,6] and has also been found in East Asia.[5,9]

The zooarchaeological record shows that taurine cattle were introduced to Northeast Asia by Afanasievo groups who arrived around 5,300 years ago.[10] Taurine cattle appear in the Yellow River Valley by about 4,500 years ago and are more common after 4,000 years ago.[11,12] One isolated individual in northeastern China is dated as early as 5,300 years ago,[13] but it is not until around 3,500 years ago that the species became widespread across the eastern Mongolian Plateau.[14] The lack of well-studied Late Neolithic/Early Bronze Age sites in the region continues to limit our understanding of early adoption. Indicine cattle have played a minor role in Northeast Asia and are less well-understood, being first present in southern China by the late Warring States period (ca. 500 BCE).[15] In East Asia today, taurine cattle breeds are more common in the north and indicine cattle breeds are more common in the south, suggesting different histories of introduction and adoption for taurine and indicine breeds. There are many taurine-indicine hybrid breeds, and admixture between domestic cattle and other indigenous East Asian bovines such as yak, gayal/mithun, and banteng is also common,[16–19] with taurine-yak hybrids especially common in Central Mongolia.[20,21] Genomic evidence suggests that ancient East Asian domestic cattle populations also hybridized with local aurochs.[22] For example, paleogenomic studies have revealed evidence for gene flow from northern Chinese aurochs into ancient East Asian domestic cattle populations on the Ordos Plateau at Shimao, Shaanxi Province (ca. 4,000 years ago),[17] traces of East Asian aurochs ancestry in modern domestic breeds, especially breeds found today on the Tibetan Plateau,[9] and evidence for aurochs-domestic cattle hybrids on the Tibetan Plateau ca. 3,700 years ago.[5]

The steppe and desert-steppe regions of eastern Mongolia provide an exciting context for exploring how the genetic history of East Asian aurochs and early cattle relates to changes in the archaeological record. Small scatters of ceramic sherds and stone tools characterize pre-pastoralist hunter-gatherer sites in western Mongolia, where there has been little research on hunter-gatherer populations who inhabited the area upon the arrival of the Afanasievo, who are known for their monumental burial architecture, fully developed pastoral lifeways, and knowledge of bronze metallurgy.[10] The record of hunting and gathering in eastern Mongolia is better known. Three millennia prior to the adoption of domestic cattle, hunter-gatherers appear to have subsisted on a wide range of plant foods, large ungulates, and small prey, but with a clear emphasis on large ungulates.[23,24] Neolithic components from Zaraa Uul (samples B11, B13, B14, and B15) and Margal (samples B21 and B23) represent typical mid-Holocene hunter-gatherer campsites fitting into a generalized pattern of decreased mobility supported by greater diet breadth, but with a continued focus on big game hunting.[23] These adaptations were prevalent across the southern and eastern Mongolian Plateau.[25] The Tamsagbulag habitation site (samples B01-B10) in eastern Mongolia represents a site type found across the southern and eastern Mongolian Plateau, characterized by communities of hunter-gatherers living in pit-dwellings and specializing in big game hunting.[26] Tamsagbulag is unique for the intensive dietary, and likely ritual, use of aurochs in addition to substantial contributions from wild equids and gazelle.[24,27,28]

About 5,500 years ago, with the onset of the first village sites (e.g., Houtaomuga and Honghe) around the Nenjiang River basin/Songnen plain of northeastern China, specialized aurochs hunting replaced an emphasis on aquatic resources as the prevailing subsistence strategy.[29–31] Mitochondrial genome sequencing of 24 individual animals from presumptive feasting pits at Houtaomuga identified one as *B. taurus* (directly dated at 5500–5300 cal BP) and the other 23 as *B. primigenius*.[11] How the taurine individual came to be present at the site and its relationship with wild cattle is unclear, but aurochs and wild equids remained central to local hunting strategies through the Late Neolithic[30] until they were largely replaced by domesticated horses and cattle by the local onset of the Bronze Age, no later than 3,500 years ago.

Bronze Age and later sites are characterized by mobile pastoralism and raising of domestic taxa such as cattle, sheep, and horses alongside continued use of wild taxa such as gazelle, deer, and hare.[14,24,32] The Prone Burial tradition presents the earliest clear evidence for full-fledged adoption of pastoralist lifeways by eastern indigenous groups and is represented by samples from Delgerkhaan Uul (B24) and Ulaanzuukh sites (B27 and B29). The Slab Grave tradition follows the Prone Burial tradition on the eastern Mongolian Plateau, beginning soon after 3,000 years ago.[14,33] These two burial traditions are distinct, but there is significant geographic overlap between them and Slab Graves often intrude upon Prone Burial grave.[14,33] Samples from Zaraa Uul (B16 and B17) and Delgerkhaan Uul (B19, B20, and B22) represent this tradition and date at 3000–2400 years. Sample B28 from Shiriin Chuluu is about 2,000 years old and dates to the Xiongnu or Hunnu Empire. One sample (B12), intrusive to Neolithic habitation contexts at Zaraa Uul, was directly dated to the Göktürk or Turkic period in the sixth century AD.

As an intermediary zone between established pastoral communities in the west and eastern hunter-gatherers and agriculturalists, the eastern Mongolian Plateau is foundational to the larger story of human-bovine relationships in East Asia, but local aurochs genomes have yet to be published. It is unclear how ancient Mongolian cattle relate to other aurochs and early cattle found at sites in China and other parts of East Asia. This study aims to fill in some of the geographic and temporal gaps in research on East Asian aurochs and domestic cattle by analyzing ancient genomes from archaeological sites in eastern Mongolia. Given the long history of interactions between humans and aurochs and the importance of cattle pastoralism in more recent Mongolian history, it is important to clarify how ancient bovine populations adapted to and with distinct cultural shifts in the region.

Here, we sequence genomes of Neolithic Mongolian aurochs pre-dating the arrival of domestic cattle in East Asia by 3000 years, and domestic Mongolian cattle genomes from the subsequent Bronze Age and Iron Age to see whether domesticated cattle completely replaced or incorporated local aurochs lineages. We compare the Mongolian samples with other studies of aurochs worldwide, and with other ancient and modern DNA studies of East Asian cattle. We find that the Neolithic Mongolian aurochs are related to previously identified post-Last Glacial Maximum (LGM) Pleistocene North Asian aurochs.[22] Bronze and Iron Age cattle from Mongolia are genetically similar to ancient cattle from Chinese archaeological sites such as Shimao,[17] suggesting that cattle pastoralism may have first been adopted across northern East Asia from a single source population. We also confirm previous findings that East Asian aurochs have left genetic signatures in modern East Asian cattle breeds, especially in northwestern China and the Tibetan Plateau.[5,9] Together, the Mongolian samples highlight a shift in local bovine population composition by at least 3,500 years ago, associated with the establishment of an indigenous Prone Burial tradition. This period marks the emergence of a developed East Asian pastoralist economy in the eastern Mongolian Plateau, defined by familiarity with bronze metallurgy, monumental burial architecture, and lifeways organized around grazing of domesticated herds.[33,34] Aurochs were replaced by their domestic counterparts during this time. The replacement of aurochs by cattle led to the establishment of unique traditions that still define local pastoralist landscapes, showing continuity between ancestral hunter-gatherer and later herding cultures.

RESULTS

Ancient DNA sequencing

We extracted ancient DNA (aDNA) from bones originating from seven archaeological sites in eastern Mongolia (Figure S1). Table S1 lists contextual information for the samples including excavation context, skeletal elements represented, and dates. DNA extraction was attempted for 27 individuals. We recovered mitochondrial genomes from 11 individuals and low-coverage genomes from 7 individuals (0.01×–0.86×, Table S2). All sequenced genomes show DNA damage patterns consistent with those of ancient DNA (Figure S2). The Neolithic samples from the sites of Tamsagbulag, Zaraa Uul, and Margal were directly radiocarbon dated to 8395–5598 cal BP and pre-date the introduction of taurine cattle. Bronze Age and later samples from the sites of Zaraa Uul, Delgerkhaan Uul, Shiriin Chuluu, and Ulaanzuukh are 3,500 years or younger and post-date the introduction of taurine cattle.

Most of our analyses only include the three highest coverage individuals representing three distinct time periods: (1) B13, a Neolithic aurochs female from Zaraa Uul, directly radiocarbon dated to 7792–7662 cal BP, 0.43× coverage; (2) B17, a late Bronze Age domestic female from Zaraa Uul, radiocarbon dated to 2932–2778 cal BP based on associated finds, 0.86× coverage; and (3) B28, an Iron Age/Xiongnu period domestic female from Shiriin Chuluu, radiocarbon dated to 1995–1897 cal BP based on associated finds, 0.28× coverage (Figure S2).

Phylogenetic relationships and ancestry of ancient Mongolian cattle

We compared the ancient Mongolian samples with a reference panel of over 300 ancient and modern cattle genomes from around the world (Figure 1A; Table S3). The Mongolian aurochs samples from our study show genetic similarity to other previously reported North Asian aurochs (Figures 1B and 1C). The highest-coverage aurochs individual (B13) is most closely related to ca. 3800-year-old aurochs Y5 from the Songnen Plain in northern China,[9] and is part of the clade that includes other North Asian aurochs (Figure 1C). The Mongolian individuals that post-date the arrival of domesticated cattle in East Asia cluster with other early domesticated cattle, especially individuals from Shimao (Figures 1B and 1C). Shimao is a 4,000-year-old site in the Ordos region of China that was one of the first sites in the Yellow River Valley to use domesticated cattle in large numbers.[35,36] These ancient East Asian cattle form a clade with modern East Asian taurine cattle breeds, and are most closely related to Yanbian and Yakutian breeds (Figure 1C). We also examined the relationship between indicine cattle breeds, hybrid cattle breeds, and North Asian aurochs and found that some Chinese hybrid cattle show some genetic affinity to North Asian aurochs as well (Figure S3).

The mitochondrial sequences of the ancient Mongolian individuals provide additional evidence that there was a population shift around 4000–3500 cal BP, or earlier. All individuals predating this shift belong to haplogroup C, which has so far been found exclusively in East Asian aurochs,[6,7] while later individuals are part of haplogroups T1, T3, and T4, all of which are found today in domesticated taurine cattle in East Asia (Figure S4; Table S4).[11,37] Most taurine individuals in our sample belong to mitochondrial haplogroup T3, which is found in the earliest taurine individual from Houtaomuga and remains common in both East Asia and western Eurasia. One individual (B20), from Slab Grave components of Delgerkhaan Uul, is haplogroup T1, which is common today in southern Europe and Africa.[38] One individual (B12) from Zaraa Uul was directly dated to the sixth century and belongs to haplogroup T4, which is distinct to East Asian cattle breeds.[39,40] We also examined the mitochondrial D-loop to compare with other ancient aurochs and taurine cattle from the surrounding region (Figure S5; Table S5). The median joining network shows separation between individuals in the C and T

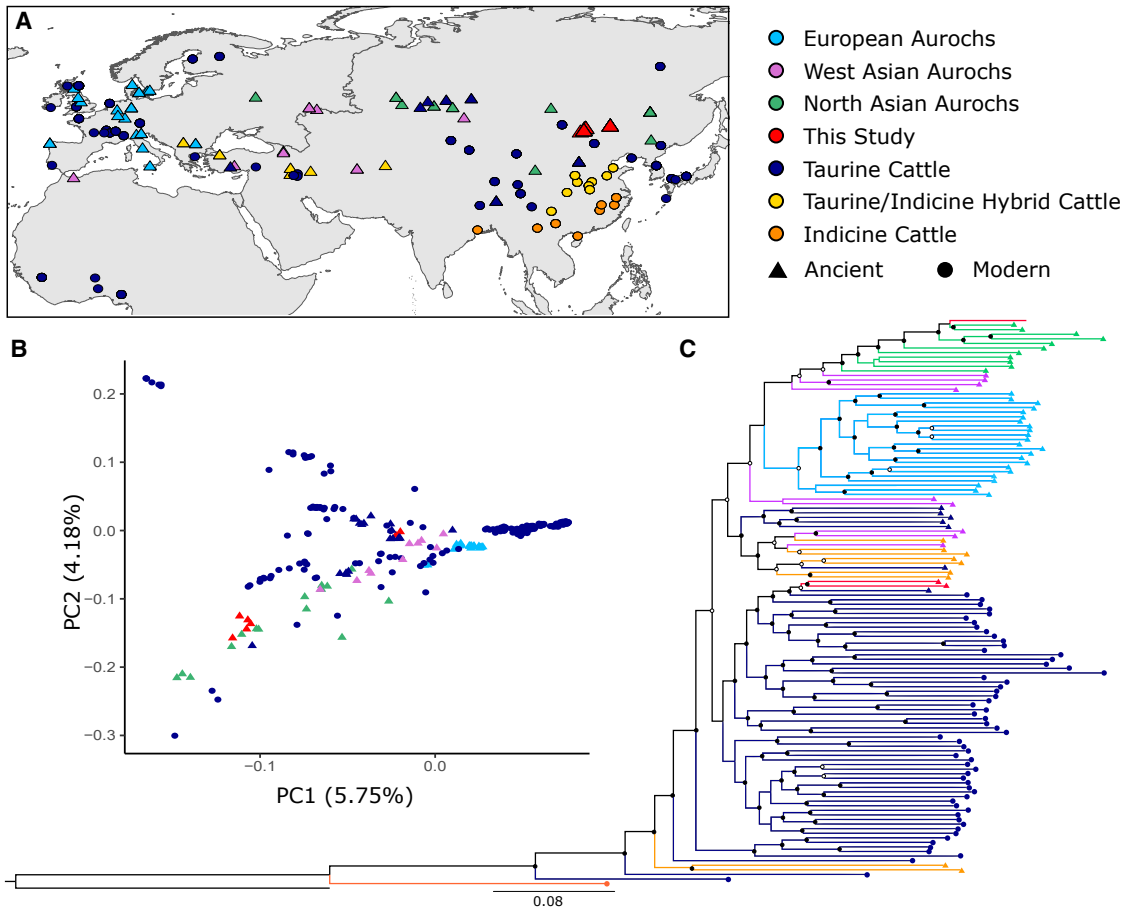

Figure 1. Geographical distributions and phylogenetic relationships of ancient Mongolian cattle compared with other published ancient and modern cattle and bovine genomes

(A) Map showing the locations of published samples and samples generated by this study, with colors indicating species (or in the case of aurochs, the geographic region they derive from) and shapes indicating ancient vs. modern samples. The published ancient cattle genome (Shimao) and aurochs genome (Songnen) that are geographically closest to our samples are indicated.

(B) PCA showing the two most significant axes for genetic diversity of ancient and modern taurine cattle and aurochs individuals. All modern genomes and ancient genomes with over 2× average coverage were used to generate the principal components, and lower-coverage ancient genomes were projected onto the PCA space. Individual Mongolian samples are labeled by name while Shimao and Songnen individuals are indicated as a whole.

(C) Maximum likelihood tree of ancient and modern taurine cattle and aurochs and the three highest coverage samples from this study (B13, B17, and B28), using Gaur as an outgroup and a Brahman *B. indicus* individual for comparison. Node bootstrap support of 99% or higher is indicated with black circles, while node bootstrap support of 90%–98% is indicated with white circles.

haplogroups, and aurochs from all time periods across East Asia belong to haplotype C.

Admixture between aurochs and cattle in East Asia

We used several methods to test for ancient admixture between aurochs and cattle in the Mongolian samples. Our admixture analysis shows that the genetic structure of the data is best explained by eight distinct ancestry sources (K = 8), with North Asian aurochs having a unique signature of ancestry relative to other aurochs populations (Figures 2 and S6). B17 and B28 are similar to ancient Shimao cattle and have shared ancestry components with northeast Asian cattle breeds such as Mishima and Yanbian. We used another approach to construct an admixture plot that is optimized for lower coverage data, which shows a similar pattern of North Asian aurochs ancestry in Tibetan Plateau cattle populations (Figure S7). One difference between the two plots is the ancestry of B13, the Neolithic individual. In Figure 2, it appears similar to the other ancient Mongolian individuals, while in Figure S7, it appears more similar to other North Asian aurochs. It is likely that the sample lacks sufficient coverage to distinguish between these two possibilities. We also examined admixture with indicine and hybrid cattle breeds, to observe whether North Asian aurochs ancestry remains in admixed cattle in Central China and our results suggest that some breeds, including Weining and Zaobei, have some North Asian aurochs ancestry (Figure S8). Finally, we used Treemix to examine gene flow between aurochs and taurine cattle, and found evidence for gene flow between North Asian aurochs and ancient taurine cattle including Shimao (Figures 3B, S9, and S10). Due to the lower coverage of the ancient samples,

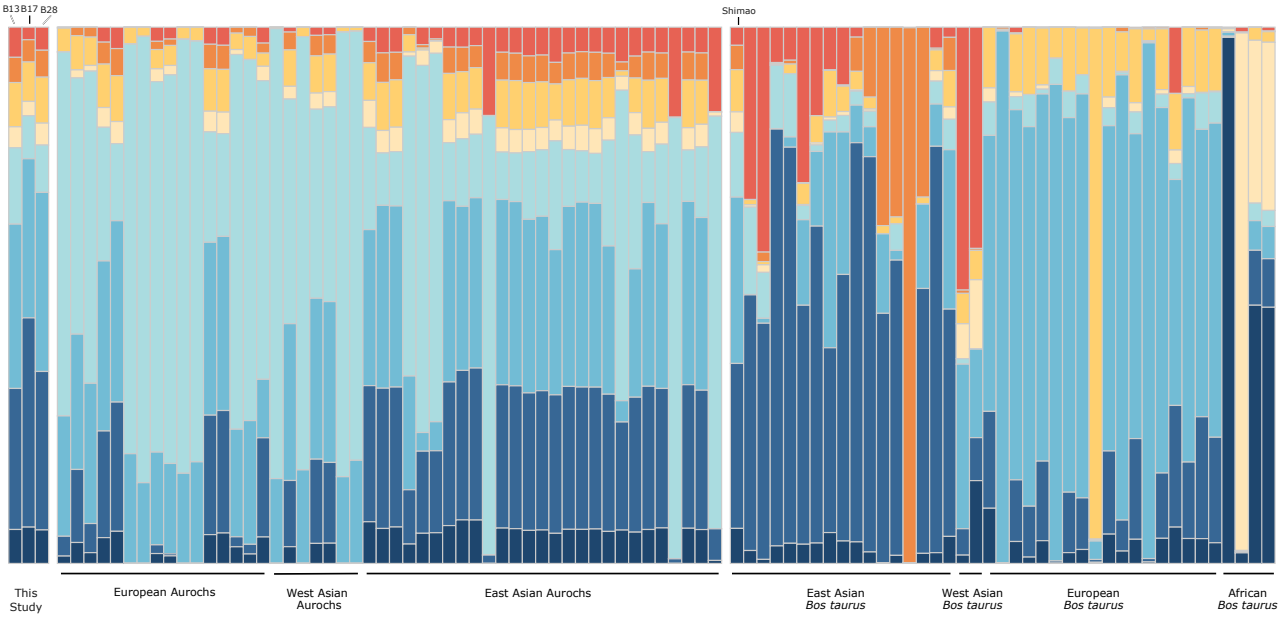

Figure 2. Admixture graph of the highest coverage Mongolian samples (B13, B17, and B28) along with aurochs, ancient cattle, and taurine cattle genomes

This plot shows K = 8, which is the lowest cross-entropy K-value for the dataset (Figure S6).

standard metrics to evaluate the fit of the plots to the data do not converge on a single best model: one, four, and five migration edges perform well across different metrics (Figures S9 and S10). Gene flow from North Asian aurochs is represented in all three of the models, although the direction and target population varies slightly.

We also used Patterson's *D* to test for introgression from North Asian aurochs into ancient domestic taurine cattle, and from ancient taurine cattle into North Asian aurochs (Table S6; Figure S11).[41] We find that ancient East Asian cattle show evidence for gene flow with North Asian aurochs (Figure S11), with later Mongolian individuals appearing to show a direct connection to earlier Mongolian aurochs (D(P_1 = B13, P_2, P_3 = Sub1, P_4 = Gaur); D = 0.397 when P_2 is B17; and D = 0.348 when P_2 is B28, Table S6). We also used F3 statistics to assess which modern cattle breeds are most closely related to our highest-coverage individual, the domesticated Bronze Age individual B17. Our results show the greatest allele sharing is with modern cattle breeds from the Tibetan Plateau and admixed breeds in Central China (Figure 3A; Table S7). Together, these analyses provide additional evidence that admixture between aurochs and taurine cattle was likely an important factor during the adoption of pastoralism in ancient East Asia. Evidence for a connection between eastern Mongolian aurochs and taurine cattle is a distinct from the hypothesis that early East Asian taurine lineages were largely formed by an introgression event around 4,500 years ago, followed by an extreme bottleneck and dispersal.[22]

DISCUSSION

Eastern Mongolia is a geographical and cultural axis point with some of the earliest clear evidence for an intensive reliance on aurochs among increasingly sedentary populations.[24,29] The region is likely to have played a role in the spread of domesticated lineages across the eastern steppes following the arrival of taurine cattle and pastoralist communities in the west, and there is some possibility that domesticated cattle arrived in the eastern Mongolian Plateau almost immediately following their arrival in Siberia and western Mongolia.[11] Our study is, therefore, critical to understanding long-standing human-bovine relationships in East Asia, which is a region increasingly recognized to have had prolonged, pre-domestication relationships with aurochs.[11,13,23,24,26,30,31] It is likewise important in moving us toward an understanding of how and why early Bronze Age societies adopted these domesticated lineages, which, as in Europe and elsewhere, eventually replaced the wild populations.

Spanning several millennia before and after the introduction of taurine cattle, our analyses have identified a significant change in the nature of bovine populations in eastern Mongolia following the introduction of domesticated taurine cattle. Notably, the eventual replacement of aurochs by domesticated cattle involved well-attested introgression between domesticated and wild species. The pre-pastoralist individuals in our study, such as B13, appear genetically similar to previously reported North Asian aurochs from Siberia and the Songnen Plain. We find that aurochs in Mongolia were likely part of this broader East Asian aurochs population, expanding the geographic and temporal coverage for aDNA datasets from northern East Asia.

The aDNA data presented here suggest that admixture was common as domestic cattle were introduced into East Asia. Despite being increasingly sedentary during the mid-Holocene, Tamsagbulag and other habitation sites in eastern Mongolia show that, beginning around 8000 years ago, some local

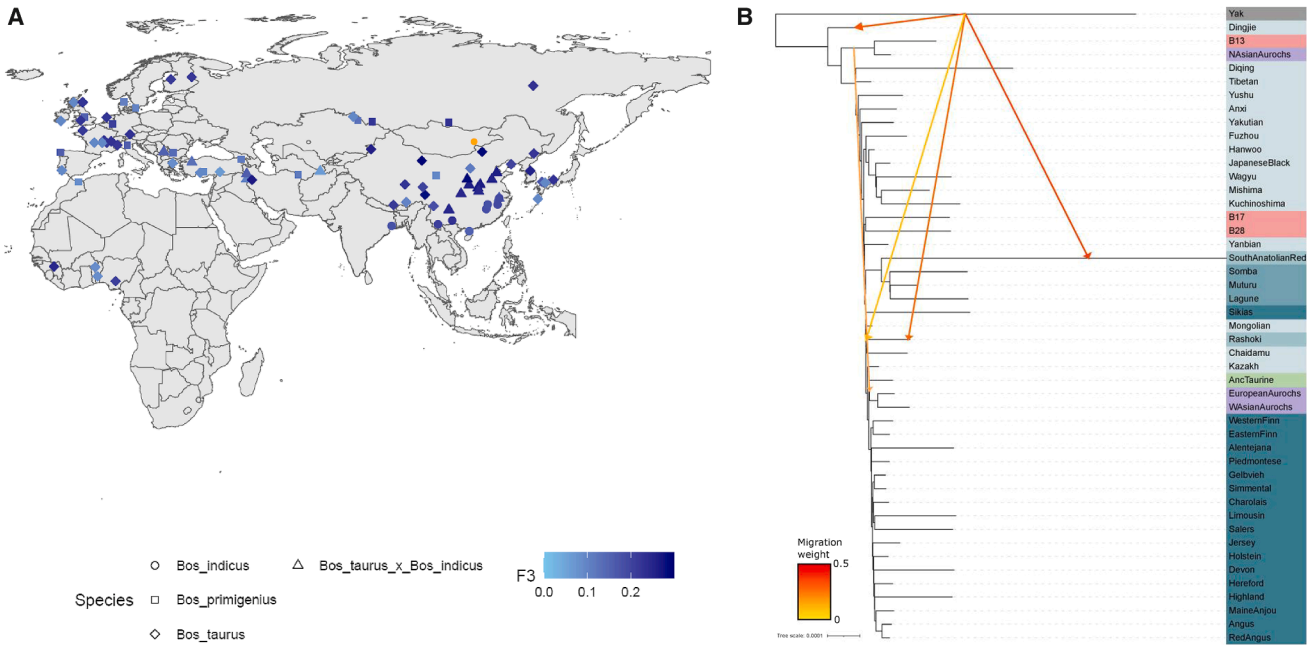

Figure 3. Admixture between Mongolian aurochs and East Asian cattle breeds

(A) F3 statistics for B17 compared with modern cattle breeds with Yak as an outgroup. Mongolian taurine cattle show similarities with cattle from the Tibetan Plateau and central China. The three closest modern breeds are Anxi, Mongolian, and Qinchuan (Table S7).

(B) Treemix plot of a well-supported number of migrations (m = 5) between taurine cattle and aurochs populations with Yak as an outgroup. Modern populations are color-coded by geographic region (light blue, Eastern Eurasia; medium blue, Africa; dark blue, Western Eurasia). There is a migration edge from ancient North Asian Aurochs (NAsianAurochs) to ancient taurine cattle including Shimao (AncTaurine).

hunter-gatherer societies were big-game hunters who relied heavily on aurochs.[23,26] Farther east on the Songnen Plain, the same pattern later emerged in the Nenjiang River Basin at an even larger scale and continued up to, and possibly beyond, the arrival of domesticated cattle.[29] For example, at Houtaomuga in Jilin Province, China, archaeologists have uncovered pits full of aurochs bones that may represent remains from large feasting events.[11,31] At this same site, geneticists identified the earliest East Asian cattle bone belonging to a taurine mtDNA haplogroup directly radiocarbon dated to 5500–5300 cal. BP.[11] Aurochs were also a key component of the Neolithic Honghe site in Heilongjiang Province, China,[30] and aDNA analyses at Honghe reveal that both *B. primigenius* and *B. taurus* remains were present in Bronze Age contexts dated to 3572–3445 cal BP.[13] Early Bronze Age sites in Central China contain both aurochs and taurine cattle remains.[4] Aurochs persisted in China until the Shang and Zhou Dynasties (ca. 1600–1050 BCE and 1046–256 BCE; 3550–2206 cal BP), and probably much later.[8,42] These zooarchaeological finds indicate that there would have been opportunities for admixture between wild and domestic herds at sites where domestic and wild populations overlapped in time and space. Indeed, taurine-aurochs hybrids have been identified on the Tibetan Plateau ca. 3,700 years ago,[5] and it is likely that additional hybrids will be identified as more ancient East Asian cattle are studied.

The post-4000 cal BP individuals in our study, including B17 and B28, are taurine cattle that are closely related to other previously reported early East Asian domestic cattle such as those from Shimao. The similarity between Bronze Age (B17), Xiongnu period (B28), and modern samples from Tibet and central China suggests that there was genetic continuity through time even when the archaeological record reflects significant cultural change. One possible hypothesis is that early domesticated cattle breeds descended from the same ancestral population of taurines introduced to East Asia by Afanasievo groups starting ca. 5,300 years ago. The earliest evidence of taurines outside this region of initial pastoralist settlement comes from the eastern edge of the Mongolian Plateau in a 5,300-year-old context associated with millennia-old traditions that combined intensive aurochs hunting and sedentary village communities. Following that, the 4000-year-old individuals from the early urban settlement of Shimao already show intermixing with North Asian aurochs populations.[17] This data shows the need to move beyond models positioning northwestern China as the primary corridor for dispersal of domesticated cattle and other herd animals. Current archaeological and genomic data support a common founding population for Mongolian and Chinese cattle, followed by localized male-dominated introgression with North Asian aurochs. However, we acknowledge the small sample size and low coverage genomes in our analyses, which limits our ability to draw definitive conclusions. This is shown by the discrepancy between the results of our different admixture analyses. Additional sampling and deeper sequencing will be needed to determine whether early East Asian domesticated cattle form a single, non-structured population, and whether introgression with aurochs occurred during the initial introduction of domestic cattle or

over a prolonged period. Improving sampling breadth and depth across East Asia would also help to clarify whether the signatures of admixture in modern cattle breeds reflect direct descent from Neolithic aurochs or later gene flow with descendant populations carrying aurochs ancestry. What is clear is that the introduction of taurine cattle does not represent full population replacement. Aurochs matrilines were largely erased, but some modern cattle breeds still carry North Asian aurochs ancestry, including hybrid cattle from Central China and taurine cattle from the Tibetan Plateau (Figures 3 and S3). This is consistent with other studies that have identified aurochs ancestry in modern cattle breeds.[6,43]

One of the most exciting insights from recent archaeological and paleogenomic research on animal domestication is the importance of wild introgression in the spread of domesticated animals and the development of modern breeds. Complete reproductive isolation of domestic populations from their wild progenitors did not take place during the domestication of most taxa. Instead, introgression or admixture between wild and domestic populations occurred frequently as domestic populations were introduced into new regions and as people bred their herds with wild stock to improve herd health and increase genetic diversity.[44,45] For example, as domesticated pigs were introduced to Europe, admixture with local wild boar erased most of their original Near Eastern ancestry signal.[46,47] Early domesticated goats have multiple highly divergent lineages that may have resulted from continuous incorporation of wild individuals into goat herds.[44,48] Wild introgression continues today, including in Mongolia, where herders both intentionally and unintentionally interbreed domesticated and wild camels, as well as domesticated horses (*Equus caballus*) and khulan (*Equus hemionus*) and goats with ibex (*Capra sibirica*).[49] As cattle were introduced to new regions of Western Eurasia[39,50–54] and Africa,[55] admixture with local wild aurochs populations also occurred. Domesticated herd animals represent specialized breeds of species that were already widely known by hunter-gatherers and early agriculturalists across Central and East Asia, as well as northern Africa, suggesting that local traditional ecological knowledge of these species was likely fundamental to successful husbandry practices.

Finally, the aDNA data presented in this study adds to the growing evidence that the period from ca. 5300–3500 years ago represents a period of significant changes in the archaeological record of East Asia associated with the intensification of cattle pastoralism in East Asia. This coincided with broader changes in subsistence, ritual practices, and landscape use. Archaeological finds of dairy products and identification of milk residues in pottery and human dental calculus suggest that milk was important to Bronze Age and later pastoralist peoples across the mountain, steppe, and desert regions of East Asia.[56–60] Cattle bones were heavily utilized for oracle bone divination in ancient China by 4,000 years ago,[61] and cattle were also used in large numbers for subsistence, bone artifact production, and ritual sacrifice at early urban centers by 3,000 years ago.[62] The incorporation of cattle into ritual practices may have built upon longer-standing relationships with indigenous bovine populations across the larger region, as demonstrated by the importance of aurochs to increasingly sedentary hunter-gatherer populations across the southern and eastern Mongolian plateau. Increasing reliance on domesticated cattle coincides with a decline in wild fauna such as deer, suggesting changes in human landscape use away from the mosaic habitats that facilitated interactions with humans.[63,64] We do not know at what stage in these transitions aurochs went extinct, but the evidence of interbreeding suggests that we should not discount the possibility that people actively managed aurochs long before and perhaps even after the introduction of taurine cattle. The history of domesticated cattle in East Asia from initial domestication to the present remains enigmatic, and further study of the archaeological and genetic history of ancient populations will be critical for understanding the unique history of North Asian aurochs and how they contributed to early cattle husbandry and modern breeds.

Limitations of the study

The conclusions presented here are preliminary, and we acknowledge the small sample size and low coverage of ancient genomes used in our analyses. There are discrepancies between the results of our different admixture analyses using pcangsd and LEA, which may be explained by the low-coverage datasets. There are also several remaining questions that we are unable to address with the current data. For example, we are unable to determine whether early East Asian domesticated cattle form a single, non-structured population. We are also unable to determine whether introgression between domestic cattle and aurochs occurred during the initial introduction of domestic cattle to Mongolia, or over a prolonged period of time after people began herding domestic cattle. Future studies that include additional sampling and deeper sequencing of aurochs and cattle from multiple time periods in Mongolian history will help address these remaining questions.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Lisa Janz (lisa.janz@utoronto.ca).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All raw reads from the project are available on the NCBI SRA archive under BioProject PRJNA1430427 (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1430427). Accession numbers are also listed in the key resources table. Other data reported in this paper will be shared by the lead contact upon request.
- Code is available on GitHub at https://github.com/kelsey-witt/cattle_aDNA_methods. Any additional information required to reanalyze the data reported in this paper are available from the lead contact upon request.
- mtDNA alignments are available at https://doi.org/10.25438/wes02.31445452.

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AUTHOR CONTRIBUTIONS

Conceptualization, L.J., K.B., and K.E.W.; methodology, K.B., K.E.W., S.W., S.M., and R.S.; investigation, K.B., K.E.W., S.W., S.M., L.J., D.P., R.S., D.O., D.B., A.C., and L.R.; visualization, K.B., K.E.W., D.P., and R.S.; funding acquisition, L.J. and K.B.; writing – original draft, K.B., K.E.W., L.J., S.W., S.M., and D.P.; writing – review and editing, all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2026.117409.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
TB2.H1.1.L1: 1	Zhao et al.[26]	B01
TB2.H1.2.L1: 27–30	Zhao et al.[26]	B02
TB2.H1.4.L1B: 10	Zhao et al.[26]	B03
TB3: 3	Zhao et al.[26]	B04
TB5	Zhao et al.[26]	B05
TB9.Q3.L2: 22	Zhao et al.[26]	B07
ZU2.T2.16.B1.L2: 1	Janz et al.[23]	B12
ZU2.T3.17.E1.L1B: 1	Janz et al.[23]	B13
ZU.18.EX-05b	This Study	B17
18_07_019	Pleuger-Dreibrodt[14]	B20
UZ.19.2015	Khatanbaatar[65] and Khatanbaatar et al.[66]	B27
FB.206.1	This Study	B28
Chemicals, peptides, and recombinant proteins		
Proteinase K	New England Biolabs	P8107S
Qiagen PE Buffer	Qiagen	19065
Qiagen Buffer EB	Qiagen	19086
NEBNext Ultra II DNA Library Prep Kit for Illumina	New England Biolabs	E7654S/L
NEBNext Multiplex Oligos	New England Biolabs	E7600S
AMPure XP magnetic beads	Beckman Coulter	A63880
Critical commercial assays		
Qubit dsDNA HS kit	Thermo Fisher Scientific	Q33231
Deposited data		
Paired-end aDNA sequencing data	This study	https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1430427
Code written for genomic analyses	This study	https://github.com/kelsey-witt/cattle_aDNA_methods
Mitochondrial DNA alignment	This study	https://doi.org/10.25438/wes02.31445452
Bos taurus Alentejana genome	Verdugo et al.[3]	ERR3305588
Bos taurus Angus01 genome	Stothard et al.[67]	SRR1525582
Bos taurus Angus02 genome	Stothard et al.[67]	SRR1525583
Bos taurus Angus03 genome	Stothard et al.[67]	SRR1525686
Bos taurus Angus04 genome	Stothard et al.[67]	SRR1525687
Bos taurus Angus05 genome	Stothard et al.[67]	SRR1525688
Bos taurus Angus06 genome	Stothard et al.[67]	SRR1355237
Bos taurus Angus07 genome	Stothard et al.[67]	SRR1365144
Bos taurus Angus08 genome	Stothard et al.[67]	SRR1425124
Bos taurus Angus09 genome	Stothard et al.[67]	SRR1365129
Bos taurus Angus10 genome	Stothard et al.[67]	SRR1346376
Bos taurus Anxi1902 genome	Lyu et al.[68]	SRR22186401
Bos taurus Anxi1906 genome	Lyu et al.[68]	SRR22186400
Bos taurus Anxi1908 genome	Lyu et al.[68]	SRR22186399
Bos taurus Anxi1909 genome	Lyu et al.[68]	SRR22186398
Bos taurus Anxi1915 genome	Lyu et al.[68]	SRR22186397
Bos taurus Anxi1917 genome	Lyu et al.[68]	SRR22186396
Bos taurus Anxi1921 genome	Lyu et al.[68]	SRR22186395

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Bos taurus Anxi1922 genome	Lyu et al.[68]	SRR22186394
Bos taurus Anxi1925 genome	Lyu et al.[68]	SRR22186393
Bos taurus Anxi1936 genome	Lyu et al.[68]	SRR22186392
Bos primigenius Baikal1 genome	Rossi et al.[6]	ERR13295485 - ERR13295504, ERR13600227
Bos taurus Bangga01 genome	Chen et al.[43]	SRR17245064, SRR17245075, SRR17245086, SRR17245089, SRR17245090, SRR17245091, SRR17245092, SRR17245093, SRR17245094, SRR17245105, SRR17245116, SRR17245127, SRR17245132 - SRR17245139
Bos taurus Bangga14 genome	Chen et al.[43]	SRR17245119 - SRR17245126, SRR17245128 - SRR17245131
Bos taurus Bangga15 genome	Chen et al.[43]	SRR17245110 -SRR17245115, SRR17245117, SRR17245118
Bos taurus Bangga33 genome	Chen et al.[43]	SRR21608681 - SRR21608686, SRR21608693, SRR21608694, SRR17245060 - SRR17245063, SRR17245065 -SRR17245074, SRR17245076 -SRR17245082
Bos grunniens Bangga67 genome	Chen et al.[43]	SRR21608679, SRR21608680, SRR21608687 - SRR21608692, SRR17245056 - SRR17245059, SRR17245095 - SRR17245104, SRR17245106, SRR17245107
Bos taurus x Bos indicus Bashan01 genome	Chen et al.[17]	SRR5507209
Bos taurus x Bos indicus Bashan02 genome	Chen et al.[17]	SRR5507208
Bos taurus x Bos indicus Bashan03 genome	Chen et al.[17]	SRR5507207
Bos taurus x Bos indicus Bashan04 genome	Chen et al.[17]	SRR5507206
Bos taurus x Bos indicus Bashan05 genome	Chen et al.[17]	SRR5507205
Bos primigenius Bed4 genome	Rossi et al.[6]	ERR13295505 - ERR13600228
Bos taurus x Bos indicus Bes1 genome	Verdugo et al.[3]	ERR3317371, ERR3317376, ERR3317377, ERR3317382
Bos taurus x Bos indicus Bes2 genome	Verdugo et al.[3]	ERR3317361, ERR3317363, ERR3317365, ERR3317367, ERR3317368
Bos taurus x Bos indicus BohaiBlack01 genome	Chen et al.[17]	SRR5507227
Bos taurus x Bos indicus BohaiBlack02 genome	Chen et al.[17]	SRR5507226
Bos taurus x Bos indicus BohaiBlack03 genome	Chen et al.[17]	SRR5507225
Bos taurus x Bos indicus BohaiBlack04 genome	Chen et al.[17]	SRR5507224
Bos taurus x Bos indicus BohaiBlack05 genome	Chen et al.[17]	SRR5507223
Bos primigenius Borly4a genome	Rossi et al.[6]	ERR13302211 -ERR13302224, ERR13600229
Bos primigenius Borly4b genome	Rossi et al.[6]	ERR13302225 - ERR13302239, ERR13600230
Bos primigenius Borlya genome	Rossi et al.[6]	ERR13302240 -ERR13302251, ERR13600231
Bos indicus Brahman01 genome	Bickhart et al.[69]	SRR2016745
Bos indicus Brahman02 genome	Bickhart et al.[69]	SRR2016748
Bos indicus Brahman03 genome	Bickhart et al.[69]	SRR2016749
Bos indicus Brahman04 genome	Bickhart et al.[69]	SRR2016795
Bos taurus x Bos indicus Bul2 genome	Rossi et al.[6]	ERR13302252 -ERR13302258, ERR13600232
Bos taurus BZL1 genome	Rossi et al.[6]	ERR13302259 -ERR13302263, ERR13600233
Bos taurus BZL2 genome	Rossi et al.[6]	ERR13302264 -ERR13302268, ERR13600234
Bos primigenius Ch22 genome	Verdugo et al.[3]	ERR3317470, ERR3317475, ERR3317476, ERR3317479
Bos taurus Chaidamu01 genome	Chen et al.[17]	SRR5507272
Bos taurus Chaidamu02 genome	Chen et al.[17]	SRR5507271
Bos taurus Chaidamu03 genome	Chen et al.[17]	SRR5507270

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Bos taurus Chaidamu04 genome	Chen et al.[17]	SRR5507269
Bos taurus Chaidamu05 genome	Chen et al.[17]	SRR5507268
Bos taurus Charolais01 genome	Stothard et al.[67]	SRR1343167
Bos taurus Charolais02 genome	Stothard et al.[67]	SRR1343168
Bos taurus Charolais03 genome	Stothard et al.[67]	SRR1343169
Bos taurus Charolais04 genome	Stothard et al.[67]	SRR1348571
Bos taurus Charolais05 genome	Stothard et al.[67]	SRR1355258
Bos taurus Charolais06 genome	Stothard et al.[67]	SRR1365122
Bos primigenius CPC98 genome	Park et al.[54]	SRR2460709, SRR2463292, SRR2463657-SRR2463661, SRR2464109-SRR2464114, SRR2464116, SRR2465352, SRR2465437, SRR2465673, SRR2465675, SRR2465676, SRR2465678-SRR2465682
Bos taurus x Bos indicus Dabieshan01 genome	Chen et al.[17]	SRR5507194
Bos taurus x Bos indicus Dabieshan02 genome	Chen et al.[17]	SRR5507193
Bos taurus Devon genome	Stothard et al.[67]	SRR1346378
Bos indicus Dianzhong01 genome	Chen et al.[17]	SRR6024567
Bos indicus Dianzhong02 genome	Chen et al.[17]	SRR6024568
Bos indicus Dianzhong03 genome	Chen et al.[17]	SRR6024565
Bos indicus Dianzhong04 genome	Chen et al.[17]	SRR6024566
Bos indicus Dianzhong05 genome	Chen et al.[17]	SRR6024563
Bos indicus Dianzhong06 genome	Chen et al.[17]	SRR6024564
Bos taurus Dingjie31 genome	Chen et al.[43]	SRR25937264
Bos taurus Dingjie44 genome	Chen et al.[43]	SRR25994665
Bos taurus Dingjie49 genome	Chen et al.[43]	SRR25937249
Bos taurus Diqing27 genome	Chen et al.[43]	SRR26265630
Bos taurus Diqing38 genome	Chen et al.[43]	SRR26265618
Bos taurus EasternFinnCattle01 genome	Weldenegodguad et al.[70]	ERR2734942
Bos taurus EasternFinnCattle02 genome	Weldenegodguad et al.[70]	ERR2734943
Bos taurus EasternFinnCattle03 genome	Weldenegodguad et al.[70]	ERR2734944
Bos taurus EasternFinnCattle04 genome	Weldenegodguad et al.[70]	ERR2734945
Bos taurus EasternFinnCattle05 genome	Weldenegodguad et al.[70]	ERR2734946
Bos taurus Fuzhou1A genome	Hou et al.[9]	SRR26081654
Bos taurus Fuzhou2A genome	Hou et al.[9]	SRR26081653
Bos taurus Fuzhou3A genome	Hou et al.[9]	SRR26081652
Bos primigenius Galicia1 genome	Rossi et al.[6]	ERR13302269 -ERR13302292, ERR13600235
Bos primigenius Galicia2 genome	Rossi et al.[6]	ERR13302293 -ERR13302296, ERR13600236
Bos primigenius Galicia3 genome	Rossi et al.[6]	ERR13302297 -ERR13302306, ERR13600237
Bos gaurus Gaur05 genome	Verdugo et al.[3]	ERS3381389
Bos taurus Gelbvieh01 genome	Stothard et al.[67]	SRR1343161
Bos taurus Gelbvieh02 genome	Stothard et al.[67]	SRR1343162
Bos taurus Gelbvieh03 genome	Stothard et al.[67]	SRR1343164
Bos taurus Gelbvieh04 genome	Stothard et al.[67]	SRR1343165
Bos taurus Gelbvieh05 genome	Stothard et al.[67]	SRR1343166
Bos taurus Gelbvieh06 genome	Stothard et al.[67]	SRR1365112
Bos taurus Gelbvieh07 genome	Stothard et al.[67]	SRR1425154
Bos taurus Gelbvieh08 genome	Stothard et al.[67]	SRR1355236
Bos taurus Gelbvieh09 genome	Stothard et al.[67]	SRR1355240
Bos taurus Gelbvieh10 genome	Stothard et al.[67]	SRR1355260

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Bos indicus Guangfeng01 genome	Chen et al.[17]	SRR5507286
Bos indicus Guangfeng02 genome	Chen et al.[17]	SRR5507285
Bos indicus Guangfeng03 genome	Chen et al.[17]	SRR5507284
Bos indicus Guangfeng04 genome	Chen et al.[17]	SRR5507283
Bos primigenius Gyu1 genome	Rossi et al.[6]	ERR13295562 -ERR13295566, ERR13302307 -ERR13302318, ERR13600238
Bos primigenius Gyu2 genome	Verdugo et al.[3]	ERR3317392, ERR3317394
Bos taurus Hanwoo01 genome	Shin et al.[71]	SRR934415
Bos taurus Hanwoo02 genome	Shin et al.[71]	SRR934417
Bos taurus Hanwoo03 genome	Shin et al.[71]	SRR934418
Bos taurus Hanwoo04 genome	Shin et al.[71]	SRR934419
Bos taurus Hanwoo05 genome	Shin et al.[71]	SRR934432
Bos taurus Hanwoo06 genome	Shin et al.[71]	SRR934433
Bos taurus Hanwoo07 genome	Shin et al.[71]	SRR934434
Bos taurus Hanwoo08 genome	Shin et al.[71]	SRR934435
Bos taurus Hanwoo09 genome	Shin et al.[71]	SRR934436
Bos taurus Hanwoo10 genome	Shin et al.[71]	SRR934437
Bos taurus Hanwoo11 genome	Shin et al.[71]	SRR934395
Bos taurus Hanwoo12 genome	Shin et al.[71]	SRR934397
Bos taurus Hanwoo14 genome	Shin et al.[71]	SRR934400
Bos taurus Hanwoo15 genome	Shin et al.[71]	SRR934401
Bos taurus Hanwoo16 genome	Shin et al.[71]	SRR934402
Bos taurus Hanwoo17 genome	Shin et al.[71]	SRR934403
Bos taurus Hanwoo18 genome	Shin et al.[71]	SRR934404
Bos taurus x Bos indicus Has3 genome	Verdugo et al.[3]	ERR3317402, ERR3317404, ERR3317406
Bos taurus x Bos indicus Has4 genome	Verdugo et al.[3]	ERR3317263, ERR3317264, ERR3317266-ERR3317269, ERR331272, ERR3317274
Bos taurus Hereford01 genome	Stothard et al.[67]	SRR1343160
Bos taurus Hereford02 genome	Stothard et al.[67]	SRR1346382
Bos taurus Hereford03 genome	Stothard et al.[67]	SRR1346383
Bos taurus Hereford04 genome	Stothard et al.[67]	SRR1346385
Bos taurus Hereford05 genome	Stothard et al.[67]	SRR1346387
Bos taurus Hereford06 genome	Stothard et al.[67]	SRR1365124
Bos taurus Hereford07 genome	Stothard et al.[67]	SRR1365126
Bos taurus Hereford08 genome	Stothard et al.[67]	SRR1365128
Bos taurus Hereford09 genome	Stothard et al.[67]	SRR1365131
Bos taurus Hereford10 genome	Stothard et al.[67]	SRR1365137
Bos taurus Highland genome	Verdugo et al.[3]	ERS3381385
Bos primigenius Hjo1 genome	Rossi et al.[6]	ERR13302319 -ERR13302326, ERR13600239
Bos taurus Holstein01 genome	Stothard et al.[67]	SRR1346386
Bos taurus Holstein02 genome	Stothard et al.[67]	SRR1346390
Bos taurus Holstein03 genome	Stothard et al.[67]	SRR1346392
Bos taurus Holstein04 genome	Stothard et al.[67]	SRR1348583
Bos taurus Holstein05 genome	Stothard et al.[67]	SRR1348592
Bos taurus Holstein06 genome	Stothard et al.[67]	SRR1365147
Bos taurus Holstein07 genome	Stothard et al.[67]	SRR1425129
Bos taurus Holstein08 genome	Stothard et al.[67]	SRR1425129
Bos taurus Holstein09 genome	Stothard et al.[67]	SRR1425134

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Bos taurus Holstein10 genome	Stothard et al.[67]	SRR1425144
Bos primigenius Hxh2 genome	Rossi et al.[6]	ERR13295382 -ERR13295484
Bos taurus JapaneseBlack01 genome	Mei et al.[72]	SRS933383
Bos taurus JapaneseBlack02 genome	Mei et al.[72]	SRS933384
Bos taurus JapaneseBlack03 genome	Mei et al.[72]	SRS933385
Bos taurus JapaneseBlack06 genome	Mei et al.[72]	SRS933386
Bos taurus JapaneseBlack09 genome	Mei et al.[72]	SRS933387
Bos taurus JapaneseBlack12 genome	Mei et al.[72]	SRS933388
Bos taurus JapaneseBlack14 genome	Mei et al.[72]	SRS933389
Bos taurus JapaneseBlack22 genome	Mei et al.[72]	SRS933390
Bos taurus JapaneseBlack23 genome	Mei et al.[72]	SRS933391
Bos taurus JapaneseBlack24 genome	Mei et al.[72]	SRS933392
Bos taurus JapaneseBlack26 genome	Mei et al.[72]	SRS933393
Bos taurus Jersey01 genome	Heaton et al.[73]	SRR2016774
Bos taurus Jersey02 genome	Heaton et al.[73]	SRR2016776
Bos taurus Jersey03 genome	Heaton et al.[73]	SRR2016799
Bos taurus Jersey04 genome	Kim et al.[74]	SRR3497613
Bos taurus Jersey05 genome	Kim et al.[74]	SRR3497611
Bos taurus Jersey06 genome	Kim et al.[74]	SRR3497467
Bos taurus Jersey07 genome	Kim et al.[74]	SRR3497466
Bos taurus Jersey08 genome	Kim et al.[74]	SRR3497465
Bos taurus Jersey09 genome	Kim et al.[74]	SRR3497464
Bos taurus Jersey10 genome	Kim et al.[74]	SRR3497462
Bos taurus Jersey11 genome	Kim et al.[74]	SRR3497451
Bos taurus Jersey12 genome	Kim et al.[74]	SRR3497162
Bos taurus Jersey13 genome	Kim et al.[74]	SRR3497161
Bos indicus Ji'an01 genome	Chen et al.[17]	SRR5507282
Bos indicus Ji'an02 genome	Chen et al.[17]	SRR5507281
Bos indicus Ji'an03 genome	Chen et al.[17]	SRR5507280
Bos indicus Ji'an04 genome	Chen et al.[17]	SRR5507279
Bos taurus x Bos indicus JiaxianRed01 genome	Chen et al.[17]	SRR5507232
Bos taurus x Bos indicus JiaxianRed02 genome	Chen et al.[17]	SRR5507231
Bos taurus x Bos indicus JiaxianRed03 genome	Chen et al.[17]	SRR5507230
Bos taurus x Bos indicus JiaxianRed04 genome	Chen et al.[17]	SRR5507229
Bos taurus x Bos indicus JiaxianRed05 genome	Chen et al.[17]	SRR5507228
Bos indicus Jinjiang01 genome	Chen et al.[17]	SRR5507278
Bos indicus Jinjiang03 genome	Chen et al.[17]	SRR5507275
Bos indicus Jinjiang04 genome	Chen et al.[17]	SRR5507274
Bos taurus Kazakh01 genome	Chen et al.[17]	SRR5507260
Bos taurus Kazakh02 genome	Chen et al.[17]	SRR5507259
Bos taurus Kazakh03 genome	Chen et al.[17]	SRR5507258
Bos taurus Kazakh04 genome	Chen et al.[17]	SRR5507257
Bos taurus Kazakh05 genome	Chen et al.[17]	SRR5507256
Bos taurus Kazakh06 genome	Chen et al.[17]	SRR5507255
Bos taurus Kazakh07 genome	Chen et al.[17]	SRR5507254
Bos taurus Kazakh08 genome	Chen et al.[17]	SRR5507253
Bos taurus Kazakh09 genome	Chen et al.[17]	SRR5507252
Bos taurus KOL10 genome	Rossi et al.[6]	ERR13302327 - ERR13302330, ERR13600241

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Bos taurus KOL9 genome	Rossi et al.[6]	ERR13302331 -ERR13302334, ERR13600242
Bos taurus Kuchinoshima genome	Kawahara-Miki et al.[75]	DRR000429 -DRR000432
Bos taurus Lagune genome	Verdugo et al.[3]	ERR3293557
Bos indicus Leiqiong01 genome	Chen et al.[17]	SRR5507190
Bos indicus Leiqiong02 genome	Chen et al.[17]	SRR5507189
Bos indicus Leiqiong03 genome	Chen et al.[17]	SRR5507188
Bos taurus Limousin genome	Stothard et al.[67]	SRR1365134
Bos taurus x Bos indicus Lingnan01 genome	Chen et al.[17]	SRR5507222
Bos taurus x Bos indicus Lingnan02 genome	Chen et al.[17]	SRR5507221
Bos taurus x Bos indicus Lingnan03 genome	Chen et al.[17]	SRR5507220
Bos taurus x Bos indicus Lingnan04 genome	Chen et al.[17]	SRR5507219
Bos taurus x Bos indicus Lingnan05 genome	Chen et al.[17]	SRR5507218
Bos taurus x Bos indicus Lingnan06 genome	Chen et al.[17]	SRR5507217
Bos taurus x Bos indicus Lingnan07 genome	Chen et al.[17]	SRR5507216
Bos taurus x Bos indicus Lingnan08 genome	Chen et al.[17]	SRR5507215
Bos taurus x Bos indicus Luxi01 genome	Chen et al.[17]	SRR5507242
Bos taurus x Bos indicus Luxi02 genome	Chen et al.[17]	SRR5507241
Bos taurus x Bos indicus Luxi03 genome	Chen et al.[17]	SRR5507240
Bos taurus x Bos indicus Luxi04 genome	Chen et al.[17]	SRR5507239
Bos taurus x Bos indicus Luxi05 genome	Chen et al.[17]	SRR5507238
Bos taurus MaineAnjou01 genome	Stothard et al.[67]	SRR1355238
Bos taurus MaineAnjou02 genome	Stothard et al.[67]	SRR1355245
Bos taurus MaineAnjou03 genome	Stothard et al.[67]	SRR1355259
Bos taurus MaineAnjou04 genome	Stothard et al.[67]	SRR1365125
Bos taurus MaineAnjou05 genome	Stothard et al.[67]	SRR1365127
Bos taurus MaineAnjou06 genome	Stothard et al.[67]	SRR1365130
Bos primigenius Mantova1 genome	Rossi et al.[6]	ERR13302335 - ERR13302343, ERR13600243
Bos taurus x Bos indicus Men1 genome	Verdugo et al.[3]	ERR3301568, ERR3301574, ERR3301576, ERR3301577, ERR3301579, ERR3301581, ERR3301583, ERR3301585, ERR3301588
Bos taurus x Bos indicus Men2 genome	Verdugo et al.[3]	ERR3317304, ERR3317306, ERR3317308, ERR3317310, ERR3317312, ERR3317314
Bos taurus Mishima01 genome	Tsuda et al.[76]	DRR001771, DRR001778, DRR001781
Bos taurus Mishima02 genome	Tsuda et al.[76]	DRR001768, DRR001775, DRR001782
Bos taurus Mishima03 genome	Tsuda et al.[76]	DRR001763, DR001765
Bos taurus Mishima04 genome	Tsuda et al.[76]	DRR001770, DRR001777, DRR001780
Bos taurus Mishima05 genome	Tsuda et al.[76]	DRR001762, DRR001772, DRR001774
Bos taurus Mishima06 genome	Tsuda et al.[76]	DRR001769, DRR001776, DRR001779
Bos taurus Mishima07 genome	Tsuda et al.[76]	DRR001764, DRR001766
Bos primigenius Mon4 genome	Rossi et al.[6]	ERR13302344 -ERR13302350, ERR13600244
Bos primigenius Mon7 genome	Rossi et al.[6]	ERR13302351 -ERR13302358, ERR13600245
Bos taurus Mongolian_MG1 genome	Chen et al.[37]	SRR10809663
Bos taurus Mongolian_MG2 genome	Chen et al.[37]	SRR10809662
Bos taurus Mongolian_MG3 genome	Chen et al.[37]	SRR10842383, SRR10809653
Bos taurus Mongolian_MG4 genome	Chen et al.[37]	SRR10842384, SRR10809655
Bos taurus Mongolian_MG5 genome	Chen et al.[37]	SRR10809652
Bos taurus Mongolian_MG6 genome	Chen et al.[37]	SRR10809651
Bos taurus Mongolian_WMG13 genome	Chen et al.[37]	SRR10809661

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Bos taurus Mongolian_WMG14 genome	Chen et al.[37]	SRR10809660
Bos taurus Mongolian_WMG15 genome	Chen et al.[37]	SRR10809659
Bos taurus Mongolian_WMG16 genome	Chen et al.[37]	SRR10809658
Bos taurus Mongolian_WMG17 genome	Chen et al.[37]	SRR10809657
Bos taurus Mongolian_WMG18 genome	Chen et al.[37]	SRR10809656
Bos taurus Mongolian_WMG7 genome	Chen et al.[37]	SRR10809650
Bos taurus Mongolian_WMG8 genome	Chen et al.[37]	SRR10809649
Bos taurus Mongolian_WMG9 genome	Chen et al.[37]	SRR10809648
Bos taurus Mongolian01 genome	Chen et al.[17]	SRR5507267
Bos taurus Mongolian02 genome	Chen et al.[17]	SRR5507266
Bos taurus Mongolian03 genome	Chen et al.[17]	SRR5507265
Bos taurus Mongolian04 genome	Chen et al.[17]	SRR5507264
Bos taurus Mongolian05 genome	Chen et al.[17]	SRR5507263
Bos taurus Mongolian06 genome	Chen et al.[17]	SRR5507262
Bos taurus Mongolian07 genome	Chen et al.[17]	SRR5507261
Bos taurus Muturu01 genome	Tijjani et al.[77]	SRR5630644
Bos taurus Muturu02 genome	Tijjani et al.[77]	SRR5630645
Bos taurus Muturu03 genome	Tijjani et al.[77]	SRR5630646
Bos taurus Muturu04 genome	Tijjani et al.[77]	SRR5630647
Bos taurus Muturu05 genome	Tijjani et al.[77]	SRR5630648
Bos taurus Muturu06 genome	Tijjani et al.[77]	SRR5630649
Bos taurus Muturu07 genome	Tijjani et al.[77]	SRR5630650
Bos taurus Muturu08 genome	Tijjani et al.[77]	SRR5630651
Bos taurus Muturu09 genome	Tijjani et al.[77]	SRR5630652
Bos taurus Muturu10 genome	Tijjani et al.[77]	SRR5630653
Bos taurus x Bos indicus Nanyang01 genome	Chen et al.[17]	SRR5507237
Bos taurus x Bos indicus Nanyang02 genome	Chen et al.[17]	SRR5507236
Bos taurus x Bos indicus Nanyang03 genome	Chen et al.[17]	SRR5507235
Bos taurus x Bos indicus Nanyang04 genome	Chen et al.[17]	SRR5507234
Bos taurus x Bos indicus Nanyang05 genome	Chen et al.[17]	SRR5507233
Bos taurus Ndama01 genome	Kim et al.[74]	SRR3693229
Bos taurus Ndama02 genome	Kim et al.[74]	SRR3693373
Bos taurus Ndama03 genome	Kim et al.[74]	SRR3693375
Bos taurus Ndama04 genome	Kim et al.[74]	SRR3693376
Bos taurus Ndama05 genome	Kim et al.[74]	SRR3693378
Bos taurus Ndama06 genome	Kim et al.[74]	SRR3693379
Bos taurus Ndama07 genome	Kim et al.[74]	SRR3693419
Bos taurus Ndama08 genome	Kim et al.[74]	SRR3693420
Bos taurus Ndama09 genome	Kim et al.[74]	SRR3694478
Bos taurus Ndama10 genome	Kim et al.[74]	SRR3694578
Bos primigenius NVL1 genome	Rossi et al.[6]	ERR13302359, ERR13302360, ERR13302361, ERR13600246
Bos primigenius NVL3 genome	Rossi et al.[6]	ERR13302362 - ERR13302365, ERR13600247
Bos primigenius Padova1 genome	Rossi et al.[6]	ERR13302366 -ERR13302374, ERR13600248
Bos primigenius Palidoro1 genome	Rossi et al.[6]	ERR13302375 - ERR13302387, ERR13600249
Bos taurus Piedmontese01 genome	Stothard et al.[67]	SRR1525596
Bos taurus Piedmontese02 genome	Stothard et al.[67]	SRR1525599
Bos taurus Piedmontese03 genome	Stothard et al.[67]	SRR1525603

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Bos taurus Piedmontese04 genome	Stothard et al.[67]	SRR1525604
Bos taurus Piedmontese05 genome	Stothard et al.[67]	SRR1525606
Bos taurus x Bos indicus Plo3 genome	Verdugo et al.[3]	ERR3317283, ERR3317285, ERR3317287 -
Bos taurus x Bos indicus Plo4 genome	Verdugo et al.[3]	ERR3317290, ERR3317292
Bos taurus x Bos indicus Qaz1 genome	Verdugo et al.[3]	ERR3317383, ERR3317384, ERR3317386, ERR3317387, ERR3317389, ERR3317390, ERR3317391
Bos primigenius QG10-29 genome	Hou et al.[9]	SRR22215646 -SRR22215650
Bos taurus x Bos indicus Qinchuan005 genome	Mei et al.[72]	SRS933333
Bos taurus x Bos indicus Qinchuan025 genome	Mei et al.[72]	SRS933345
Bos taurus x Bos indicus Qinchuan053 genome	Mei et al.[72]	SRS933349
Bos taurus x Bos indicus Qinchuan069 genome	Mei et al.[72]	SRS933352
Bos taurus x Bos indicus Qinchuan070 genome	Mei et al.[72]	SRS933328
Bos taurus x Bos indicus Qinchuan075 genome	Mei et al.[72]	SRS933354
Bos taurus x Bos indicus Qinchuan079 genome	Mei et al.[72]	SRS933356
Bos taurus x Bos indicus Qinchuan087 genome	Mei et al.[72]	SRS933360
Bos taurus x Bos indicus Qinchuan090 genome	Mei et al.[72]	SRS933361
Bos taurus x Bos indicus Qinchuan102 genome	Mei et al.[72]	SRS933365
Bos taurus Rashoki01 genome	NextGen Project	ERR454987
Bos taurus Rashoki02 genome	NextGen Project	ERR454988
Bos taurus Rashoki03 genome	NextGen Project	ERR454989
Bos taurus Rashoki04 genome	NextGen Project	ERR454991
Bos taurus Rashoki05 genome	NextGen Project	ERR454992
Bos taurus Rashoki06 genome	NextGen Project	ERR454993
Bos taurus Rashoki07 genome	NextGen Project	ERR454994
Bos taurus Rashoki08 genome	NextGen Project	ERR454990
Bos taurus RedAngus01 genome	Stothard et al.[67]	SRR1525580
Bos taurus RedAngus02 genome	Stothard et al.[67]	SRR1525581
Bos taurus RedAngus03 genome	Stothard et al.[67]	SRR1525600
Bos taurus RedAngus04 genome	Stothard et al.[67]	SRR1525613
Bos taurus RedAngus05 genome	Stothard et al.[67]	SRR1525614
Bos taurus RedAngus06 genome	Stothard et al.[67]	SRR1343172
Bos taurus RedAngus07 genome	Stothard et al.[67]	SRR1355239
Bos taurus RedAngus08 genome	Stothard et al.[67]	SRR1365103
Bos taurus RedAngus09 genome	Stothard et al.[67]	SRR1365113
Bos taurus RedAngus10 genome	Stothard et al.[67]	SRR1425153
Bos primigenius Rhi1 genome	Rossi et al.[6]	ERR13302388 -ERR13302400, ERR13600250
Bos primigenius Rhi2 genome	Rossi et al.[6]	ERR13302401 - ERR13302435, ERR13600251
Bos primigenius Rhi3 genome	Rossi et al.[6]	ERR13302436 -ERR13302445, ERR13600252
Bos primigenius ROS001 genome	Rossi et al.[6]	ERR13600253
Bos primigenius ROS002 genome	Rossi et al.[6]	ERR13302446 -ERR13302454, ERR13600254
Bos taurus Salers genome	Stothard et al.[67]	SRR1525608
Bos taurus Shiderti10 genome	Rossi et al.[6]	ERR13302456 - ERR13302464, ERR13600255
Bos taurus Shimao01 genome	Chen et al.[17]	SRR6942512
Bos taurus Shimao02 genome	Chen et al.[17]	SRR6942513
Bos taurus Shimao03 genome	Chen et al.[17]	SRR6942510
Bos taurus Shimao04 genome	Chen et al.[17]	SRR6942511
Bos taurus Shimao05 genome	Chen et al.[17]	SRR6942508

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Bos taurus Shimao06 genome	Chen et al.[17]	SRR6942509
Bos taurus Shimao07 genome	Chen et al.[17]	SRR6942506
Bos taurus Shimao08 genome	Chen et al.[17]	SRR6942507
Bos taurus Sikias genome	Verdugo et al.[3]	ERR3293559
Bos taurus Simmental01 genome	Stothard et al.[67]	SRR1525617
Bos taurus Simmental02 genome	Stothard et al.[67]	SRR1525618
Bos taurus Simmental03 genome	Stothard et al.[67]	SRR1525619
Bos taurus Simmental04 genome	Stothard et al.[67]	SRR1525620
Bos taurus Simmental05 genome	Stothard et al.[67]	SRR1525621
Bos taurus Simmental06 genome	Stothard et al.[67]	SRR1525700
Bos taurus Simmental07 genome	Stothard et al.[67]	SRR1525701
Bos taurus Simmental08 genome	Stothard et al.[67]	SRR1525702
Bos taurus Simmental09 genome	Stothard et al.[67]	SRR1525703
Bos taurus Simmental10 genome	Stothard et al.[67]	SRR1525705
Bos primigenius Ska1 genome	Rossi et al.[6]	ERR13302465 - ERR13302468, ERR13600256
Bos primigenius Ska3 genome	Rossi et al.[6]	ERR13302469, ERR13302470, ERR13600257
Bos taurus Somba genome	Verdugo et al.[3]	ERR3305591
Bos primigenius Songnen_Y13 genome	Hou et al.[9]	SRR17200709, SRR17200710, SRR17200711, SRR17200713, SRR17200726 -SRR17200729
Bos primigenius Songnen_Y14 genome	Hou et al.[9]	SRR17200689, SRR17200691 -SRR17200700, SRR17200702 - SRR17200708, SRR17200721, SRR17200722, SRR17200724, SRR17200725, SRR17200730 - SRR17200733
Bos primigenius Songnen_Y25 genome	Hou et al.[9]	SRR17200677, SRR17200678, SRR17200679, SRR17200690, SRR17200701, SRR17200712, SRR17200723, SRR17200734, SRR17200745, SRR17200764, SRR17200775, SRR17200780 - SRR17200783, SRR17200816, SRR17200817, SRR17200818
Bison priscus Songnen_Y48 genome	Hou et al.[9]	SRR17200739 - SRR17200742, SRR17200765 - SRR17200770
Bos primigenius Songnen_Y5 genome	Hou et al.[9]	SRR21609177 - SRR21609184, SRR17200714 - SRR17200720, SRR17200762, SRR17200763, SRR17200784 - SRR17200791, SRR17200803 - SRR17200815
Bos primigenius Songnen_Y54 genome	Hou et al.[9]	SRR17200750, SRR17200792, SRR17200793, SRR17200795 - SRR17200802
Bos primigenius Songnen_Y58 genome	Hou et al.[9]	SRR17200748, SRR17200749
Bos primigenius Songnen_Y6 genome	Hou et al.[9]	SRR17200735 - SRR17200738, SRR17200758 - SRR17200761
Bison priscus Songnen_Y8 genome	Hou et al.[9]	SRR17200743, SRR17200744, SRR17200746, SRR17200747, SRR17200751, SRR17200752, SRR17200754 - SRR17200757
Bos taurus SouthAnatolianRed genome	Verdugo et al.[3]	ERS3410015
Bos taurus Sub1 genome	Verdugo et al.[3]	ERR3317317, ERR3317320, ERR3317322-ERR3317324, ERR3317326, ERR3317327, ERR3317329, ERR3317330, ERR3317332, ERR3317333, ERR3317335, ERR3317338, ERR3317341, ERR3317345, ERR3317349, ERR3317350, ERR3317353, ERR3317355, ERR3317357, ERR3317358
Bos primigenius Tango1 genome	Rossi et al.[6]	ERR13295552 - ERR13295556, ERR13600258

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Bos primigenius Tango2 genome	Rossi et al.[6]	ERR13295557 -ERR13295561, ERR13600259
Bos primigenius Th7 genome	Verdugo et al.[3]	ERR3317487, ERR3317488, ERR3317490, ERR3317492, ERR3317493, ERR3317495 - ERR3317498, ERR3317503
Bos taurus Tibetan01 genome	Chen et al.[17]	SRR5507251
Bos taurus Tibetan02 genome	Chen et al.[17]	SRR5507250
Bos taurus Tibetan03 genome	Chen et al.[17]	SRR6024571, SRR5507249
Bos taurus Tibetan04 genome	Chen et al.[17]	SRR6024572, SRR5507248
Bos taurus Tibetan06 genome	Chen et al.[17]	SRR5507246
Bos taurus Tibetan07 genome	Chen et al.[17]	SRR5507245
Bos taurus Tibetan08 genome	Chen et al.[17]	SRR5507244
Bos taurus Tibetan09 genome	Chen et al.[17]	SRR5507243
Bos primigenius Tri1 genome	Rossi et al.[6]	ERR13295528 -ERR13295551, ERR13600260
Bos primigenius Tula1 genome	Rossi et al.[6]	ERR13302471 - ERR13302509, ERR13600261
Bos primigenius Uralsk1 genome	Rossi et al.[6]	ERR13302510 - ERR13302516, ERR13600262
Bos primigenius Uzzo1 genome	Rossi et al.[6]	ERR13302517 - ERR13302532, ERR13600263
Bos primigenius Var1 genome	Rossi et al.[6]	ERR13302533 -ERR13302544, ERR13600264
Bos primigenius Var2 genome	Rossi et al.[6]	ERR13302545 - ERR13302564, ERR13600265
Bos primigenius Vratsa1 genome	Rossi et al.[6]	ERR13302565 -ERR13302585, ERR13600266
Bos primigenius Vratsa2 genome	Rossi et al.[6]	ERR13302586 - ERR13302591, ERR13600267
Bos taurus Wagyu genome	Verdugo et al.[3]	ERR3293561
Bos taurus x Bos indicus Wandong01 genome	Chen et al.[17]	SRR5507192
Bos taurus x Bos indicus Wandong02 genome	Chen et al.[17]	SRR5507191
Bos indicus Wannan01 genome	Chen et al.[17]	SRR6024573, SRR5507199
Bos indicus Wannan02 genome	Chen et al.[17]	SRR6024574, SRR5507198
Bos indicus Wannan03 genome	Chen et al.[17]	SRR5507197
Bos indicus Wannan04 genome	Chen et al.[17]	SRR5507196
Bos indicus Wannan05 genome	Chen et al.[17]	SRR5507195
Bos taurus x Bos indicus Weining01 genome	Chen et al.[17]	SRR5507204
Bos taurus x Bos indicus Weining02 genome	Chen et al.[17]	SRR5507203
Bos taurus x Bos indicus Weining03 genome	Chen et al.[17]	SRR5507202
Bos taurus x Bos indicus Weining04 genome	Chen et al.[17]	SRR5507201
Bos taurus x Bos indicus Weining05 genome	Chen et al.[17]	SRR5507200
Bos indicus Wenshan01 genome	Chen et al.[17]	SRR6024561
Bos indicus Wenshan03 genome	Chen et al.[17]	SRR6024562
Bos indicus Wenshan04 genome	Chen et al.[17]	SRR6024569
Bos indicus Wenshan05 genome	Chen et al.[17]	SRR6024570
Bos indicus Wenshan06 genome	Chen et al.[17]	SRR6024577
Bos indicus Wenshan07 genome	Chen et al.[17]	SRR6024578
Bos indicus Wenshan08 genome	Chen et al.[17]	SRR6024575
Bos indicus Wenshan09 genome	Chen et al.[17]	SRR6024576
Bos taurus WesternFinnCattle01 genome	Weldenegodguad et al.[70]	ERR2734947
Bos taurus WesternFinnCattle02 genome	Weldenegodguad et al.[70]	ERR2734948
Bos taurus WesternFinnCattle03 genome	Weldenegodguad et al.[70]	ERR2734949
Bos taurus WesternFinnCattle04 genome	Weldenegodguad et al.[70]	ERR2734950
Bos taurus WesternFinnCattle05 genome	Weldenegodguad et al.[70]	ERR2734951
Bos grunniens Yak01 genome	Qiu et al.[78]	SRR2058046
Bos grunniens Yak02 genome	Qiu et al.[78]	SRR2059936

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Bos grunniens Yak03 genome	Qiu et al.[78]	SRR2059966
Bos grunniens Yak04 genome	Qiu et al.[78]	SRR2059950
Bos grunniens Yak05 genome	Qiu et al.[78]	SRR2059951
Bos grunniens Yak06 genome	Qiu et al.[78]	SRR2059952
Bos grunniens Yak07 genome	Qiu et al.[78]	SRR2059962
Bos grunniens Yak08 genome	Qiu et al.[78]	SRR2059963
Bos grunniens Yak09 genome	Qiu et al.[78]	SRR2059964
Bos grunniens Yak10 genome	Qiu et al.[78]	SRR2059969
Bos grunniens Yak12 genome	Qiu et al.[78]	SRR2059965
Bos grunniens Yak13 genome	Qiu et al.[78]	SRR2062306
Bos taurus Yakutian01 genome	Weldenegodguad et al.[70]	ERR2734952
Bos taurus Yakutian02 genome	Weldenegodguad et al.[70]	ERR2734953
Bos taurus Yakutian03 genome	Weldenegodguad et al.[70]	ERR2734954
Bos taurus Yakutian04 genome	Weldenegodguad et al.[70]	ERR2734955
Bos taurus Yakutian05 genome	Weldenegodguad et al.[70]	ERR2734956
Bos taurus Yanbian00 genome	Chen et al.[17]	SRR5507273
Bos taurus Yanbian01 genome	Shen et al.[79]	SRR10112122
Bos taurus Yanbian02 genome	Shen et al.[79]	SRR10112121
Bos taurus Yanbian03 genome	Shen et al.[79]	SRR10112120
Bos taurus Yanbian04 genome	Shen et al.[79]	SRR10112119
Bos taurus Yanbian05 genome	Shen et al.[79]	SRR10112118
Bos taurus Yanbian06 genome	Shen et al.[79]	SRR10112117
Bos primigenius YoA genome	Rossi et al.[6]	ERR13302592 -ERR13302598, ERR13600268
Bos taurus Yushu01 genome	Chen et al.[43]	SRS19051002
Bos taurus Yushu02 genome	Chen et al.[43]	SRS19051001
Bos taurus Yushu03 genome	Chen et al.[43]	SRS19050999
Bos taurus x Bos indicus Zaobei01 genome	Chen et al.[17]	SRR5507214
Bos taurus x Bos indicus Zaobei02 genome	Chen et al.[17]	SRR5507213
Bos taurus x Bos indicus Zaobei03 genome	Chen et al.[17]	SRR5507212
Bos taurus x Bos indicus Zaobei04 genome	Chen et al.[17]	SRR5507211
Bos taurus x Bos indicus Zaobei05 genome	Chen et al.[17]	SRR5507210
Bos primigenius Zea1 genome	Rossi et al.[6]	ERR13302599 - ERR13302602, ERR13600269
Bos primigenius Zea2 genome	Rossi et al.[6]	ERR13302603, ERR13302604, ERR13600270
CPC98 mitochondrial genome	Edwards et al.[80]	GU985279
DQ124377 mitochondrial genome	GenBank	DQ124377
DQ124383 mitochondrial genome	GenBank	DQ124383
DQ124389 mitochondrial genome	GenBank	DQ124389
DQ124401 mitochondrial genome	GenBank	DQ124401
DQ124412 mitochondrial genome	GenBank	DQ124412
DQ124418 mitochondrial genome	GenBank	DQ124418
DSQ02C mitochondrial genome	Zhang et al.[81]	OQ924184
DSQ03C mitochondrial genome	Zhang et al.[81]	OQ924185
DSQ04C mitochondrial genome	Zhang et al.[81]	OQ924186
DSQ05C mitochondrial genome	Zhang et al.[81]	OQ924187
EU177831 mitochondrial genome	Achilli et al.[39]	EU177831
EU177839 mitochondrial genome	Achilli et al.[39]	EU177839
EU177840 mitochondrial genome	Achilli et al.[39]	EU177840
EU177841 mitochondrial genome	Achilli et al.[39]	EU177841

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
EU177854 mitochondrial genome	Achilli et al.[39]	EU177854
EU177858 mitochondrial genome	Achilli et al.[39]	EU177858
EU177862 mitochondrial genome	Achilli et al.[39]	EU177862
EU177863 mitochondrial genome	Achilli et al.[39]	EU177863
EU177864 mitochondrial genome	Achilli et al.[39]	EU177864
EU177867 mitochondrial genome	Achilli et al.[39]	EU177867
EU177868 mitochondrial genome	Achilli et al.[39]	EU177868
EU177870 mitochondrial genome	Achilli et al.[39]	EU177870
FJ971081 mitochondrial genome	Achilli et al.[39]	FJ971081
FJ971085 mitochondrial genome	Achilli et al.[39]	FJ971085
FJ971087 mitochondrial genome	Achilli et al.[39]	FJ971087
FJ971088 mitochondrial genome	Achilli et al.[39]	FJ971088
HH01C mitochondrial genome	Zhang et al.[13]	OQ160842
HH02C mitochondrial genome	Zhang et al.[13]	OQ160843
HH03C mitochondrial genome	Zhang et al.[13]	OQ160844
HH04C mitochondrial genome	Zhang et al.[13]	OQ160845
HH05C mitochondrial genome	Zhang et al.[13]	OQ160846
HH07C mitochondrial genome	Zhang et al.[13]	OQ160847
HH08C mitochondrial genome	Zhang et al.[13]	OQ160848
HH09C mitochondrial genome	Zhang et al.[13]	OQ160849
HH10C mitochondrial genome	Zhang et al.[13]	OQ160850
HH11C mitochondrial genome	Zhang et al.[13]	OQ160851
HH12C mitochondrial genome	Zhang et al.[13]	OQ160852
HH13C mitochondrial genome	Zhang et al.[13]	OQ160853
HH15C mitochondrial genome	Zhang et al.[13]	OQ160854
HH16C mitochondrial genome	Zhang et al.[13]	OQ160855
HT1 mitochondrial genome	Cai et al.[11]	MG279460
HT2 mitochondrial genome	Cai et al.[11]	MG279461
HT3 mitochondrial genome	Cai et al.[11]	MG279462
HT4 mitochondrial genome	Cai et al.[11]	MG279463
HT6 mitochondrial genome	Cai et al.[11]	MG279464
HT7 mitochondrial genome	Cai et al.[11]	MG279465
HT8 mitochondrial genome	Cai et al.[11]	MG279466
HT9 mitochondrial genome	Cai et al.[11]	MG279467
HT10 mitochondrial genome	Cai et al.[11]	MG279468
HT11 mitochondrial genome	Cai et al.[11]	MG279469
HT12 mitochondrial genome	Cai et al.[11]	MG279470
HT13 mitochondrial genome	Cai et al.[11]	MG279471
HT14 mitochondrial genome	Cai et al.[11]	MG279472
HT15 mitochondrial genome	Cai et al.[11]	MG279473
HT16 mitochondrial genome	Cai et al.[11]	MG279474
HT17 mitochondrial genome	Cai et al.[11]	MG279475
HT20 mitochondrial genome	Cai et al.[11]	MG279476
HT22 mitochondrial genome	Cai et al.[11]	MG279477
HT23 mitochondrial genome	Cai et al.[11]	MG279478
HT24 mitochondrial genome	Cai et al.[11]	MG279479
HT27 mitochondrial genome	Cai et al.[11]	MG279480
HT28 mitochondrial genome	Cai et al.[11]	MG279481

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
HT30 mitochondrial genome	Cai et al.[11]	MG279482
HT31 mitochondrial genome	Cai et al.[11]	MG279483
JN817304 mitochondrial genome	Bonfiglio et al.[38]	JN817304
JN817327 mitochondrial genome	Bonfiglio et al.[38]	JN817327
JN817328 mitochondrial genome	Bonfiglio et al.[38]	JN817328
JQ437479 mitochondrial genome	Zeyland et al.[82]	JQ437479
KF525852 mitochondrial genome	Zhang et al.[7]	KF525852
KR106993 mitochondrial genome	GenBank	KR106993
KT184451 mitochondrial genome	Olivieri et al.[83]	KT184451
KT184471 mitochondrial genome	Olivieri et al.[83]	KT184471
LC537308 mitochondrial genome	Mannen et al.[40]	LC537308
MN200825 mitochondrial genome	Xia et al.[84]	MN200825
MN200842 mitochondrial genome	Xia et al.[84]	MN200842
MT576705 mitochondrial genome	Xia et al.[85]	MT576705
MT576706 mitochondrial genome	Xia et al.[85]	MT576706
MT576707 mitochondrial genome	Xia et al.[85]	MT576707
MT576708 mitochondrial genome	Xia et al.[85]	MT576708
MT576709 mitochondrial genome	Xia et al.[85]	MT576709
MT576710 mitochondrial genome	Xia et al.[85]	MT576710
MT576715 mitochondrial genome	Xia et al.[85]	MT576715
MT576726 mitochondrial genome	Xia et al.[85]	MT576726
MT576748 mitochondrial genome	Xia et al.[85]	MT576748
MT576756 mitochondrial genome	Xia et al.[85]	MT576756
MT576765 mitochondrial genome	Xia et al.[85]	MT576765
MT576785 mitochondrial genome	Xia et al.[85]	MT576785
MT576800 mitochondrial genome	Xia et al.[85]	MT576800
MT576801 mitochondrial genome	Xia et al.[85]	MT576801
MT576805 mitochondrial genome	Xia et al.[85]	MT576805
MT576820 mitochondrial genome	Xia et al.[85]	MT576820
MT576824 mitochondrial genome	Xia et al.[85]	MT576824
MT576827 mitochondrial genome	Xia et al.[85]	MT576827
MT576831 mitochondrial genome	Xia et al.[85]	MT576831
MT576835 mitochondrial genome	Xia et al.[85]	MT576835
MT576836 mitochondrial genome	Xia et al.[85]	MT576836
MT576840 mitochondrial genome	Xia et al.[85]	MT576840
MT576841 mitochondrial genome	Xia et al.[85]	MT576841
MT576842 mitochondrial genome	Xia et al.[85]	MT576842
MW414140 mitochondrial genome	GenBank	MW414140
MW414151 mitochondrial genome	GenBank	MW414151
NC_006295 mitochondrial genome	GenBank	NC_006295
NC_006380 mitochondrial genome	GenBank	NC_006380
NC_006853 mitochondrial genome	GenBank	NC_006853
NC_025563 mitochondrial genome	Na et al.[86]	NC_025563
NC_049568 mitochondrial genome	GenBank	NC_049568
Nelore mitochondrial genome	GenBank	NC_005971
SM09C mitochondrial genome	Zhang et al.[81]	OQ924188
SM10C mitochondrial genome	Zhang et al.[81]	OQ924189
SM13C mitochondrial genome	Zhang et al.[81]	OQ924190

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
SM17C mitochondrial genome	Zhang et al.[81]	OQ924191
TC03C mitochondrial genome	Zhang et al.[81]	OQ924192
TC04C mitochondrial genome	Zhang et al.[81]	OQ924193
TS01C mitochondrial genome	Zhang et al.[81]	OQ924181
TS03C mitochondrial genome	Zhang et al.[81]	OQ924182
V00654 mitochondrial genome	Anderson et al.[87]	V00654
XB04C mitochondrial genome	Zhang et al.[81]	OQ924183
Oligonucleotides		
Cattle mitochondrial D-loop control region primer	Troy et al.[2]	L16022
Cattle mitochondrial D-loop control region primer	Troy et al.[2]	H16178
Cattle mitochondrial D-loop control region primer	Cai et al.[11]	L16137
Cattle mitochondrial D-loop control region primer	Cai et al.[11]	H16315
Software and algorithms		
OxCal v. 4.4.2	Bronk Ramsey[88]	https://c14.arch.ox.ac.uk/oxcal.html
AdapterRemoval v. 2	Schubert et al.[89]	https://adapterremoval.readthedocs.io/en/stable/
bwa v. 0.7.15	Li[90]	https://bio-bwa.sourceforge.net/bwa.shtml
SAMtools v. 1.10	Li et al.[91]	https://www.htslib.org/
Qualimap v. 2.3	Okonechnikov et al.[92]	http://qualimap.conesalab.org/
DamageProfiler	Neukamm et al.[93]	https://github.com/Integrative-Transcriptomics/DamageProfiler
AMBER	Dolenz et al.[94]	https://github.com/tvandervalk/AMBER
ANGSD v. 0.930	Korneliussen et al.[95]	https://github.com/ANGSD/angsd
IQ-Tree v. 2.3.2	Minh et al.[96]	https://iqtree.github.io/
MEGA 11	Tamura et al.[97]	https://www.megasoftware.net/
PopArt	Leigh et al.[98]	https://popart.maths.otago.ac.nz/
Eigensoft v. 6.0	Patterson et al.[99]	https://github.com/DReichLab/EIG
LEA	Frichot et al.[100]	https://doi.org/10.18129/B9.bioc.LEA
AdmixturePlotter	N/A	https://github.com/TCLamnidis/AdmixturePlotter
TreeMix	Pickrell et al.[101]	http://treemix.googlecode.com
popstats	Skoglund et al.[102]	https://github.com/pontussk/popstats
AdmixTools	Meisner et al.[103]	https://github.com/DReichLab/AdmixTools
OptM	Fitak[104]	https://cran.r-project.org/web/packages/OptM
Sexing Script for Ancient DNA	DeFlamingh et al.[105]	https://github.com/adeflamingh/de_Flamingh_et_al_2020_G3.git

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Ancient aurochs and cattle

Skeletal material from 27 individual aurochs were analyzed as a part of this study. After examining DNA coverage, eleven had sufficient data for mitochondrial DNA-based analyses and six had sufficient data for nuclear genome-based analyses, for a total of twelve individuals. Details on the age, context and origin of each sample is detailed in Table S1.

For comparison, we used a reference panel of ancient cattle genomes, including ancient taurine cattle from the 4000-years-old site of Shimao in the Ordos region of China. These genomes are publicly accessible and were used for both whole-genome[3,6,9,17,43,54] and mitochondrial DNA analyses.[3,6,7,9,11,13,17,43,80–85,87] A summary of metadata for the whole-genome reference individuals is available in Table S3 and a summary of metadata for the mitochondrial reference individuals is available in Table S4.

Modern cattle

For comparison, we also used a reference panel of modern taurine and indicine cattle breeds which are publicly accessible, both for whole-genome[3,9,17,37,43,67–79] and mitochondrial DNA analyses.[38,39,43,50,81,83–87,106] A summary of metadata for the whole-genome reference individuals is available in Table S3 and a summary of metadata for the mitochondrial reference individuals is available in Table S4.

METHOD DETAILS

Radiocarbon dating

Dates for individual samples, where available, are reported in Table S1. Seven samples had direct or secure indirect dates that were previously reported elsewhere (UGAMS-, OxA-). Nine of the samples were directly dated using AMS 14C for this study (UOC-). Dates for B16 and B17 are on associated human remains from the same tomb. Remaining samples were assigned to a period based on other dates from same stratigraphic association; those samples were selected from associated faunal remains based on their context (e.g., securely mapped, locational significance). Bone collagen for all samples dated in this study was extracted and purified at the Trent Environmental Archaeology Laboratory (TEAL) using Centriprep 30 kDa centrifugal ultrafilters according to the UCI-KCCAMS procedure.[107] The samples were prepared alongside a woolly mammoth bone with an infinite radiocarbon age (Hollis Mine Mammoth, Fmc = 0.0031 ± 0.0009) and two secondary standards that have been measured multiple times (Umingmak Wale, Fmc = 0.4011 ± 0.0009; Banks Island Musk Ox, Fmc = 0.6489 ± 0.0011). The >30 kDa collagen extracts were sent to the A. E. Lalonde AMS Laboratory where radiocarbon analyses were performed on a 3 MV tandem accelerator mass spectrometer built by High Voltage Engineering (HVE). 12,13,14C+3 ions were measured at 2.5 MV terminal voltage with Ar stripping.[108] The fraction of modern carbon, F14C, was calculated according to[109] as the ratio of the sample 14C/12C ratio to the standard 14C/12C ratio (in our case Ox-II) measured in the same data block. Both 14C/12C ratios were background-corrected and the result was corrected for spectrometer and preparation fractionation using the AMS measured 13C/12C ratio and normalized to δ13C (PDB). Radiocarbon ages were calculated as $-8033\ln(F14C)$ and reported in 14C yr BP (BP = AD 1950) as described by.[109] Calibration was performed using OxCal v4.4.2[88] and the IntCal20 calibration curve.[110]

Ancient DNA sample preparation

A total of 27 bone or tooth samples were analyzed at the Williams Ancient DNA Laboratory with HEPA filtered positive airflow at the University of Illinois at Chicago (UIC), which is used exclusively for ancient DNA research and physically separated from the post-PCR laboratory. Rigorous contamination controls followed standard procedures, including multiple negative controls at all stages of analysis, the sterilization of surfaces and instruments by UV light, and the decontamination of the work area and equipment with 10% sodium hypochlorite solution. Before the DNA extraction, samples were decontaminated by submerging them in a 10% sodium hypochlorite solution for 4 min and subsequently rinsed in DNAse free water on a tube rocker for 15 min, repeating the rinse if necessary or until the water was clear.

DNA extraction

The DNA extraction followed a modified silica-spin column method.[111] The decontaminated samples were ground into a powder and approximately 120 mg of bone powder was incubated for at least 18 h at 37°C in lysis buffer (0.45M EDTA pH 8.0, 20mg/20 mL Proteinase K). Afterward, 1 mL of sample supernatant was transferred to a Zymo-Spin V Extender Assembly along with 13 mL of binding buffer (guanidine hydrochloride, sodium acetate, Tween 20, and silica suspension). The extracts were purified using QIAGEN PE buffer and eluted with QIAGEN Buffer EB. Each sample was extracted several times along with no more than 6 samples at a time and a negative control. DNA quantity was measured using a Qubit quantification platform. As a further check, extracted DNA samples were amplified and visualized on acrylamide gels in a laboratory located in another building on campus.[112] Two sets of primers that target cattle mitochondrial D-loop control regions were used (L16022/H16178 and L16137/H16315.[4,16] Six samples did not show evidence of DNA and received no further analysis.

Next-generation sequencing

Genomic libraries were prepared for next-generation sequencing using the NEBNext® Ultra™ II DNA Library Prep kit for Illumina® with NEBNext® Multiplex Oligos (Dual Index primers) and purified using AMPure XP magnetic beads (Beckman Coulter). The NEBNext® Ultra™ II protocol was followed, with adaptor dilution at 1:15 and cleanup of adaptor-ligated DNA was carried out without size selection. The binding time with the beads was extended to 10 min. PCR amplification of the libraries included 14 cycles of denaturation at 98°C for 10 s and annealing/extension at 65°C for 75 s. Thirteen libraries were sequenced at the Genome Research Core at UIC, and an additional 10 samples were sequenced at the Rush University Medical Center Genomics and Microbiome Core Facility. The library fragments were visualized on D1000 and D5000 ScreenTape Systems in both labs. An initial run was performed on an Illumina® MiniSeq to assess the number of reads that mapped to cattle DNA sequence. Quality assessment was undertaken by the UIC Research Bioinformatics Core Facility. Endogenous read percentages ranged from 14 to 97%, with an average of 43%. Two samples (B1 and B17) were selected for deeper coverage sequencing because of their high quality. The highest endogenous percentage (97% DNA reads) came from B17, the only petrous bone sample collected. An Illumina® NovaSeq was used to generate 2×150 paired end reads.

Alignment to reference cattle genome

All raw reads were analyzed using a standard pipeline optimized for ancient samples. Adapters were removed using AdapterRemoval v2[89] with a quality trim, a removal of Ns, and a minimum length of 25 base pairs (AdapterRemoval –trimns –trimqualities –minlength 25). We used a reference genome that combined the autosomes and X chromosome from BosTau9 (ARS-UCD2.0), the

Y chromosome from BosTau7, and the mitochondrial reference sequence (accession V00654.1). The Burrows-Wheeler Alignment Tool version 0.7.15 with the 'aln' function[90] was used to align the raw sequenced reads to the reference with a 1% missing alignment allowance and a 2 gap open limit (bwa aln -n 0.01 -o 2), and sampe was used to combine the mapped pairs. The resulting sam files were converted to bam files using the SAMtools version 1.10 view command, which removed unaligned reads and reads with a mapping quality less than 25 (samtools view -b -S -F 4 -q 25).[91] SAMtools was also used to sort the reads and remove duplicates (samtools sort and samtools rmdup, respectively). We used Qualimap version 2.3[92] to assess sequencing depth and genome coverage. Table S2 lists total genome coverage, number of nucleotides, and average coverage for each sample.

All ancient comparative samples downloaded from the Sequence Read Archive (Table S3) as fastq files were aligned using the same pipeline, starting at the "bwa aln" step (with samse used instead of sampe in the case of single-end ancient sequences). All modern comparative samples downloaded from the Sequence Read Archive (Table S3) as fastq files were aligned using a similar pipeline that used the "bwa mem" command for initial alignment and the same steps as above to remove low quality/unaligned reads, sort reads and remove duplicates.

Quality control of NGS data

We used DamageProfiler[93] to authenticate ancient sequences. Typical ancient DNA damage patterns have parabolic distributions with more C to T misincorporations at the 5 prime ends of reads and more G to A misincorporations at the 3 prime ends of reads. DamageProfiler deamination curves for the 12 samples included in our analyses are shown in Figure S2.

To assess whether the use of BosTau9 as our reference was introducing reference bias, we used AMBER to compare mapping efficacy of our new samples to the *Bos taurus* and *Bubalus bubalis* genomes.[94] Bam files were filtered to include unique reads only prior to analysis with AMBER. The results suggest that using the *B. taurus* reference genome results in less biased mapping (Figure S11).

SNP calling

The program ANGSD ver. 0.930[95] was used to call variants. The method uses a genotype likelihood method, which accounts for some of the uncertainty surrounding ancient DNA SNP calls. Haploid calling was performed for all of the ancient and modern samples, calling the most common base at each position using the SAMtools model of genotype likelihood calling and filtering for quality ("angsd -doHaploCall 2 -doCounts 1 -GL 1 -C 50 -uniqueOnly 1 -remove_bads 1 -minQ 25 -minMapQ 30"). We also filtered the data to only retain SNPs with transversions, as transitions can also be caused by DNA damage. We used multiple subsets of the data depending on the analysis. Our most complete dataset included modern taurine, indicine, and admixed cattle; ancient aurochs genomes from Western and Eastern Eurasia; ancient cattle from the Middle East and East Asia; domesticated and wild yak; and a single gaur individual as outgroup. A "Taurine and Indicine" dataset included ancient and modern taurine, indicine, and admixed cattle and aurochs (excluding yaks), and a "Taurine" dataset included ancient and modern taurine cattle and aurochs (excluding indicine and admixed cattle and yaks). For each of these datasets, some analyses called for higher-coverage data, and in those cases we used a "High Coverage" dataset that included all modern individuals, all published ancient genomes with an average coverage of 2× or higher, and three ancient Mongolian individuals from this study: B13, B17, and B28.

Phylogenies and networks

A whole-genome phylogeny was constructed using the SNP data for the "High Coverage Bovines" set. The vcf file was converted to a phylip alignment using a python script called "vcf2phylip.py" (https://github.com/edgardomortiz/vcf2phylip/blob/master/vcf2phylip.py) and a maximum likelihood tree was created using IQ-TREE v2.3.2[96] using 1000 bootstraps. We used a substitution model identified by ModelFinder[113] as part of tree construction, which used a generalized time reversible substitution model, empirical base frequencies, and a generalized gamma model with 6 categories (GTR+F+R6).

We used SAMtools[91] to extract complete mitochondrial genomes from the sample bam files and then made an alignment using MUSCLE in MEGA11.[97] We constructed a maximum likelihood tree for the complete mitochondrial genomes using IQ-TREE v2.3.2[96] using 1000 bootstraps (Figure S4).

We also compared the mtDNA D-loop region (16022–(16315) with previously published ancient aurochs and taurine cattle samples from China and surrounding regions of northern Asia. We identified variable nucleotide positions as shown in Table S5. We used PopArt[98] to construct a median joining network for the D-loop alignment, epsilon 0 (Figure S5). Individuals included in the mitochondrial genome or D-loop analyses include north Asian aurochs from Siberia and West Asia (samples date from ca. 41,000 ca; BP to ca. 5,000 cal BP),[6] aurochs from Songnen in the Amur region of Heilongjiang Province (samples date from ca. 10,000 to ca. 3,300 cal BP),[9] aurochs and *Bos taurus* (one individual, HT31) from Houtaomuga (ca. 6300–5000 cal BP),[11] aurochs and *Bos taurus* from Honghe (ca. 4500–3500 cal BP),[13] taurine cattle from Bangga on the Tibetan Plateau (ca. 2600 cal BP),[43] taurine cattle from Bronze Age Dashanqian in Inner Mongolia (ca. 4000–3500 cal BP),[81] taurine cattle from Bronze Age Shimao in the Ordos region of Shaanxi Province (ca. 4000–3800 cal BP),[17,81] taurine cattle from Late Neolithic Taosi in Shanxi Province (ca. 4500–4100 cal BP), taurine cattle from Bronze Age Xubao in Henan Province (4500–4000 cal BP), and taurine cattle from the Tsaraam cemetery in Buryatia, Russian Federation (ca. 1900–1800 cal BP).[81]

Principal component analysis

We used smartpca from eigensoft v. 6.0[99] to create a Principal Component Analysis. A python script was used to convert the vcf to the input files for smartPCA, and modern taurine cattle and ancient aurochs and taurine cattle with an average depth of coverage of at least 2× were used in the calculation of the eigenvectors, while the low-coverage ancient individuals were projected onto the PCA (lsqproject: YES in the parameter file). We also made a similar plot using our "Taurine and Indicine" dataset (Figure S3).

Admixture

We used the "High Coverage" dataset for admixture analyses, and used two approaches that are designed to work well with ancient DNA and missing data. Our first approach used angsd,[95] which called genotype likelihoods using the SAMtools model (-GL (1) for all sites with genotype data for 231 individuals (-minInd (231) where the number of individuals is equal to the number of modern samples plus half the number of ancient individuals, producing a Beagle file output (-doGlf 2). The major allele was polarized to the reference genome and allele frequencies for each allele were calculated (-doMajorMinor 1 -doMaf 2). We then used PCAngsd to calculate admixture proportions for K = 2–8.[103] Admixture proportions were also calculated using the R package LEA,[100] using 50 repetitions and testing K = 1–8. The run with the least cross-entropy was chosen as the best for each value of K. Visualization was performed using the R script AdmixturePlotter (https://github.com/TCLamnidis/AdmixturePlotter). Admixture proportions were calculated for both the Taurine and Taurine and Indicine datasets.

TreeMix

TreeMix version 1.13[101] was used to create a TreeMix plot using the High Coverage Bovines, ancient *Bos taurus* and *primigenious* individuals, modern *Bos taurus* individuals, and yak (*Bos grunniens)* individuals as an outgroup to identify possible sources of gene flow (Figure S9).

Sex identification

Genetic sexing of the higher coverage ancient Mongolian individuals (B13, B17, B28) was performed using a script developed by de Flamingh et al. (2020)[105] that compares average sequencing depth of the autosomes to the X chromosome. A 95% confidence interval was calculated for the ratio of X depth to autosome depth. An interval of 0.8 or above was considered female, while an X:autosome ratio confidence interval of 0.6 or below was considered male.

QUANTIFICATION AND STATISTICAL ANALYSIS

Introgression scans (*D* statistics)

To test for the presence of introgression in ancient or modern bovine populations, we utilized Patterson's *D* statistic which uses observed site pattern counts as a proxy for genealogical relationships to assess if there are more discordant topologies than expected under neutrality.[114]

To test whether North Asian aurochs admixed with ancient East Asian domesticated cattle populations, we used the following configurations by permuting all possible combinations of P_2 and P_3:

$$P_1 = \text{Sub1}; P_2 = (\text{B17}, \text{B28}, \text{Shimao05}, \text{Banga33}); P_3 = (\text{B13}, \text{Baikal1}, \text{Tula1}, \text{Gyu1}, \text{Songnen\_Y5}); P_4 = \text{Gaur}$$

To test whether our samples that postdate the arrival of domesticated cattle to East Asia admixed with domesticated cattle, we used the following configurations by permuting P_2:

$$P_1 = \text{B13}; P_2 = (\text{B17}, \text{B28}); P_3 = \text{Sub1}; P_4 = \text{Gaur}$$

We assessed significance by using a weighted block-jackknifing procedure to estimate the standard error and subsequently compute *Z*-scores as described in[41] with a block size of 50 kb, which was determined based on known patterns of LD-decay in cattle following.[3] To ensure the robustness of our standard error estimates, we repeated these analyses for block sizes of 500 kb, 1 Mb, and 5 Mb for comparison. As was done in Verdugo et al.,[3] we filtered out any configurations that did not have at least 200 *ABBA* + *BABA* sites and considered a configuration statistically significant if the absolute value of the *Z* score was greater than or equal to three. The *D* statistics results are shown in Table S6 and Figure S11.

F3 statistics

We used F3 statistics to identify the modern cattle populations that were most closely related to ancient East Asian cattle (Shimao05 and B17, the highest-coverage samples from each region). F3 statistics were calculated using popstats,[102] with qp3pop from AdmixTools[114] used to corroborate results. For popstats, transposed plink files and populations for comparison were used as input, with the additional flags: –informative –not23 –f3vanilla. Qp3pop used eigenfiles, with no additional flags or modifications from the default. Plink 2.0[115] and convertf from AdmixTools were used to filter and reformat data.[114] Results for B17 are shown in Figure 3 and results for Shimao are in Table S7.

Demographic model validation

For admixture plots generated using LEA,[100] the run with the least cross-entropy was chosen as the best for each value of K for both the "Taurine" and the "Taurine and Indicine" dataset. For Treemix runs, OtpM[104] was used to determine the optimal number of migrations edges from a range of 1–7 (Figure S10).

ADDITIONAL RESOURCES

All scripts needed to reproduce all analyses are available at https://github.com/kelsey-witt/cattle_aDNA_methods.