

This is a repository copy of *Ancient cattle genomics, origins, and rapid turnover in the Fertile Crescent*.

White Rose Research Online URL for this paper:
<https://eprints.whiterose.ac.uk/149232/>

Version: Accepted Version

Article:

Verdugo, Marta Pereira, Mullin, Victoria E, Scheu, Amelie et al. (38 more authors) (2019) Ancient cattle genomics, origins, and rapid turnover in the Fertile Crescent. *Science*. pp. 173-176. ISSN 0036-8075

<https://doi.org/10.1126/science.aav1002>

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

Title: Ancient cattle genomics, origins and rapid turnover in the Fertile Crescent

Authors: Marta Pereira Verdugo^{1†}, Victoria E. Mullin^{1,2†}, Amelie Scheu^{1,3†}, Valeria Mattiangeli¹, Kevin G. Daly¹, Pierpaolo Maisano Delser^{1,4}, Andrew J. Hare¹, Joachim Burger³, Matthew J. Collins^{5,6}, Ron Kehati⁷, Paula Hesse⁸, Deirdre Fulton⁹, Eberhard W. Sauer¹⁰, Fatemeh A. Mohaseb^{12,13}, Hossein Davoudi^{13,14,15}, Roya Khazaeli¹³, Johanna Lhuillier¹⁶, Claude Rapin¹⁷, Saeed Ebrahimi¹⁸, Mutalib Khasanov¹⁹, S. M. Farhad Vahidi²⁰, David E. MacHugh^{21,22}, Okan Ertuğrul²³, Chaido Koukouli-Chrysanthaki²⁴, Adamantios Sampson²⁵, George Kazantzis²⁶, Ioannis Kontopoulos⁵, Jelena Bulatovic²⁷, Ivana Stojanović²⁸, Abdesalam Mikdad²⁹, Norbert Benecke³⁰, Jörg Linstädter³¹, Mikhail Sablin³², Robin Bendrey^{10,33}, Lionel Gourichon³⁴, Benjamin S. Arbuckle³⁵, Marjan Mashkour^{12,13,14}, David Orton⁵, Liora Kolska Horwitz³⁶, Matthew D. Teasdale^{1,5} and Daniel G. Bradley^{1*}

Affiliations:

¹ Smurfit Institute of Genetics, Trinity College Dublin, Dublin, D02 PN40, Ireland.

² Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK.

³ Palaeogenetics Group, Institute of Organismic and Molecular Evolution (iOME), Johannes Gutenberg-University Mainz, 55099 Mainz, Germany.

⁴ Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK.

⁵ BioArCh, University of York, York YO10 5DD, UK.

⁶ Museum of Natural History, University of Copenhagen, Copenhagen, Denmark.

⁷ 448 Shvil Hachalav Street Nir Banim 7952500, Israel.

⁸ Jewish Studies Program, Department of Classics and Ancient Mediterranean Studies, The Pennsylvania State University, 108 Weaver Building, University Park, PA 16802, USA.

⁹ Department of Religion, Baylor University, Waco, TX 76798-7284, USA.

¹⁰ School of History, Classics and Archaeology, University of Edinburgh, Old Medical School, Teviot Place, Edinburgh EH8 9AG, UK.

¹¹ Tabriz Islamic Art University, Department of Archaeology and Archaeometry, 5164736931, Tabriz, Iran.

¹² Archéozoologie, Archéobotanique (UMR 7209), CNRS, MNHN, UPMC, Sorbonne Universités, Paris, France.

¹³ Archaeozoology section, Archaeometry Laboratory, University of Tehran, Tehran, Iran.

¹⁴ Osteology Department, National Museum of Iran, Tehran, Iran.

¹⁵ Department of Archaeology, Faculty of Humanities, Tarbiat Modares University, 111-14115 Tehran, Iran.

¹⁶ Archéorient Université Lyon 2/CNRS UMR 5133, Maison de l'Orient et de la Méditerranée, 7 rue Raulin, 69365 Lyon, France.

¹⁷ Archéologie d'Orient et d'Occident (AOROC, UMR 8546, CNRS ENS), Centre d'archéologie, 45 Rue d'Ulm, 75005 Paris, France.

- ¹⁸ Faculty of Literature and Humanities, Islamic Azad University, Damavand Avenue, Imam Hossein Square, Tehran, Iran.
- ¹⁹ Uzbekistan Institute of Archaeology of the Academy of Sciences of the Republic of Uzbekistan, Abdullaeva street 3, 703051 Samarkand, Uzbekistan.
- ²⁰ Agricultural Biotechnology Research Institute of Iran-North branch (ABRII), Agricultural Research, Education and Extension Organization, Rasht, Iran.
- ²¹ Animal Genomics Laboratory, UCD School of Agriculture and Food Science, University College Dublin, Dublin, D04 V1W8, Ireland.
- ²² UCD Conway Institute of Biomolecular and Biomedical Research, University College Dublin, Dublin, D04 V1W8, Ireland.
- ²³ Veterinary Faculty, Ankara University, Ankara, Turkey.
- ²⁴ Hellenic Ministry of Culture and Sports, Department of Prehistoric and Classical Antiquities, and Museums, 68 Ethnikis Antistaseos, Serres, 62 122 Greece.
- ²⁵ University of the Aegean, Department of Mediterranean Studies, Rhodes, Greece.
- ²⁶ Archaeological Museum of Aeani, 500 04, Kozani, Western Macedonia, Greece.
- ²⁷ Laboratory for Bioarchaeology, Department of Archaeology, University of Belgrade, Cika Ljubina 18-20, 11000 Belgrade, Serbia.
- ²⁸ Institute of Archaeology, Knez Mihailova 35/4, 11000 Belgrade, Serbia.
- ²⁹ Institut National des Sciences de l'Archéologie et du Patrimoine de Maroc (INSAP) Hay Riad, Madinat al Ifrane, Argle rues 5 et 7, Rabat Instituts, 10000 Rabat, Morocco.
- ³⁰ Department of Natural Sciences, German Archaeological Institute, 14195 Berlin, Germany.
- ³¹ Deutsches Archäologisches Institut, Kommission für Archäologie Außereuropäischer Kulturen (KAAK), Dürenstr. 35-37, 53173 Bonn, Germany.
- ³² Zoological Institute of the Russian Academy of Sciences, 199034 St Petersburg, Russia.
- ³³ Department of Archaeology, University of Reading, Whiteknights Box 226, Reading RG6 6AB, UK
- ³⁴ University Côte d'Azur, CNRS, CEPAM (UMR 7264), Nice, France.
- ³⁵ Department of Anthropology, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA
- ³⁶ National Natural History Collections, Faculty of Life Sciences, The Hebrew University, Jerusalem, Israel

† These authors contributed equally to this work.

* Corresponding author. Email: dbradley@tcd.ie

Abstract: Genome-wide analysis of 67 ancient Near Eastern cattle, *Bos taurus*, remains reveal regional variation that has since been obscured by admixture in modern populations. Comparisons of genomes of early domestic cattle to their aurochs progenitors identify diverse origins with separate introgressions wild stock. A later region-wide Bronze Age shift indicates rapid and widespread introgression of zebu, *Bos indicus*, from the Indus Valley. This process was likely stimulated at the onset of the current geological age, ~4.2ka, by a widespread multi-century drought. In contrast to genomewide admixture, mtDNA stasis supports that this introgression was male-driven, suggesting that selection of arid-adapted zebu bulls enhanced herd survival. This human-mediated migration of zebu-derived genetics has continued through millennia, altering tropical herding on each continent.

One Sentence Summary: Ancient Near Eastern cattle show ancestry from multiple aurochs strains plus a massive zebu influx at the onset of the Meghalayan Age.

The extinct Eurasian aurochs (*Bos primigenius*) was domesticated *ca.* 10,500 BP within the restricted locality of the Upper Euphrates and Tigris drainages of the Fertile Crescent (1, 2). However, the true extent and nature of interactions between humans and aurochs resulting in modern day domestic cattle are obscure.

Mitochondrial DNA (mtDNA) diversity in modern *Bos taurus* cattle suggests a highly restricted initial domestic pool of ~80 females (3–5). However, a more complex relationship with wild populations is evidenced by introgression from local aurochs into British cattle and the genomic divergence of *B. indicus* (zebu) cattle from the Indus Valley region (6, 7). Zebu genomic influence is pervasive in modern Near Eastern herds (8). Two theories account for this: one suggests an origin from genomically intermediate Near Eastern aurochs whereas a second hypothesizes they resulted from an introgression of domestic zebu genomes into the region from the east, either in a discrete active process, perhaps responding to climate fluctuation, or a passive diffusion over many millennia (9).

In order to analyse now-obscured early cattle genome strata from the region of *Bos taurus* domestication we retrieved genome-wide data from 67 ancient bovines (including six aurochs). These date from Mesolithic to early Islamic periods and despite poor preservation, typical of the region, we obtained an average genome coverage of 0.9× (Table S1).

The pattern of genetic variation in extant cattle is well established. European *B. taurus*, West African *B. taurus* and *B. indicus* of South Asian origin, represent three distinct apices in plotted principal components (PC) (Fig. 1A). Geographically intermediate populations, such as Near Eastern and East African animals, fall in genetically intermediate positions (7, 8, 10). Projecting ancient cattle genomes against this genetic landscape (Fig. 1A) we observe that to the left of PC1, earlier (Neolithic and Bronze Age) genomes fall in three geographical clusters (*a*, Balkans; *b*, Anatolia/Iran; and *c*, southern Levant) along with modern European and African *B. taurus* while *B. indicus* breeds are separated and represented on the far right of the PC plot (Fig. 1A). This confirms that cattle origins included two divergent aurochs populations that formed the basis of the *indicus-taurus* divide.

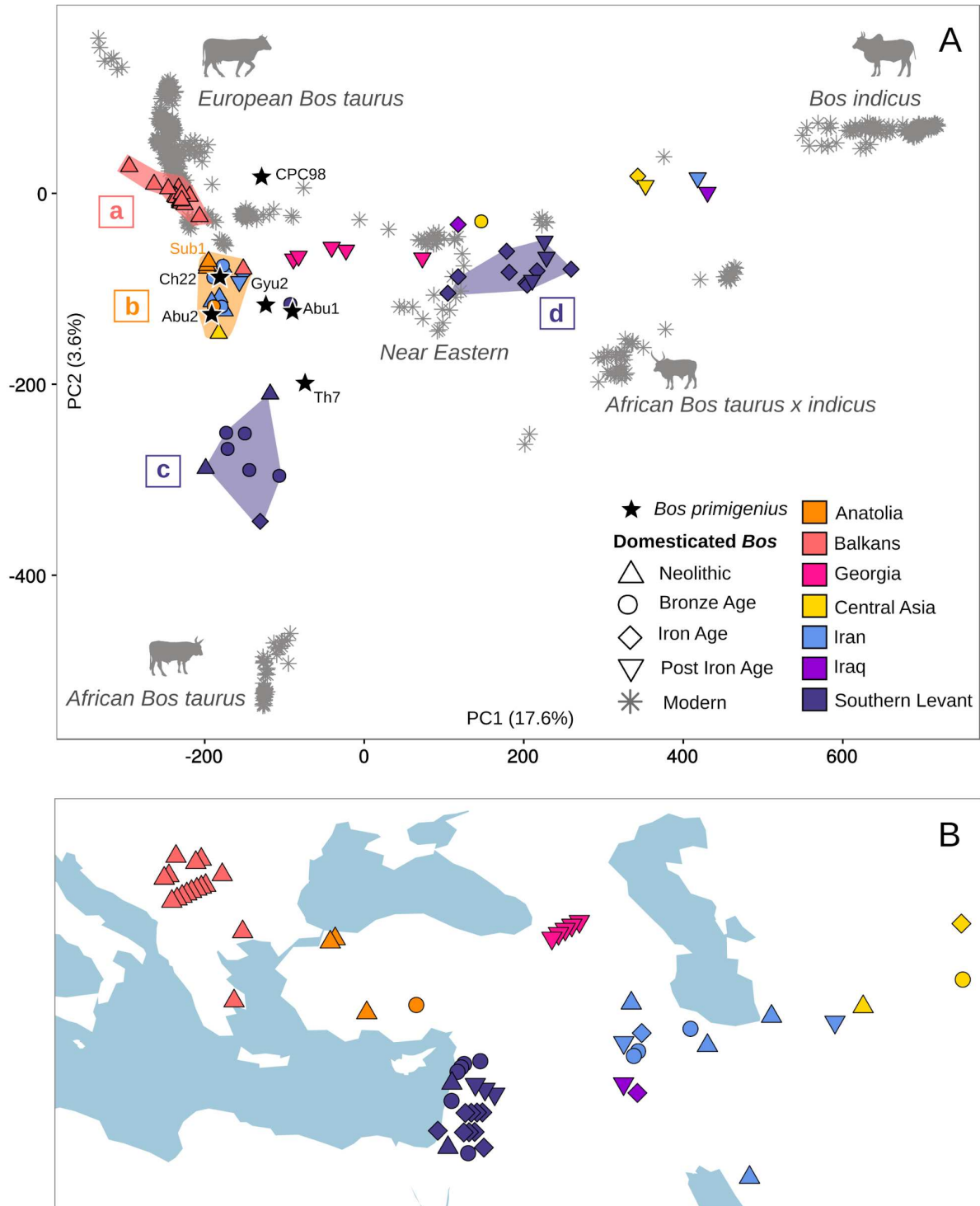


Fig. 1. Projection Procrustes principal components analysis of ancient cattle. (A) Ancient animals are projected on modern 770K Bovine SNP genotypes, shown as background gray asterisks (Figs. S1-2). Four clusters are highlighted: (a) Neolithic Balkans, which plot with modern Europeans; (b) a group of mainly Anatolian and Iranian cattle close to four aurochs from the Near East; Levantine cattle fall in two groups: (c) a cluster of earlier samples and (d) a cluster of later samples close to contemporary Near Eastern cattle with *B. indicus* admixture. (B) Approximate geographical distribution of ancient sample sites.

Six ancient aurochs genomes provide additional context, including four from the greater Near East: two ~9,000 yr old samples from the Levantine Aceramic village of Abu Ghosh (*Abu1* and *Abu2*), a 7,500 yr old sample from the early Anatolian settlement, Çatalhöyük (*Ch22*) and a 7,000 yr old Armenian aurochs (*Gyu2*) (11). These four fall close to the Anatolia/Iran ancient domestic cattle cluster (Fig. 1A, cluster *b*) and reveal this as the oldest ancestral stratum of *B. taurus*. The genomic signature of this earliest population has been obscured in modern Near Eastern cattle by later admixture. From this group we sequenced a well-preserved 8,000 yr old Anatolian genome (*Sub1*) (11) to 13.5× coverage and use this in *D* statistics testing for zebu introgression in other ancient individuals (Fig. 2).

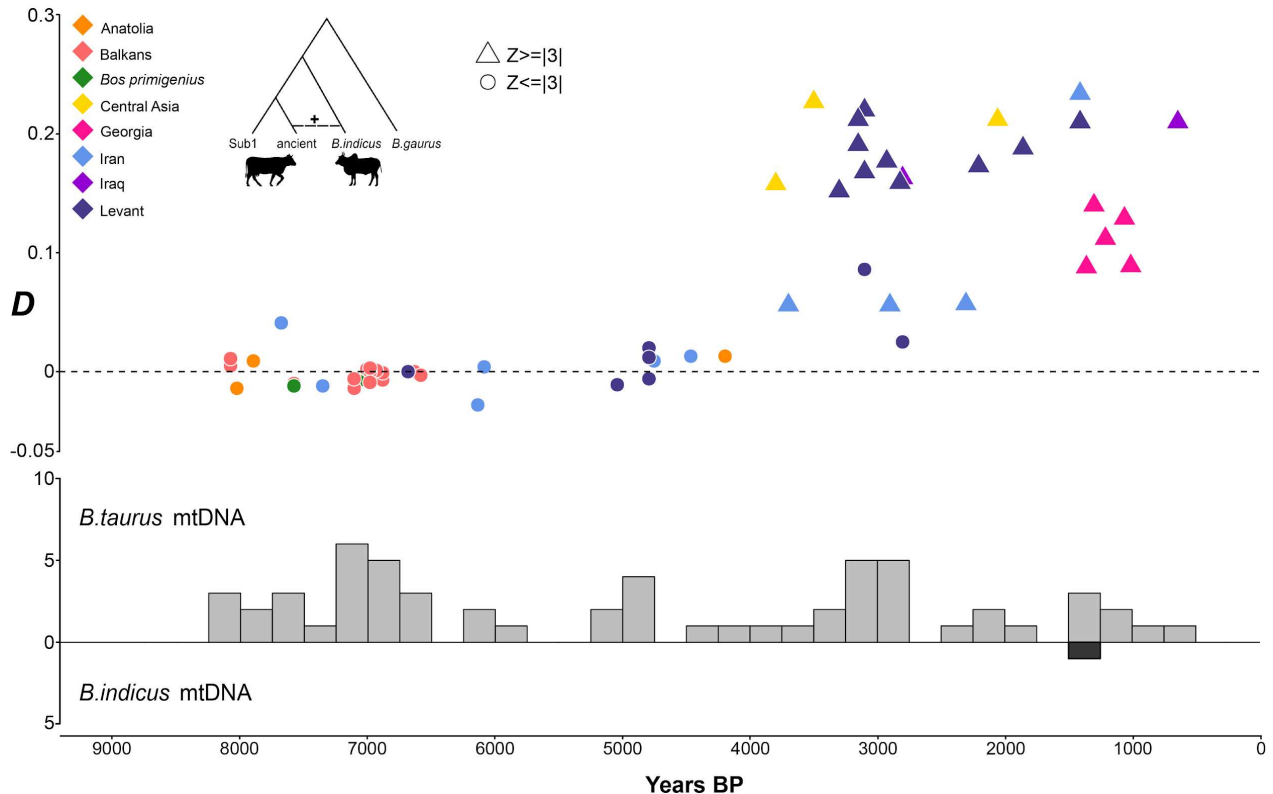


Fig. 2. Zebu introgression through time in the greater Near East. Whole genome *D* statistic calculations with a gaur (*B. gaurus*) as an outgroup and the Neolithic Anatolian domestic genome *Sub1* as a representative non-admixed individual (see inset). A step change in zebu introgression is apparent *circa* 4,000 BP. MtDNA counts of taurine (gray) and the single zebu (black) mtDNA within ancient domestic cattle are graphed (bottom, with a shared time axis) in 250 yr intervals.

B. indicus cattle are adapted to, and predominate in, modern arid and tropical regions of the world (11). Zebu cattle originated *ca.* 8,000 BP (12). However, despite archaeological evidence for contact between the Fertile Crescent region and the Indus Valley (9), it is 4,000 years before the influence of the zebu genome is detectable in ancient Southwest Asian cattle (Fig. 2). However, after ~4,000 BP, hybrid animals (median 35% indicine ancestry) are found across the Near East, from Central Asia and Iran to the Caucasus and Mediterranean shores of the southern Levant (Table S2, Fig. S1). In this period, depictions and osteological evidence for *B. indicus* also appear within the region (9, 13). In contrast to autosomal data, but similar to earlier work (14), we find

persistence of *taurus* mitochondria, suggesting introgression may have been mediated by bulls (Fig. 2).

This sharp influx may have been stimulated by the onset of a period of increased aridity known as the 4.2ka abrupt climate change event (9, 15–17). This multi-century drought, coincided with empire collapse in both Mesopotamia and Egypt as well as a decline in the Indus Civilisation and has been accepted as the boundary defining the onset of our current geological age, the Meghalayan (18).

Three features of this post ~4,000 BP zebu influx attest that it was likely driven by adaptation and/or human agency rather than passive diffusion. First, the extent of indicine introgression does not follow a simple East to West gradient; for example, it is pronounced in Levantine genomes from the western edge of the Near East. Second, the introgression was widespread, and took place in a relatively restricted time interval following four millennia of barely detectable *B. indicus* influence. Third, it was plausibly driven by bull choice as we observe up to ~70% autosomal genome change but a retained substratum of *Bos taurus* mtDNA haplotypes (Fig. 2; Table S3). Hybrid *taurus-indicus* herds may have enabled the survival of communities under stress and perhaps facilitated expansion of herding into more peripheral regions. Restocking following herd decline may have been a factor. Westward human migration has been documented around this time (19, 20) along with archaeological evidence for the appearance of other South Asian taxa such as water buffalo and Asian elephants in the Near East (21) suggesting the movement of large animals by people.

Prior to zebu admixture ancient southern Levantine animals occupy a unique space within the PC plot (fig. 1A; cluster *c*), towards modern African cattle and adjacent to a 9,000 BP Epipalaeolithic Moroccan aurochs (Th7). A 7,000 BP Mesolithic British aurochs genome (CPC98) (6) also plots away from the core Anatolia/Iran ancestral Near Eastern cluster and close to Neolithic Balkan (cluster *a*) and modern European cattle. These genetic affinities in ancient cattle suggest an early secondary recruitment from diverse wild populations.

Concordantly, *D* statistic tests of allele sharing by cattle population pairs with three divergent aurochsen confirm that early cattle exhibit asymmetric relationships with different wild populations (Fig. 3). The most extreme deviations are found in comparisons featuring the *B. taurus* Levantine population (Fig. 1 cluster *c*); these share the least affinity with the British and Armenian aurochsen ($Z > 5.67$; $P < 10^{-5}$) but more with the Moroccan Epipalaeolithic sample. We infer that a distinct strain of aurochs, probably from the Levant and similar to those ranging across North Africa, had considerable input into early cattle in the southern Levant. The Mesolithic British aurochs also shows asymmetric affinity with the Neolithic Balkans samples, implying that the hybridization of European aurochs (6) was initiated over 7,000 years ago, close to the onset of human herding of cattle in Europe. These findings are supported by a qpgraph analysis (Figs. S2, S3) Although each of these three aurochsen have divergent mtDNA haplotypes falling outside normal *B. taurus* variation, ancient domesticates display typical modern domestic haplotypes (Fig S4). This points toward common matrilineal origins for domestic taurine cattle, and suggests that introgression may have been *via* mating with wild males. Sexually mature bulls because of size and aggression were likely the most dangerous stock within Neolithic villages and thus unsupervised field insemination by aurochs bulls may have played a role in early herd management (22).

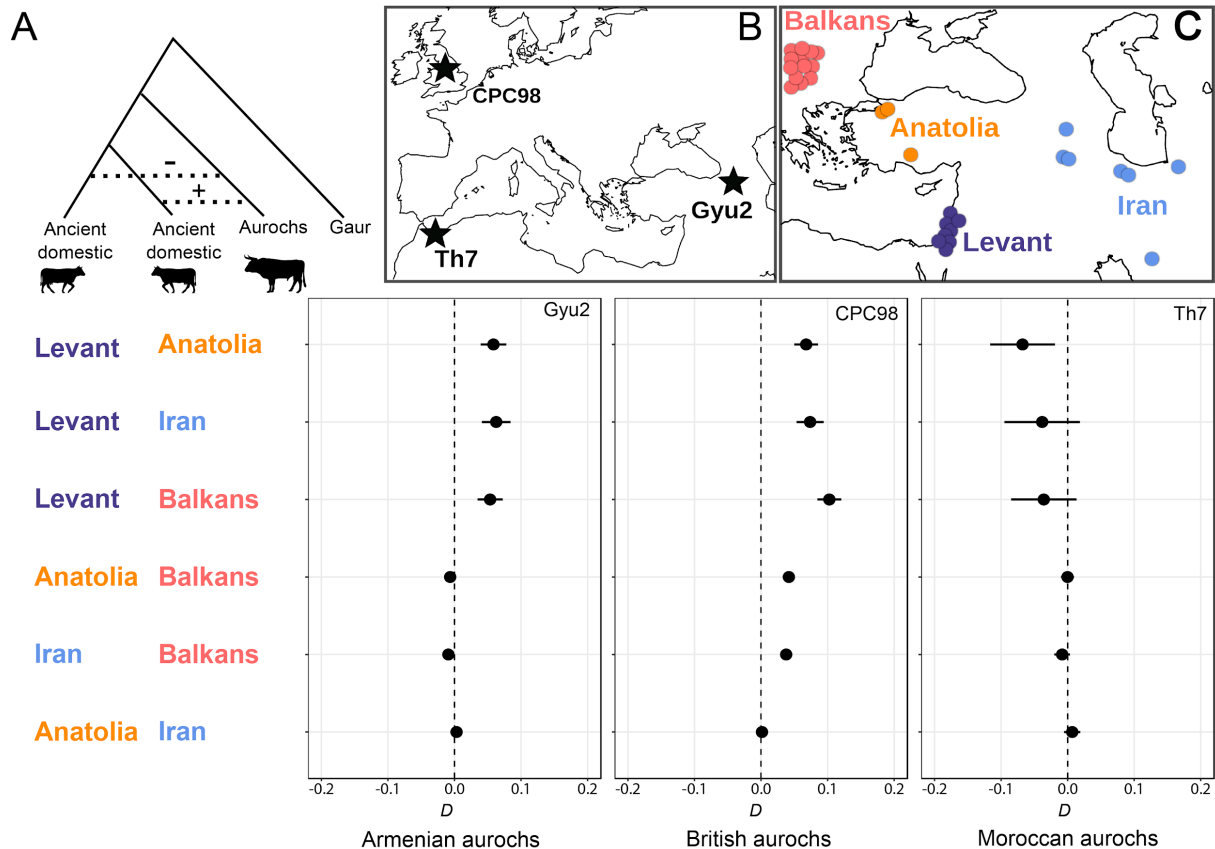


Figure 3 - Clade integrity of ancient population pairs with respect to aurochs introgression. Bars denote two standard errors. **(A)** The test $D(gaur, aurochs; ancient\ group1, ancient\ group2)$ reveals asymmetric affinities of aurochs genomes with pre-4,000 BP cattle populations. Levantine cattle show reduced allele sharing relative to other populations with the Armenian (Gyu2) and British (CPC98) aurochs, but more with the Moroccan aurochs (Th7). Balkan cattle show asymmetric affinities with the British aurochs. **(B)** Geographical location of aurochs tested. **(C)** Distribution of ancient domestic cattle groups tested.

Distinct genotypes and phenotypes in *B. taurus* cattle native to Africa, such as tolerance of tropical infections, have been attributed to either local domestication or introgression from African aurochs (10, 23). However, ancient Levantine genome affinity with North African aurochs hints that this distinctiveness may have origins in the southern Fertile Crescent. Supporting this, the *Bos taurus* mtDNA haplogroup (T1) which is almost fixed in African cattle populations (24) is the most frequent in the southern Levant, including earliest samples, but was not found among other ancient domesticates (table S3).

In sum, *Bos taurus* were initially derived from a restricted northern Fertile Crescent genetic background but early domestic cattle outside this region gained heterogeneous inputs from diverse aurochs strains including contributions specific to European and African cattle ancestors. After ~4,200 BP, gross genome turnover reflecting the spread of *B. indicus* and likely associated with climate change was effected by cattle herders throughout Southwest and Central Asia, representing the start of a global *B. indicus* genome diaspora (25) that continues today.

1. D. Helmer, L. Gourichon, H. Monchot, J. Peters, M. S. Segui, in *The First Steps of Animal Domestication*, J.-D. Vigne, J. Peters, D. Helmer, Eds. (Oxbow Books, Oxford, 2005), pp. 86–95.
2. H. Hongo, J. Pearson, B. Öksüz, G. Ilgezdi, The process of ungulate domestication at Cayönü, Southeastern Turkey: a multidisciplinary approach focusing on *Bos* sp. and *Cervus elaphus*. *Anthropozoologica*. **44**, 63–78 (2009).
3. C. S. Troy *et al.*, Genetic evidence for Near-Eastern origins of European cattle. *Nature*. **410**, 1088–1091 (2001).
4. R. Bollongino *et al.*, Modern taurine cattle descended from small number of near-eastern founders. *Mol. Biol. Evol.* **29**, 2101–2104 (2012).
5. A. Scheu *et al.*, The genetic prehistory of domesticated cattle from their origin to the spread across Europe. *BMC Genet.* **16**, 54 (2015).
6. S. D. E. Park *et al.*, Genome sequencing of the extinct Eurasian wild aurochs, *Bos primigenius*, illuminates the phylogeography and evolution of cattle. *Genome Biol.* **16**, 234 (2015).
7. Bovine HapMap Consortium *et al.*, Genome-wide survey of SNP variation uncovers the genetic structure of cattle breeds. *Science*. **324**, 528–532 (2009).
8. R. T. Loftus *et al.*, A microsatellite survey of cattle from a centre of origin: the Near East. *Mol. Ecol.* **8**, 2015–2022 (1999).
9. R. Matthews, Zebu: Harbingers of doom in Bronze Age western Asia? *Antiquity*. **74**, 438–446 (2002).
10. D. E. MacHugh, M. D. Shriver, R. T. Loftus, P. Cunningham, D. G. Bradley, Microsatellite DNA variation and the evolution, domestication and phylogeography of taurine and zebu cattle (*Bos taurus* and *Bos indicus*). *Genetics*. **146**, 1071–1086 (1997).
11. See the supplementary materials.
12. A. K. Patel, R. H. Meadow, in *The Oxford Handbook of Zooarchaeology*, U. Albarella, M. Rizzetto, H. Russ, K. Vickers, S. Viner-Daniels, Eds. (Oxford University Press, Oxford, 2017), pp. 280–303.
13. C. Grigson, The fauna of Tell Nebi Mend (Syria) in the Bronze and Iron Age—a diachronic overview. Part 1: Stability and change—animal husbandry. *Levantina*. **47**, 5–29 (2015).
14. M. Meiri *et al.*, Eastern Mediterranean Mobility in the Bronze and Early Iron Ages: Inferences from Ancient DNA of Pigs and Cattle. *Sci. Rep.* **7**, 701 (2017).
15. M. H. Wiener, The interaction of climate change and agency in the collapse of civilizations ca. 2300–2000 BC. *Radiocarbon*. **56**, S1–S16 (2014).
16. A. Sharifi *et al.*, Abrupt climate variability since the last deglaciation based on a high-resolution, multi-proxy peat record from NW Iran: The hand that rocked the Cradle of Civilization? *Quat. Sci. Rev.* **123**, 215–230 (2015).
17. M. Staubwasser, H. Weiss, Holocene climate and cultural evolution in late prehistoric–early historic West Asia. *Quat. Res.* **66**, 372–387 (2006).

18. M. J. C. Walker *et al.*, Formal subdivision of the Holocene Series/Epoch: a Discussion Paper by a Working Group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). *J. Quat. Sci.* **27**, 649–659 (2012).
19. M. Haber *et al.*, Continuity and Admixture in the Last Five Millennia of Levantine History from Ancient Canaanite and Present-Day Lebanese Genome Sequences. *Am. J. Hum. Genet.* **101**, 274–282 (2017).
20. I. Lazaridis *et al.*, Genomic insights into the origin of farming in the ancient Near East. *Nature.* **536**, 419–424 (2016).
21. C. Çakırlar, S. Ikram, “When elephants battle, the grass suffers.” Power, ivory and the Syrian elephant. *Levant.* **48**, 167–183 (2016).
22. J. Peters, B. S. Arbuckle, N. Pöllath, in *The Neolithic in Turkey, VOL. 6*, M. Özdoğan, N. Başgelen, P. Kuniholm, Eds. (Archaeology and Art Publications, Istanbul, 2012), pp. 1–65.
23. J. E. Decker *et al.*, Worldwide patterns of ancestry, divergence, and admixture in domesticated cattle. *PLoS Genet.* **10**, e1004254 (2014).
24. D. G. Bradley, D. E. MacHugh, P. Cunningham, R. T. Loftus, Mitochondrial diversity and the origins of African and European cattle. *Proc. Natl. Acad. Sci. U. S. A.* **93**, 5131–5135 (1996).
25. N. Chen *et al.*, Whole-genome resequencing reveals world-wide ancestry and adaptive introgression events of domesticated cattle in East Asia. *Nat. Commun.* **9**, 2337 (2018).
26. L. K. Horwitz, in *The Neolithic Site of Abu Gosh. The 1995 Excavations.*, H. Khalaily, O. Marder, Eds. (Israel Antiquities Authority Reports, 2003), vol. 19, pp. 87–101.
27. P. Ducos, L. K. Horwitz, in *The Neolithic Site of Abu Gosh. The 1995 Excavations.*, H. Khalaily, O. Marder, Eds. (Israel Antiquities Authority Reports, 2003), vol. 19, pp. 103–120.
28. M. Lechevallier *et al.*, Abou Gosh et Beisamoun. Deux gisements du VII millénaire avant l’ère chrétienne en Israël. *Mémoires et Travaux du Centre de Recherches Préhistoriques Français de Jérusalem Jérusalem.* **2** (1978).
29. A. Öztan, 2000 yılı Acemhöyük kazıları. *Kazı Sonuçları Toplantısı.* **23**, 327–333 (2001).
30. N. Özgüç, Acemhöyük kazıları. Excavations at Acemhöyük. *Anadolu.* **10**, 29–52 (1966).
31. B. S. Arbuckle, Zooarchaeology at Acemhöyük 2013. *Anadolu/Anatolia.* **39**, 55–68 (2013).
32. D. Šljivar, D. Jacanović, Veliko Laole-Belovode, Vinča Culture Settlement in Northeastern Serbia. *Préhistoire Européenne.* **8**, 175–188 (1996).
33. D. Boric, in *Metals and Societies: Studies in honour of Barbara S. Ottaway*, T. L. Kienlin, B. W. Roberts, Eds. (Habelt, Bonn, 2009), *Universitätsforschungen zur prähistorischen Archäologie*, p. 468.
34. M. Radivojević *et al.*, On the origins of extractive metallurgy: new evidence from Europe. *J. Archaeol. Sci.* **37**, 2775–2787 (2010).
35. R. Matthews, W. Matthews, K. R. Raheem, K. R. Aziz, in *The Archaeology of the Kurdistan Region of Iraq and Adjacent Regions*, K. Kopanias, J. MacGinnis, Eds. (Archaeopress, 2016).

36. D. Nikolic, J. Zecevic, *Blagotin : istrazivanja 1989 - 1999 = Blagotin : excavations and research 1989 - 1999* (Filozofski Fakultet u Beogradu, Centar za Arheoloska Istrazivanja, Beograd, 2001).
37. H. J. Greenfield, T. L. J. Greenfield, S. Jezik, Subsistence and settlement in the Early Neolithic of temperate SE Europe: a view from Blagotin, Serbia. *Archaeologia Bulgarica*. **18**, 1–33 (2014).
38. A. Whittle, L. Bartosiewicz, D. Borić, P. Pettitt, M. P. Richards, In the beginning : new radiocarbon dates for the Early Neolithic in northern Serbia and south-east Hungary. *Antaeus*. **25**, 63–118 (2002).
39. M. Garašanin, Iskopavanja na Bubnju kod Niša, prethodni izveštaj za 1954-1956. godinu. *Starinar*. **7-8**, 269–274 (1958).
40. D. Milanović, T. Trajković-Filipović, *Stara iskopavanja na lokalitetu Bubanj* (Narodni muzej u Nišu, Niš, 2015).
41. T. Trajković-Filipović, D. Milanović, A. Bulatović, Reviziona arheološka iskopavanja lokaliteta Bubanj kod Niša u 2008. godini. *Zbornik Narodnog Muzeja u Nišu*. **16-17**, 309–318 (2008).
42. A. Bulatović, M. V. Linden, Absolute Dating of Copper and Early Bronze Age Levels at the Eponymous Archaeological Site Bubanj (Southeastern Serbia). *Radiocarbon*. **59**, 1047–1065 (2017).
43. A. Bayliss *et al.*, Getting to the Bottom of It All: A Bayesian Approach to Dating the Start of Çatalhöyük. *J World Prehist*, 1–26 (2015).
44. A. Marciniak *et al.*, Fragmenting times: interpreting a Bayesian chronology for the Late Neolithic occupation of Çatalhöyük East, Turkey. *Antiquity*. **89**, 154–176 (2015).
45. D. Orton *et al.*, A tale of two tells: dating the Çatalhöyük West Mound. *Antiquity*. **92**, 620–639 (2018).
46. I. Hodder, Çatalhöyük: the leopard changes its spots. A summary of recent work. *Anatolian Studies*. **64**, 1–22 (2014).
47. N. Russell, K. C. Twiss, D. C. Orton, G. A. Demirergi, Changing animal use at Neolithic Çatalhöyük, Turkey. *Archaeozoology of the Near East X*. Peeters Press, Leuven, 45–68 (2013).
48. M. Degerbøl, B. Fredskild, *The Urus (Bos Primigenius Bojanus) and Neolithic Domesticated Cattle (Bos Taurus Domesticus Linné) in Denmark: With a Revision of Bos-remains from the Kitchen Middens. Zoological and Palynological Investigations* (Munksgaard, 1970).
49. M. Mashkour *et al.*, in *Sasanian Persia between Rome and the Steppes of Eurasia*, E. W. Sauer, Ed. (Edinburgh University Press, 2017), pp. 74–95.
50. E. W. Sauer *et al.*, Northern outpost of the Caliphate: maintaining military forces in a hostile environment (the Dariali Gorge in the Central Caucasus in Georgia). *Antiquity*. **89**, 885–904 (2015).
51. C. Grigson, in *Archaeology, Anthropology and Cult* (Routledge, London, 2016), pp. 225–329.
52. O. W. Muscarella, The Excavation of Hasanlu: An Archaeological Evaluation. *Bull. Am. Schools Orient. Res.*, 69–94 (2006).
53. R. H. Dyson, O. W. Muscarella, Constructing the Chronology and Historical Implications of Hasanlu IV. *Iran*. **27**, 1–27 (1989).
54. M. D. Danti, *Hasanlu V: The Late Bronze and Iron I Periods* (University of Pennsylvania Press,

2013).

55. M. D. Danti, M. M. Voigt, & Dyson, R. H, in *A View from the Highlands: Archaeological studies in honour of Charles Burney*, A. Sagona, Ed. (Leuven: Peeters, 2004), pp. 583–616.
56. M. Danti, M. Cifarelli, Iron II Warrior Burials at Hasanlu Tepe, Iran. *Iranica Antiqua*. **50**, 61–157 (2015).
57. S. Kroll, Hasanlu Period III – Annotations and Corrections. *Iranica Antiqua*. **48**, 175–195 (2013).
58. R. H. Dyson, Digging in Iran: Hasanlu 1958. *Expedition*. **1**, 4–18 (1959).
59. R. H. Dyson, The Achaemenid Painted Pottery of Hasanlu IIIA. *Anatolian Studies*. **49**, 101–110 (1999).
60. H. Davoudi, thesis, PhD thesis in Archaeology, Tarbiat Modares University, Iran (2017).
61. F. Broushaki *et al.*, Early Neolithic genomes from the eastern Fertile Crescent. *Science*. **353**, 499–503 (2016).
62. C. Gaunitz *et al.*, Ancient genomes revisit the ancestry of domestic and Przewalski’s horses. *Science*, eaao3297 (2018).
63. E. Van den Brink *et al.*, Two Roman-Byzantine subsurface features at Horbat Castra, at the Foot of Mount Carmel. *Atiqot*. **75**, 71–127 (2013).
64. A. Abedi *et al.*, Excavation at Kul Tepe (Hadishahr), North-Western Iran, 2010: First Preliminary Report. *Ancient Near Eastern Studies*. **51**, 33–165 (2014).
65. A. Abedi, B. Omrani, Kura-Araxes culture and North-Western Iran: New perspectives from Kul Tepe Jolfa (Hadishahr). *Paléorient*, 55–68 (2015).
66. H. Davoudi *et al.*, in *Archaeozoology of the Near East XII*, C. Çakırlar, J. Chahoud, R. Berthon & S. Pilaar Birch, Ed. (Barkhuis Publishing & University of Groningen, Groningen, 2018), pp. 91–108.
67. Y. Majidzadeh, *The archaeological excavation of Ozbaki*. 2 vols (ICHTO press, Tehran, Iran, 2011).
68. M. Mashkour, A. F. Mohaseb, in *The archaeological excavation of Ozbaki, Vol. 1, Art and architecture*, Y. Majidzadeh, Ed. (ICHTO press, Tehran, 2011), p. 273–30, 597–601.
69. J. Roodenberg, S. Alpaslan Roodenberg, *Life and Death in a Prehistoric Settlement in Northwest Anatolia. The Ilipinar Excavations, volume III* (Nederlands Instituut voor het Nabije Oosten, Leiden, 2008).
70. L. Gourichon, D. Helmer, in *Life and Death in a Prehistoric Settlement in Northwest Anatolia. The Ilipinar Excavations, volume III*, J. Roodenberg, S. Alpaslan Roodenberg, Eds. (Nederlands Instituut voor het Nabije Oosten, Leiden, 2008), pp. 435–448.
71. A. Abolahrar, M. Zare, S. Ebrahimi, in *The Neolithic of the Iranian Plateau: recent research*, K. Roustaei, M. Mashkour, Eds. (Ex Oriente, Berlin, 2016).
72. M. Mashkour, A. Mohaseb, K. Debue, in *The Origins of State Organizations in Prehistoric Highland Fars, Excavations at Tall-e Bakun*, A. Alizadeh, Ed. (Oriental Institute Publications, 128, Chicago, Illinois, 2006), pp. 101–105.
73. S. Pollock *et al.*, Excavations at Monjukli Depe, Meana-Čaača Region, Turkmenistan 2010.

Archäologische Mitteilungen aus Iran und Turan. **43**, 169–237 (2011).

74. E. C. Kansa, S. W. Kansa, T. E. Levy, in *Integrating zooarchaeology, 9th ICAZ Conference, Durham*, M. Maltby, Ed. (Oxbow Books, Oxford, 2006), pp. 76–91.
75. T. E. Levy *et al.*, Egyptian-Canaanite Interaction at Nahal Tillah, Israel (ca. 4500-3000 BCE): An Interim Report on the 1994-1995 Excavations. *Bull. Am. Schools Orient. Res.*, 1–51 (1997).
76. Z. Lorzadeh, thesis, Institute for Near Eastern Archaeology, Goethe University Frankfurt. (2018).
77. W. Hauser, C. K. Wilkinson, *The museum's excavations at Nishapur* (Metropolitan Museum of Art, 1942).
78. R. Khazaeli, thesis, University of Tehran (2013).
79. D. Boric, in *Metals and Societies: Studies in honour of Barbara S. Ottaway*, T. L. Kienlin, B. W. Roberts, Eds. (Habelt, Bonn, 2009), *Universitätsforschungen zur prähistorischen Archäologie*, p. 468.
80. Stalio, Pločnik-Prokuplje – naselje. *Arheološki pregled*. **2**, 33–36 (1960).
81. D. Šljivar, J. Kuzmanović-Cvetković, Pločnik kod Prokuplja, istraživanja u. *Glasnik Srpskog arheološkog društva*. **14**, 79–85 (1997).
82. M. Radivojević, J. Kuzmanović-Cvetković, Copper minerals and archaeometallurgical materials from the Vinča culture sites of Belovode and Pločnik: overview of the evidence and new data. *Starinar*, 7–30 (2014).
83. J. Bulatović, thesis, University of Belgrade (2018).
84. C. Koukouli-Chryssanthaki, H. Todorova, I. Aslanis, I. Vajsov, M. Valla, in *The Struma/Strymon River Valley in Prehistory e in the Steps of James Harvey Gaul, Proceedings of the International Symposium, Strymon Praehistoricus* (2007), vol. 27, p. 43e78.
85. C. Koukouli-Chrysanthaki, T. H., I. Aslanis, V. I., M. Valla, in *A Century of research in Prehistoric Macedonia, proceedings of the International Conference, 251-260. Thessaloniki*, E. Stefani, N. Merousis, A. Dimoula, Eds. (Archaeological Museum of Thessaloniki., 2014).
86. G. Kazantzis, U. Albarella, Size and shape of Greek Late Neolithic livestock suggest the existence of multiple and distinctive animal husbandry cultures. *Journal of Archaeological Science: Reports*. **9**, 630–645 (2016).
87. G. Kazantzis, in *Communities, Landscape and Interaction in Neolithic Greece, Proceedings of the International Conference Rethymno 29th 30th May 2015*, A. Sarris, E. Kalogiropoulou, T. Kalayci, L. Karimali, Eds. (2017), vol. 20 of *International Monographs in Prehistory, Archaeological Series*, pp. 291–315.
88. A. Sampson, Ed., *The Sarakenos cave at Akraephnion, Boeotia, Greece, Vol. I: The Neolithic and the Bronze Age* (Archeobooks, 2008).
89. A. Sampson *et al.*, Sarakenos cave in Boeotia, from Palaeolithic to the Early Bronze Age. *Eurasian Prehistory*. **6**, 199–231 (2009).
90. M. Kaczanowska, J. K. Kozłowski, A. Sampson, Eds., *The Sarakenos cave at Akraephnion, Boeotia, Greece, Vol. II: The early Neolithic, the Mesolithic and the final Palaeolithic* (Archeobooks, 2016).

91. A. Marciszak, The common weasel *Mustela nivalis* L., 1766 from Sarakenos Cave (Greece) and the difficulty to distinguish small mustelid species in the fossil record. *Acta Zool. Cracov.* **59**, 25–35 (2016).
92. J. Wilczyński, T. Tomek, A. Pryor, in *The Sarakenos Cave at Akraephnion, Boeotia, Greece Vol. II The Early Neolithic, the Mesolithic and the Final Palaeolithic (Excavations in Trench A)*, M. Kaczanowska, J. K. Kozłowski, A. Sampson, Eds. (Archaeobooks, 2016), pp. 81–150.
93. Z. M. Bochenski *et al.*, Who ate the birds: the taphonomy of Sarakenos Cave, Greece. *Archaeol. Anthropol. Sci.* (2017), doi:10.1007/s12520-017-0488-3.
94. A. Crnobrnja, Z. Simić, M. Janković, Late Vinča culture settlement at Crkvine in Stubline: Household organization and urbanization in the Late Vinča culture period. *Starinar*, 9–25 (2009).
95. M. Spasić, S. Živanović, Foodways architecture: storing, processing and dining structures at the Late Neolithic Vinča culture site at Stubline. *Documenta Praehistorica.* **42**, 219–230 (2015).
96. M. Spasić, A Group Find of Neolithic Figurines of the Vinča Culture from Stubline, Serbia. *Les Carnets de l'ACoSt* (2014), doi:10.4000/acost.217.
97. J. Bordaz, Current Research in the Neolithic of South Central Turkey: Suberde, Er Baba and Their Chronological Implications. *Am. J. Archaeol.* **77**, 282–288 (1973).
98. B. S. Arbuckle, Revisiting Neolithic Caprine Exploitation at Suberde, Turkey. *J. Field Archaeol.* **33**, 219–236 (2008).
99. D. Perkins Jr, P. Daly, A hunters' village in neolithic Turkey. *Sci. Am.* **219**, 97–106 (1968).
100. B. S. Arbuckle, thesis, Harvard University (2006).
101. B. S. Arbuckle, C. A. Makarewicz, The early management of cattle (*Bos taurus*) in Neolithic central Anatolia. *Antiquity.* **83**, 669–686 (2009).
102. J. Linstädter, I. Medved, M. Solich, G.-C. Weniger, Neolithisation process within the Alboran territory: Models and possible African impact. *Quat. Int.* **274**, 219–232 (2012).
103. R. Hutterer, J. Linstädter, J. Eiwanger, A. Mikdad, Human manipulation of terrestrial gastropods in Neolithic culture groups of NE Morocco. *Quat. Int.* **320**, 83–91 (2014).
104. S. Masuda, in *Proceedings of the 1st annual symposium of archaeological research in Iran, 1972*, F. Bagherzadeh, Ed. (1973), pp. 1–5.
105. A. Tsuneki, The site of Tappeh Sang e Chakhmaq. *The first farming village in northeast Iran and Turan: Tappeh Sang-e Chakhmaq and beyond*, 5–8 (2014).
106. K. Roustaei, M. Mashkour, M. Tengberg, Tappeh Sang-e Chakhmaq and the beginning of the Neolithic in north-east Iran. *Antiquity* (2015).
107. T. Nakamura, Radiocarbon dating of charcoal remains excavated from Tappeh Sang-e Chakhmaq. *The first farming village in northeast Iran and Turan: Tappeh Sang-e Chakhmaq and beyond*, 9–12 (2014).
108. M. Mashkour *et al.*, Neolithisation of eastern Iran: new insights through the study of the faunal remains of Tappeh Sang-e Chakhmaq. *The first farming village in northeast Iran and Turan: Tappeh Sang-e Chakhmaq and beyond*, 27–32 (2014).

109. L. E. Stager, J. D. Schloen, D. M. Master, *Ashkelon 1: Introduction and Overview (1985-2006)* (Eisenbrauns, Winona Lake., 2008).
110. B. Hesse, D. N. Fulton, P. Wapnish, in *Ashkelon 3: The Seventh Century B.C.*, L. E. Stager, D. M. Master, J. D. Schloen, Eds. (Eisenbrauns, Winona Lake., 2011), pp. 615–643.
111. A. Gopher, R. Greenberg, in *Dan I: A Chronicle of the Excavations, the Pottery Neolithic, the Early Bronze Age, and the Middle Bronze Age Tombs.*, A. Biran, D. Ilan, R. Greenberg, Eds. (Hebrew Union College-Jewish Institute of Religion., 1996), *Annual of the Nelson Glueck School of Biblical Archaeology*, pp. 67–81.
112. L. K. Horwitz, Animal Remains from the Pottery Neolithic Levels at Tel Dan. *Mitekufat Haeven: Journal of the Israel Prehistoric Society*. **20**, 114–118 (1987).
113. A. Ben-Tor, R. Bonfil, S. Zuckerman, TEL QASHISH: A VILLAGE IN THE JEZREEL VALLEY—Final Report of the Archaeological Excavations (1978–1987). *Qedem Reports*. **5**, III–449 (2003).
114. J. S. E. Lev-Tov, A preliminary report on the Late Bronze and Iron Age faunal assemblages from Tell es-Safi/Gath. *Tell es-Safi/Gath I: The*. **2005**, 610 (1996).
115. Ron Kehati, Amit Dagan, Liora Kolska Horwitz, Iron Age Animal Husbandry at Tell es-Sâfi/Gath: Notes on the Fauna from Area D. *Near Eastern Archaeology*. **81**, 41–44 (2018).
116. E. Galili, L. K. Horwitz, V. Eshed, B. Rosen, in *Under the Sea: Archaeology and Palaeolandscapes of the Continental Shelf*, G. N. Bailey, J. Harff, D. Sakellariou, Eds. (Springer International Publishing, Cham, 2017), pp. 105–130.
117. L. K. Horwitz, E. Galili, J. Sharvit, O. Lernau, Fauna from five submerged Pottery Neolithic sites off the Carmel coast. *Journal of the Israel Prehistoric Society*. **32**, 147–174 (2002).
118. E. Tchernov, A. Drori, Economic patterns and environmental conditions at Hirbet El-Msas during the Early Iron Age. *V. Fritz and A. Kempinski, Die Ergebnisse der Ausgrabungen auf der Hirbat el Msas (Tel Masos)*. **1975**, 213–222 (1972).
119. B. Hesse, Animal Use at Tel Miqne-Ekron in the Bronze Age and Iron Age. *Bull. Am. Schools Orient. Res.*, 17–27 (1986).
120. E. F. Maher, thesis, University of Illinois at Chicago (2004).
121. J. S. E. Lev-Tov, thesis, University of Tennessee, Knoxville (2000).
122. T. Dothan, Y. Garfinkel, S. Gitin, *Tel Miqne-Ekron Excavations 1985-1988, 1990, 1992-1995: Field IV Lower--the Elite Zone* (Eisenbrauns, 2016).
123. T. Dothan, S. Gitin, Tel Miqne-Ekron. *New Encyclopedia of Archaeological Excavations in the Holy Land* (ed. E. Stern et al, 3–1051 (2012).
124. L. K. Horwitz, E. Dahan, in *Yoqne'am I. The Late Periods.*, A. Ben-Tor, M. Avissar, Y. Portugali, Eds. (Qedem Reports 3, Jerusalem, 1996), pp. 246–255.
125. A. Ben-Tor, D. Ben-Ami, A. Livneh, *Yoqne'am III: The Middle and Late Bronze Ages: Final Report of the Archaeological Excavations (1977-1988)* (The Hebrew University, Jerusalem, 2007), vol. 7 of *Qedem Reports* .

126. S. Cohen, *Excavations at Tel Zahara (2006--2009): Final Report: The Hellenistic and Roman Strata* (BAR International Reports, Oxford, 2013), vol. 255.
127. L. K. Horwitz, S. Hellwing, E. Tchernov, in *Excavations at Tel Dalit: An Early Bronze Age Walled Town in Central Israel*, R. Gophna, B. Cresson, E. Friedmann, Eds. (Ramot Publishing Tel Aviv University, 1996), pp. 193–216.
128. A. M. Pollard, H. Davoudi, I. Mostafapour, H. R. Valipour, H. Fazeli Nashli, A new radiocarbon chronology for the Late Neolithic to Iron Age in the Qazvin Plain, Iran. *Int. J. Des. Nat. Ecodyn.* **19**, 110–151 (2013).
129. M. Mashkour, thesis, Université de Paris I-Sorbonne (2001).
130. M. Mashkour, Chasse et élevage au nord du Plateau central iranien entre le Néolithique et l'Âge du Fer. *Paléorient.* **28**, 27–42 (2002).
131. M. Mashkour, M. Fontugne, C. Hatte, Investigations on the evolution of subsistence economy in the Qazvin Plain (Iran) from the Neolithic to the Iron Age. *Antiquity* (1999)
132. K. Kaniuth, in *South Asian archaeology and art 2012. Volume 1, Man and environment in prehistoric and protohistoric South Asia: new perspectives*, V. Lefèvre, A. A. Didier, B. Mutin, Eds. (Turnhout, Brepols, 2016), pp. 117–12.
133. M. Kh. Isamidinoy, R. Kh. Sulejmanov, Kurgan (stratigrafia i periodizacija) (Tashkent, FAN, 1984).
134. Sulejmanov, R. Kh., *Drevnij Nakhshab* (Tashkent, FAN, 2000).
135. S. Pääbo *et al.*, Genetic analyses from ancient DNA. *Annu. Rev. Genet.* **38**, 645–679 (2004).
136. C. Gamba *et al.*, Genome flux and stasis in a five millennium transect of European prehistory. *Nat. Commun.* **5**, 5257 (2014).
137. D. Y. Yang, B. Eng, J. S. Wayne, J. C. Dudar, S. R. Saunders, Technical note: improved DNA extraction from ancient bones using silica-based spin columns. *Am. J. Phys. Anthropol.* **105**, 539–543 (1998).
138. D. E. MacHugh, C. J. Edwards, J. F. Bailey, D. R. Bancroft, D. G. Bradley, The extraction and analysis of ancient DNA from bone and teeth: a survey of current methodologies. *Anc. Biomol.* **3**, 81–102 (2000).
139. M. Meyer, M. Kircher, Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harb. Protoc.* **2010**, db.prot5448 (2010).
140. B. Bramanti *et al.*, Genetic discontinuity between local hunter-gatherers and central Europe's first farmers. *Science.* **326**, 137–140 (2009).
141. L. R. Botigué *et al.*, Ancient European dog genomes reveal continuity since the Early Neolithic. *Nat. Commun.* **8**, 16082 (2017).
142. M. Kircher, S. Sawyer, M. Meyer, Double indexing overcomes inaccuracies in multiplex sequencing on the Illumina platform. *Nucleic Acids Res.* **40**, e3 (2012).
143. R. T. Loftus, D. E. MacHugh, D. G. Bradley, P. M. Sharp, P. Cunningham, Evidence for two independent domestications of cattle. *Proc. Natl. Acad. Sci. U. S. A.* **91**, 2757–2761 (1994).

144. A. Achilli *et al.*, Mitochondrial genomes of extinct aurochs survive in domestic cattle. *Curr. Biol.* **18**, R157–8 (2008).
145. C. Murray, E. Huerta-Sanchez, F. Casey, D. G. Bradley, Cattle demographic history modelled from autosomal sequence variation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 2531–2539 (2010).
146. L. M. Cassidy *et al.*, Capturing goats: documenting two hundred years of mitochondrial DNA diversity among goat populations from Britain and Ireland. *Biol. Lett.* **13** (2017), doi:10.1098/rsbl.2016.0876.
147. C. B. Ramsey, Bayesian Analysis of Radiocarbon Dates. *Radiocarbon.* **51**, 337–360 (2009).
148. P. J. Reimer *et al.*, IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. *Radiocarbon.* **55**, 1869–1887 (2013).
149. S. Andrews, FastQ screen. https://www.bioinformatics.babraham.ac.uk/projects/fastq_screen/ (2011).
150. M. Martin, Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet.journal.* **17**, 10–12 (2011).
151. H. Li, R. Durbin, Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics.* **25**, 1754–1760 (2009).
152. H. Li *et al.*, The Sequence Alignment/Map format and SAMtools. *Bioinformatics.* **25**, 2078–2079 (2009).
153. A. McKenna *et al.*, The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Res.* **20**, 1297–1303 (2010).
154. F. García-Alcalde *et al.*, Qualimap: evaluating next-generation sequencing alignment data. *Bioinformatics.* **28**, 2678–2679 (2012).
155. S. Anderson *et al.*, Complete sequence of bovine mitochondrial DNA. Conserved features of the mammalian mitochondrial genome. *J. Mol. Biol.* **156**, 683–717 (1982).
156. G. Sempéré *et al.*, WIDDE: a Web-Interfaced next generation database for genetic diversity exploration, with a first application in cattle. *BMC Genomics.* **16**, 940 (2015).
157. S. Purcell *et al.*, PLINK: a tool set for whole-genome association and population-based linkage analyses. *Am. J. Hum. Genet.* **81**, 559–575 (2007).
158. H. Jónsson, A. Ginolhac, M. Schubert, P. L. F. Johnson, L. Orlando, mapDamage2.0: fast approximate Bayesian estimates of ancient DNA damage parameters. *Bioinformatics.* **29**, 1682–1684 (2013).
159. C. Wang *et al.*, Ancestry estimation and control of population stratification for sequence-based association studies. *Nat. Genet.* **46**, 409–415 (2014).
160. C. Wang, X. Zhan, L. Liang, G. R. Abecasis, X. Lin, Improved Ancestry Estimation for both Genotyping and Sequencing Data using Projection Procrustes Analysis and Genotype Imputation. *Am. J. Hum. Genet.* **96**, 926–937 (2015).
161. H. Wickham, *ggplot2: Elegant Graphics for Data Analysis (Use R!)* (Springer, 1st ed. 2009. Corr. 3rd printing 2010 edition., 2010).

162. N. Patterson *et al.*, Ancient admixture in human history. *Genetics*. **192**, 1065–1093 (2012).
163. D. Reich, K. Thangaraj, N. Patterson, A. L. Price, L. Singh, Reconstructing Indian population history. *Nature*. **461**, 489–494 (2009).
164. W. Haak *et al.*, Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature*. **522**, 207–211 (2015).
165. R. E. Green *et al.*, A draft sequence of the Neandertal genome. *Science*. **328**, 710–722 (2010).
166. E. Y. Durand, N. Patterson, D. Reich, M. Slatkin, Testing for ancient admixture between closely related populations. *Mol. Biol. Evol.* **28**, 2239–2252 (2011).
167. T. S. Korneliussen, A. Albrechtsen, R. Nielsen, ANGSD: Analysis of Next Generation Sequencing Data. *BMC Bioinformatics*. **15**, 356 (2014).
168. S. Soraggi, C. Wiuf, A. Albrechtsen, Powerful Inference with the D-Statistic on Low-Coverage Whole-Genome Data. *G3* (2017), doi:10.1534/g3.117.300192.
169. D. H. Alexander, J. Novembre, K. Lange, Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* **19**, 1655–1664 (2009).
170. M. Gouy, S. Guindon, O. Gascuel, SeaView version 4: A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Mol. Biol. Evol.* **27**, 221–224 (2010).
171. S. Guindon *et al.*, New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Syst. Biol.* **59**, 307–321 (2010).
172. V. Lefort, J.-E. Longueville, O. Gascuel, SMS: Smart Model Selection in PhyML. *Mol. Biol. Evol.*, msx149 (2017).
173. A. Rambaut, FigTree, a graphical viewer of phylogenetic trees. See <http://tree.bio.ed.ac.uk/software/figtree> (2007).
174. A. Achilli *et al.*, The multifaceted origin of taurine cattle reflected by the mitochondrial genome. *PLoS One*. **4**, e5753 (2009).
175. S. Bonfiglio *et al.*, Origin and spread of *Bos taurus*: new clues from mitochondrial genomes belonging to haplogroup T1. *PLoS One*. **7**, e38601 (2012).
176. A. Olivieri *et al.*, Mitogenomes from Egyptian Cattle Breeds: New Clues on the Origin of Haplogroup Q and the Early Spread of *Bos taurus* from the Near East. *PLoS One*. **10**, e0141170 (2015).
177. J. F. Bailey *et al.*, Ancient DNA suggests a recent expansion of European cattle from a diverse wild progenitor species. *Proc. Biol. Sci.* **263**, 1467–1473 (1996).
178. C. J. Edwards *et al.*, Mitochondrial DNA analysis shows a Near Eastern Neolithic origin for domestic cattle and no indication of domestication of European aurochs. *Proc. Biol. Sci.* **274**, 1377–1385 (2007).
179. H. Zhang *et al.*, Morphological and genetic evidence for early Holocene cattle management in northeastern China. *Nat. Commun.* **4**, 2755 (2013).
180. S. Bonfiglio *et al.*, The enigmatic origin of bovine mtDNA haplogroup R: sporadic interbreeding

- or an independent event of *Bos primigenius* domestication in Italy? *PLoS One*. **5**, e15760 (2010).
181. N. Patterson *et al.*, Ancient admixture in human history. *Genetics*. **192**, 1065–1093 (2012).
 182. P. Kumar *et al.*, Admixture analysis of South Asian cattle. *Heredity*. **91**, 43–50 (2003).
 183. J. A. Cahill *et al.*, Genomic Evidence of Widespread Admixture from Polar Bears into Brown Bears during the Last Ice Age. *Mol. Biol. Evol.* **35**, 1120–1129 (2018).
 184. W. Y. Low *et al.*, Chromosome-level assembly of the water buffalo genome surpasses human and goat genomes in sequence contiguity. *Nat. Commun.* **10**, 260 (2019).
 185. U. J. Ikhatua, O. W. Ehoche, J. E. Umoh, Effects of restricted water on feed intake, nutrient utilization and nitrogen metabolism in Zebu cattle. *J. Agric. Sci.* **105**, 463–467 (1985).
 186. G. D. Phillips, The relationship between water and food intakes of European and zebu type steers. *J. Agric. Sci.* **54**, 231–234 (1960).
 187. N. Silanikove, The struggle to maintain hydration and osmoregulation in animals experiencing severe dehydration and rapid rehydration: the story of ruminants. *Exp. Physiol.* **79**, 281–300 (1994).
 188. J. M. King, *Livestock water needs in pastoral Africa in relation to climate and forage* (ILCA, 1983).
 189. M. N. Brew *et al.*, Water intake and factors affecting water intake of growing beef cattle. *Livest. Sci.* **140**, 297–300 (2011).
 190. S. Dikmen, R. G. Mateescu, M. A. Elzo, P. J. Hansen, Determination of the optimum contribution of Brahman genetics in an Angus-Brahman multibreed herd for regulation of body temperature during hot weather. *J. Anim. Sci.* **96**, 2175–2183 (2018).
 191. P. J. Hansen, Physiological and cellular adaptations of zebu cattle to thermal stress. *Anim. Reprod. Sci.* **82-83**, 349–360 (2004).
 192. W. J. A. Payne, J. Hodges, *Tropical cattle: origins, breeds and breeding policies* (Blackwell Science Ltd, 1997).
 193. J. S. Whitmore, *Drought Management on Farmland* (Springer Science & Business Media, 2013).
 194. A. R. Freeman *et al.*, Admixture and diversity in West African cattle populations. *Mol. Ecol.* **13**, 3477–3487 (2004).
 195. M. Felius, *Cattle breeds: An encyclopedia* (C Misset bv, Doetinchem, 1995).
 196. Nigeria. Federal Dept. of Livestock and Pest Control Services, *Nigerian Livestock Resources: National synthesis* (Resources Inventory and Management Limited, 1992).
 197. R. J. Davis, P. J. Watts, R. W. Tucker, Environmental Sustainability Assessment of the Australian Feedlot Industry (2011), (available at <https://www.mla.com.au/download/finalreports?itemId=734>).
 198. C. J. Edwards *et al.*, A complete mitochondrial genome sequence from a mesolithic wild aurochs (*Bos primigenius*). *PLoS One*. **5**, e9255 (2010).
 199. J. Zeyland *et al.*, Complete mitochondrial genome of wild aurochs (*Bos primigenius*) reconstructed from ancient DNA. *Pol. J. Vet. Sci.* **16**, 265–273 (2013).

200. J. Kim *et al.*, The genome landscape of indigenous African cattle. *Genome Biol.* **18**, 34 (2017).
201. H. D. Daetwyler *et al.*, Whole-genome sequencing of 234 bulls facilitates mapping of monogenic and complex traits in cattle. *Nat. Genet.* **46**, 858–865 (2014).

Acknowledgments: This work was funded by ERC Investigator grant 295729-CodeX. D.G.B. conceived of the project and designed research, with input from J.B. and M.C.; M.P.V., V.E.M., A.S., V.M., K.G.D, M.D.T and A.J.H. performed ancient DNA laboratory work; M.D.T. and V.M. performed modern DNA laboratory work; M.P.V. and V.E.M performed the computational analyses with input from D.G.B., M.D.T., P.M.D and K.G.D; other coauthors provided data and samples. D.G.B., M.P.V., V.E.M, A.S., M.D.T. wrote the paper and supplementary information with input from all coauthors. We would also like to acknowledge Science Foundation Ireland Award 12/ERC/B2227, Trinseq and the SFI/HEA Irish Centre for High-End Computing (ICHEC). We thank L. Frantz, G. Larson and M. Djamali for valuable suggestions. We thank Lara Cassidy for helpful discussions and scripts, and Ricardo Verdugo for contributions in figure design. We thank excavators, archaeozoologists and museums who permitted sampling of bones from their excavations and collections without which this project would not have been possible including Dr. E. Galili; Prof. T. Levy, Dr. C. Grigson, Prof. R. Gophna, Prof. A. Maeir, Dr. S. Gitin, Prof. A. Ben-Tor, Prof. D. Master, Dr. E. van den Brink, Prof. S. Cohen, Dr. E. Rosenstock, Prof. P. Biehl, Prof. I. Hodder, Dr. J.J. Roodenberg, Dr. S. Alpaslan Roodenberg, Dr. D. Helmer, Haskel Greenfield, Jasna Vuković, Miljana Radivojević, Ben Roberts, Miroslav Marić, Gordana Grabež, Julka Kuzmanović-Cvetković, Aleksandar Bulatović, Miloš Spasić, Eva Rosenstock, Kai Kaniuth. We thank the Israel Antiquities Authority for permitting sampling of the Israeli sites (under permit). We thank the Çatalhöyük Research Project and Ministry of Culture and Tourism of the Republic of Turkey. We thank the Iranian Cultural Heritage Handicraft and Tourism organisation and the National Museum of Iran (NMI) and Jebrael Nokandeh, director, and Dr Fereidoun Biglari, Cultural Deputy. We are grateful to Dr H. Laleh and Dr A. Aliyari Directors of the Archaeometry Laboratory of the University of Tehran. The ATM Project of MNHN supported sampling of several sites as well as the LIA HAOMA CNRS project. The participation of ZIN RAS (state assignment № AAAA-A17-117022810195-3) to this research is acknowledged. M.D.T. was partially supported by the Marie Skłodowska-Curie Individual Fellowship H2020-MSCA-IF-2016 747424 (SCRIBE). V.E.M was partially supported by the NERC Grant NE/P012574/1, M.J.C acknowledges support from DNRF128. Raw reads and mitochondrial sequences have been deposited at the European Nucleotide Archive (ENA) with project number: PRJE31621. Mitochondrial phylogenies are available at XXXXXX. The authors declare no conflict of interest.



Supplementary Materials for

**Ancient cattle genomics, origins and rapid turnover in the
Fertile Crescent**

Marta Pereira Verdugo†, Victoria E. Mullin†, Amelie Scheu†, Valeria Mattiangeli, Kevin G. Daly, Pierpaolo Maisano Delser, Andrew J. Hare, Joachim Burger, Matthew J. Collins, Ron Kehati, Paula Hesse, Deirdre Fulton, Eberhard W. Sauer, Fatemeh A. Mohaseb, Hossein Davoudi, Roya Khazaeli, Johanna Lhuillier, Claude Rapin, Saeed Ebrahimi, Mutalib Khasanov, S. M. Farhad Vahidi, David E. MacHugh, Okan Ertuğrul, Chaido Koukouli-Chrysanthaki, Adamantios Sampson, George Kazantzis, Ioannis Kontopoulos, Jelena Bulatovic, Ivana Stojanović, Abdesalam Mikdad, Norbert Benecke, Jörg Linstädter, Mikhail Sablin, Robin Bendrey, Lionel Gourichon, Benjamin S. Arbuckle, Marjan Mashkour, David Orton, Liora Kolska Horwitz, Matthew D. Teasdale and Daniel G. Bradley*

†Equally contributed

*Corresponding author: Daniel G. Bradley - dbradley@tcd.ie

This PDF file includes:

Materials and Methods
Figs. S1 to S14
Tables S1 to S13

Materials and Methods

Archaeological sites and context

1. Abu Gosh, Israel

The site of **Abu Ghosh** is situated in the Judean Hills, ca. 12 km west of the city of Jerusalem (Israel). The mid Pre-Pottery Neolithic B (ca. 7500-6000 BC) deposits at the site yielded rich assemblages of lithic artefacts, groundstone vessels and faunal remains were associated with architectural remains of rectangular houses, plaster floors and stone-built installations. Two *Bos primigenius* specimens were analysed in this study, identified to species on the basis of the size and robusticity of the remains, supported by the *Bos* age profile (26–28).

<i>Abu1</i>	1336-9/6306	7500-6000 BCE	MPPNB
<i>Abu2</i>	1995, A7, 2249, 1312	7500-6000 BCE	Mid-Late PPNB

2. Acemhöyük, Turkey

Acemhöyük is a large mound site located on the Aksaray plain in central Turkey. The site has been excavated since 1962 by Dr. Nimet Özgüç and more recently by Prof. Dr. Aliye Öztan of Ankara University (29, 30). Acemhöyük's primary occupation sequence spans the Early and Middle Bronze Age periods (2800-1750 BC) when it represents a major fortified urban settlement with central administrative complexes including palaces. In the Middle Bronze Age, the settlement, which may have been known as the kingdom of *Purushattum* or possibly *Ulluma*, was heavily involved in international trade and political networks with evidence for intensive interaction with city states in northern Mesopotamia.

Specimen *Ace1* (Unique bone number: AC13918) derives from excavation square BB/50, mekan 2, from a trash pit feature (çöp çukürü) which was excavated in 2014. It is assigned to stratigraphic layer XI representing the Early Bronze Age. 11 radiocarbon dates for level XI contexts range from 2900-2300 cal BC. Based on a sample of 300 specimens identified to the genus or species level, the faunal assemblage from this Early Bronze Age locus consists of sheep and goats (54% NISP) and cattle (44%) with less than one percent pig, dog, deer, fox and equids (31). Specimen AC13918 represents a complete petrous bone identified as *Bos* sp. and probably represents domestic cattle. The vast majority of *Bos* specimens at Acemhöyük fall within the morphological and biometric range of domestic cattle rather than *Bos primigenius* and this specimen does not exhibit any features (e.g., large size) suggesting it might derive from an aurochs. However, three specimens from excavation area BB/50 do exhibit very large body size and perhaps represent *Bos primigenius*, indicating that wild aurochs may have been present in the vicinity of the settlement in the Bronze Age and may have occasionally been hunted. No skeletal evidence for *Bos indicus* has been identified from *Bos* remains at Acemhöyük.

Acel *AC13918, AC14 BB/50* *c.2500 cal BC* *Early Bronze Age*

3. *Belovode-Veliko Laole, Serbia*

The site of Belovode is situated near the village of Veliko Laole, around 140 km southeast of Belgrade, Serbia, in the immediate vicinity of Rivers Mlava and Velika Morava (32). It is a large, multi-layered settlement of the Late Neolithic Vinča culture and is important for numerous archaeometallurgical features including the earliest secure dates for copper smelting, starting at around 5000 BC (33, 34). Two *Bos taurus* specimens were included in the study, identified as domestic on the basis of size. Both derive from stratigraphic Phase 3 (5050/4925-4900/4800 BC) in recent excavations of Trench 18 by Radivojević, Roberts, and Marić.

<i>Bell</i>	<i>Bell13-102260</i>	<i>T18, layer 13</i>	<i>Phase 3</i>	<i>5050/4925-4900/4800 BC</i>	<i>Late Neolithic</i>
<i>Bell</i>	<i>Bell13-102355</i>	<i>T18, feature 32, layer 13</i>	<i>Phase 3</i>	<i>5050/4925-4900/4800 BC</i>	<i>Late Neolithic</i>

4. *Bestansur, Iraq*

The site of **Bestansur** is located some 30 km southeast of Sulaimaniyah in the foothills of the Zagros Mountains, Iraqi Kurdistan. The site was excavated as part of the Central Zagros Archaeological Project under the direction of Prof Roger Matthews and Dr Wendy Matthews (University of Reading). The site is a multi-period settlement including an extensive Early Neolithic site of at least 1.0 hectare overlain in places by Iron Age (Neo-Assyrian and Sassanian) occupation (Matthews et al. 2016). Two *Bos* samples were analysed from post-Neolithic levels at Bestansur in this study. Domestic animals dominate the post-Neolithic fauna at the site, with only relatively few remains identified to wild taxa. Amongst the domestic taxa, goats, sheep and pigs are best represented, followed by cattle (none of which demonstrated any features suggestive of aurochs). Both samples derive from mixed deposits later in the sequence at the site, with Bes1 (directly dated to 911-609 cal BC) deriving from an arbitrarily defined unit below the topsoil within Trench 10 (35), and Bes2 (directly dated to 1292-1399 cal AD) deriving from a pit stratigraphically immediately below this unit.

<i>Bes1</i>	<i>ID:6507</i>	<i>Excavated: 2014</i>	<i>911–609 BC</i>	<i>Iron Age</i>
		<i>Context: 1727</i>		
<i>Bes2</i>	<i>ID:6602</i>	<i>Excavated:2014</i>	<i>1292-1399 cal.</i>	<i>Medieval AD</i>
		<i>Context: 1718</i>		

5. *Blagotin, Serbia*

Blagotin-Polje is a small site in central Serbia, about 26 km from the town of Trstenik, belonging to the earliest phase of the Early Neolithic Starčevo-Körös-Criş complex (36). Typically for this period, the site consists of a cluster of pits, some interpreted as pit-dwellings, and no apparent above-ground architecture (37). The two *Bos taurus* left petrous bones analysed here were identified as domestic based on size. One derives from the large central pit-feature, Zemunica 7, which features three late 7th millennium BC radiocarbon dates (38), making it the earliest-dated published Neolithic feature in the Danube basin at time of writing. The other is from the nearby Zemunica 6, which, based on stratigraphy, artefactual dating, and similarity of the features themselves, is likely to be very close in date to Zemunica 7.

<i>Bla1</i>	<i>BLJhIII</i>	<i>Zemunica 6</i>	<i>c.6200-6000 BC</i>		<i>Early Neolithic</i>
<i>Bla2</i>	<i>BLFa19</i>	<i>Zemunica 7</i>	<i>c.6200-6000 BC</i>	<i>[dates from same feature]</i> <i>OxA-8760, 7230 ± 50;</i> <i>OxA-8609, 7270 ± 50;</i> <i>OxA-8608, 7480 ± 55</i>	<i>Early Neolithic</i>

6. *Bubanj, Serbia*

Bubanj is located on a plain 15 km west of the town of Niš in southeastern Serbia, close to the confluence of the Nišava and Južna Morava Rivers. With cultural layers dating from the Early Neolithic, through the Eneolithic and Early Bronze Age to the Early Iron Age—covering a time span of about five thousand years—Bubanj is a site of great importance for understanding the development of metal age societies of the central Balkans (39–41). The site covered area about 5 ha, and consisted of three plateaux, but was mostly destroyed in the 20th century: until recently only a small northeastern portion of the site was preserved (c. 200 m²), less the 1% of its original area, and this preserved part was fully excavated during excavation campaigns in 2008-2014.

The Early Eneolithic horizon at Bubanj is dated to the second half of the fifth millennium BC, c. 4400-4200 cal BC (42). Sheep and goat (taken together) are the most numerous taxa in this phase at 33.4% NISP (Bulatović 2018, total NISP=2719), followed by domestic cattle (30.5%), domestic pig (14.7%) and red deer (7.5%). A single domestic cattle (*Bos taurus*) petrous bone from this horizon was analysed in this study.

<i>Bub1</i>	<i>BU 12/261/2</i>	<i>ca.6000-5600 BC</i>
-------------	--------------------	------------------------

7. *Çatalhöyük, Turkey*

The double tell settlement of **Çatalhöyük** is located on the Konya Plain in central Turkey. The Neolithic East Mound, famous for its rich cattle symbolism and multiple layers of densely packed houses, was occupied c. 7100 to 5950 BC (43, 44). Occupation shifted to the less well-known West Mound - traditionally considered Chalcolithic - from perhaps 6200 BC, before final abandonment around 5550 BC (45). Cattle in the earlier levels of the site have been interpreted as wild based on size and herd demographics, with clearly domestic cattle appearing around 6500-6400 BC (46, 47). The single sample analysed here derives from a pit in Trench 2 on the West Mound, the latest dated feature at the site at c. 5750-5550 BC based on five radiocarbon dates, including one from the same context (2910) as the sample. The specimen, a metatarsal, is identified as *Bos primigenius* based on size, with a log10-standard index of +0.05, calculated using the Ullerslev Cow (48) as a standard.

<i>Ch22</i>	2910.	<i>West Mound</i>	<i>c.5570-5550 BC (based</i>	<i>[date from same</i>	<i>Early</i>
	<i>F171</i>	<i>Trench 2</i>	<i>on all dates from pit fill)</i>	<i>context]</i>	<i>Chalcolithic</i>
				<i>OxA-11762, 6662 ± 38</i>	

8. *Dariali Tamara Fort, Georgia*

In the border zone between Georgia and Russia in the Kazbegi region, **Dariali Tamara Fort** (Coordinates: UTM 38N 469400, 4731800) sits on top of a high flat outcrop on the west bank of the Tergi river with excellent views of the pass. The site was investigated within an ERC project “Persia and its Neighbors“ directed by Eberhard Sauer (the University of Edinburgh) and Konstantin Pitshelauri (Tbilissi State University) . Excavations at the site indicated several occupations mainly between ca. 400–1000 AD which was first a military Fort from the Sasanian period. The site was re-occupied between the late 13th and early 15th centuries AD. Following this, there is no evidence for occupation until the 20th century. A large number of animal bones (approximately half a tonne) have been studied during four seasons of excavation by a team of archaeozoologists. The domestic herbivores (sheep, goat and cattle) are dominant in the faunal remains. Very interestingly, specimens of Caucasian tur (*Capra caucasica*) were also found among the remains (49, 50). Good preservation allowed paleogenetic analysis of several species in this site.

<i>Kaz1</i>		<i>(F.062) Phase 5c-7b</i>	<i>c. 10th century - modern</i>	<i>Medieval</i>
-------------	--	----------------------------	---------------------------------	-----------------

<i>Kaz2</i>		<i>(F.088) Phase 5b-c</i>	<i>c. 9th-11th AD</i>	<i>Medieval</i>
-------------	--	---------------------------	-----------------------	-----------------

<i>Kaz3</i>	(F.094) Phase 4	<i>c. 7th-8th c., perhaps 7th c., 2nd half</i>	<i>Medieval</i>
<i>Kaz4</i>	Phase 5	<i>7-10th c.</i>	<i>Medieval</i>
<i>Kaz5</i>	(F.078) Phase 5a	<i>651-766 AD (79.5%: 651-715)</i>	<i>Medieval</i>

9. Gilat, Israel

The site of **Gilat** lies in the northern Negev of Israel, ca. 1 km east of the town of Ofakim. The site dates to the Ghassulian, Chalcolithic culture (ca. 4300–3300 BC) and has been interpreted as a permanent settlement, probably a ritual center (sanctuary). Site subsistence was based on agro-pastoralism (the latter based on domestic caprines) and trade (51). The single *Bos* sample analysed in this study was identified as that of a domestic animal.

<i>Gill</i>	1992/M1-N1/773/5451	<i>c.4300–3300 BC</i>	<i>Chalcolithic</i>
-------------	---------------------	-----------------------	---------------------

10. Gyumri, Armenia

This is a petrous bone from a skull identified unambiguously as *Bos primigenius* from size and morphology (Fig S5). It was discovered in 1891 in the Gyumri district, Armenia and is held as deposit No. 11138 in the Zoological Institute, Russian Academy of Sciences, St Petersburg. It is directly dated at 5036-5076 cal. BC.

<i>Gyu2</i>	11138	<i>5036-5076 cal. BC</i>
-------------	-------	--------------------------

11. Hasanlu, Iran

Tepe Hasanlu is one of the key sites of northwestern Iran, due to its long-term occupation and well-defined stratigraphy. Hasanlu is located in the Solduz valley on the southern shore of Lake Urmia at 1043 m ASL, Western Azerbaijan province. Robert H. Dyson Jr. directed 10 seasons of excavations at Hasanlu from 1956 to 1977 (52, 53). The site was occupied during 10 different cultural periods from the Late Neolithic (period X) to the Ilkhanid dynasty (period I) (54). Hasanlu Period VII can be linked to the Early Bronze Age from the first half of the third millennium to the late third millennium BC (3000-2100 cal BC) (55). The most represented periods in the site are the Late Bronze (period V) and Iron Age (period IV-III) (56). Hasanlu period IIIc and b, are attributed to Iron Age III (Uartian period) and period IIIa allocated to the Achaemenid Empire (550-530 cal BC), for which no substantial architectural remains have been found (57). Period II is also a debated issue but generally assigned to the Seleucid or Parthian period, post-Achaemenid (58, 59). The sample Has1-MV167 belongs to the collapse of mud-brick wall (Campaign

1974, Op.W23, St.12, Loc.14, Level VIb) from the Middle Bronze Age (1900-1600 BC). Sample Has3-MV169 was chosen from the trash lenses (Campaign 1972, Op.U22, St.20, Level VIIA) in the building level of the Early Bronze Age II (2700-2200 BC), which C14 dating of this layer dated back to 2470 Cal. BC. Sample Has4-MV170 belongs to the collapse within the burned building VI (Campaign 1974, Op.W23, St.4, Loc.7, Level IVb) from the Iron Age II (1050-800 BC). Sample Has5-MV171 was selected from ashy layer (Campaign 1972, Op.T20E, St.2, Loc.3, Level II-IIIa) of Historical period (550-275 BC). Faunal remains of this site are very abundant and very well preserved. The assemblage was studied in the Osteology Department of National Museum of Iran by H. Davoudi within a PhD Thesis under the supervision of M. Mashkour in Tarbiat Modares University, Iran (60). The osteological material from human, dog, goat, sheep, horse of this site were analysed in several paleogenetic studies (61, 62).

<i>Has1</i>	<i>1900-1600 BC</i>	<i>Middle Bronze Age</i>
<i>Has3</i>	<i>2700-2200 BC (C14: 2470 cal BC)</i>	<i>Early Bronze II</i>
<i>Has4</i>	<i>1050-800 BC</i>	<i>Iron Age II</i>
<i>Has5</i>	<i>550-275 BC</i>	<i>Achaemenid / Seleuco-Parthian</i>

12. Horvat Castra, Israel

Horvat Castra (Qastra) lies on the southern outskirts of the city of Haifa, northern Israel. Excavations revealed remains of a large Roman and Christian-Byzantine settlement including two churches, a cemetery, dwellings and industrial installations (wine and oil presses, pottery and lime kilns) as well as cave fills (63). The *Bos* sample analysed here derives from one of the Byzantine period cave fills.

<i>Cas1</i>	<i>E/5316/5872</i>	<i>324-638 AD</i>	<i>Byzantine</i>
-------------	--------------------	-------------------	------------------

13. Koktepe, Uzbekistan

Koktepe, 30 kilometers north of Samarkand in the Zerafshan Valley, was founded for the first time during the second half of the second millennium BC in the cultural context of the handmade painted ware (Yaz I period). After a long interruption of its urban life, the city was resettled in the seventh-sixth century BC (during the Middle Iron Age, Yaz II period), as the first capital of Sogdiana known as Gava. It was then fortified with a monumental wall that protected proto-urban institutions mainly represented by a sanctuary. Around 540 BC, the city was incorporated into the Achaemenid empire of Cyrus II (Yaz III period), before his successor Darius I moved the capital to Samarkand. During this period Koktepe remained the seat of a regional sanctuary, before being transformed into a fortress after the conquest of Alexander the Great. Until its abandonment during the Seleucid period (third century BC) the site was based in an agricultural economic context that has provided the bone samples analyzed here.

<i>Kok1</i>	<i>K806-NISP-1</i>	<i>2nd-1st Millennia BC</i>	<i>Iron Age</i>
-------------	--------------------	-----------------------------	-----------------

14. Kul Tepe, Azerbaijan, Iran

Kul Tepe, near Jolfa, is located 10 km south of the Araxes River in Western Azerbaijan province. The site, excavated by Akbar Abedi and Hamid Khatib Shahidi in 2010, is a multi-period mound about 6 ha in size and rising 19 m above the surrounding lands. Eight main occupation periods were identified: Early, Middle and Late Chalcolithic, Early, Middle and Late Bronze Age, Iron III, Urartian, and Achaemenid periods (64, 65). Faunal remains were studied at the Archaeozoology section, Archaeometry laboratory of the University of Tehran by H. Davoudi under the supervision of M. Mashkour. The domestic species, cattle, sheep and goats, were always the most important source of animal products at site. The wild species indicate the presence of a mosaic environmental around the site, ranging from the steppe to forested areas (66). Animal remains are exceptionally well preserved in all layers at Kul Tepe. The sample Azer1-AH23 belongs to the building floor (Tr.III, Loc.3008, RN.3040) from the Late Chalcolithic period (C14 dating: 4260-4050 Cal. BC).

<i>Azer1</i>	<i>AH23</i>	<i>4260-4050 cal BC</i> <i>(95.4%)</i>	<i>Late Chalcolithic (LC3)</i>
--------------	-------------	---	--------------------------------

15. Maral Tappeh, Iran

Maral Tappeh is one of the settlements of the Ozbaki archaeological complex located in the Savojbolagh county of Alborz province, in the southern foothills of Elburz Mountains in the northern part of the Central Plateau of Iran. Excavations from 1998 to 2005 were conducted by Y. Madjidzadeh and uncovered a long cultural sequence from the Late Neolithic to the Median period (67). Maral Tepe belongs to the Early and Middle Chalcolithic and Median period (Iron Age III). The cattle sample Mar1 belongs to Early Chalcolithic (second half of fifth millennium BC- *circa* 4300-4000 BC) (68).

<i>Mar1</i>	<i>MT Per 1 (A237)</i>	<i>c. 4300-4000 BC</i>	<i>Early Chalcolithic</i>
-------------	------------------------	------------------------	---------------------------

16. Mentese, Turkey

Located in the Bursa province (Turkey), close to the Iznik Lake, the site of **Mentese** is one of the oldest settlements of Northwest Anatolia (69). This village was established half way the 7th millennium by Neolithic farmers who bred cattle and small ruminants and cultivated an array of food plants. It has been established that the population of Mentese shared strong genetic similarities with Neolithic farmers in the Balkans and central Europe. The zooarchaeological study indicates a significant shift from the predominance of domestic cattle at the beginning towards a more sheep-based subsistence patterns in the later Neolithic levels (70). Cattle and sheep were both exploited for their meat and milk (dairy products)

and the use of bovines for transport or traction is also attested by pathological phalanges. Hunting, fowling and mollusc gathering played a minor role while fishing seems to be very scarce. According to the biometric analysis, most of the cattle bones belong clearly to domestic animals but the presence of aurochs cannot be excluded. Among the two specimens analysed, Men1 comes from the rubble from the Neolithic layers (ca. 6400-5700 cal BC) and Men2 was directly dated to the beginning of the 6th millennium BC (6048-5893 cal BC).

<i>Men1</i>	<i>JK95-7-3-166-180('97)d</i>	<i>ca. 6400-5700 cal BC</i>	<i>Neolithic</i>
<i>Men2</i>	<i>13/07/2000 Sq.13/Layer100/#600</i>	<i>7998-7843 cal. BP</i>	<i>Neolithic</i>

17. Mianroud, Fars, Iran

Tepe Mianroud is located in the Marvdasht Plain in Fars province. This mounded site with 3.7 ha at present, is highly damaged by earth-removing and agricultural activities. So far three seasons of excavations conducted at the site between 2008 and 2010 by S. Ebrahimi, M. Zare, and A. Abolahrar. The stratigraphic trench provided the complete cultural sequence of the site including Late Neolithic to Chalcolithic. The sample Far1-MV176 was selected from the Late Neolithic contexts (Tr.W23, L.54), the time span between 6000-5500 BC (71). The faunal remains of Tepe Mianroud were studied by A.F. Mohaseb, M. Mashkour and H. Fathi, at the Archaeozoology section, Archaeometry Laboratory of the University of Tehran, Iran. Domesticated caprines, and then cattle, are the most dominant animals in the assemblage and there is not the variety of hunted and herded species in comparison to the other contemporaneous sites in the region. The results are valuable for understanding the spread of domestication in southwest of Iran (72).

<i>Far1</i>	<i>#158/MMMR8</i>	<i>c. 6000-5500 BC</i>	<i>Late Neolithic (PN)</i>
-------------	-------------------	------------------------	----------------------------

18. Monjukli Depe, Turkmenistan

The settlement **Monjukli Depe** is located in the Meana-Čaača region at the foothills of the eastern Kopet Dag mountain range close to the Iranian border. It has occupational layers dating to the late Neolithic Džejtun Culture (between 6400 and 5900 calBC) and the Chalcolithic Meana Horizon (between around 5100 and 4500 calBC) (73). From the 2077 identifiable bones only 49 stem from wild animals. The remaining domestic faunal assemblage is largely dominated by sheep and goat (over 90% in both, the Neolithic and Chalcolithic contexts). Cattle and especially pig were of only limited significance.

<i>Mon1</i>	<i>Unit D, Locus 416, RN</i>	<i>5100-4500 cal BC</i>	<i>Chalcolithic</i>
-------------	------------------------------	-------------------------	---------------------

19. Nahal Tillah, Israel

The **Nahal Tillah** Early Bronze Age I site (ca. 4500-3000 BC) (also known as the Halif Terrace site or the Silo site), is located in the northern Negev desert (Israel), adjacent to ancient trade routes running north-south along the Mediterranean coast and northwards through the Judean hills abutting the coastal plain. Based on attributes of the ceramic and faunal assemblages, the excavators have suggested that an Egyptian population may have inhabited the site (74, 75). A single domestic cattle bone from the site proved suitable for analysis.

<i>Nahl</i>	1994/Area A1/Locus123/Basket 992	3300-3050 BC	Early Bronze Age I
-------------	--	--------------	--------------------

20. Nishapur Kohandēž, Central Khorasan, Iran

The ancient city of **Kohandēž** is located two kilometers to the south-east of the present city of **Nishapur** in the east of Iran is about 5 ha. Nishapur with Herat, Balkh and Merv, composed the historical Great Khurasan during the Islamic period. According to the historical sources, the city was founded during the Sasanian period became the Capital of Khurasan during the Mid-Islamic period. Agropastoralism was among the important economic activities of this region during these periods (76). The site was initially excavated by Metropolitan Museum (77). Several other excavations took place subsequently. The faunal remains of Kohandēž were studied in the Archaeozoology section, Archaeometry Laboratory of the University of Tehran, in the framework of MA thesis of R. Khazaeli supervised by M. Mashkour and H. Laleh (78). Animal bones were C14 dated within this project and we could establish that the settlement in Kohandēž predated the Sasanian period and began from the Parthian period. Sheep, goat, and cattle, were the main animal resource of Kohandēž.

<i>Khol</i>	#121/MMNKD2 (2016.01.18)	06.702 1195-10- 1195	prob 5th-8th AD	Islamic Period
-------------	-----------------------------	-------------------------	-----------------	----------------

21. Pločnik, Serbia

Pločnik is a Late Neolithic Vinča culture site on the left bank of the Toplica river, 19 km west of the town of Prokuplje in southern Serbia. The settlement was occupied for c. 600 years, c.5200–4650 cal BC (79) and is estimated at c. 100 ha at its greatest extent.

Pločnik has been excavated in several campaigns since its discovery in 1926, with numerous copper artefacts and traces of early metallurgical activity discovered across the settlement (80, 81), as well as the unique find of an *in situ* metallurgical workshop for casting and/or repair of metal tools. Aimed at understanding these metallurgical activities (82), recent excavations (2012-2013) also recovered large quantities of animal remains (83). Domestic cattle dominate the assemblage with sheep and goat (taken together) the second most frequent taxon, followed by domestic pig. Red deer is the most abundant hunted species. Eight domestic cattle (*Bos taurus*) petrous bones from the horizons excavated in 2012-2013 excavation seasons, and dated to the different phases of the Late Neolithic Vinča culture, were analyzed in this study.

Plo1	Horizon 5	97, Feature 38, spit 25	5275/5125-5100/5000 cal BC	Middle Neolithic
Plo2	Horizon 3	155, spit 16	5025/4950-4850-4650 cal BC	Late Neolithic
Plo3	Horizon 4	196, spit 24	5100/5000-5025/4950 cal BC	Middle Neolithic
Plo4	Horizon 4	230, spit 20	5100/5000-5025/4950 cal BC	Late Neolithic
Plo5	Horizon 2	197, spit 13	4850/4650-4600/4500 cal BC	Late Neolithic
Plo6	Horizon 5	97, Feature 38, spit 25	5275/5125-5100/5000 cal BC	Middle Neolithic
Plo7	Horizon 4	196, spit 24	5100/5000-5025/4950 cal BC	Late Neolithic
Plo8	Horizon 4	233, spit 20	5100/5000-5025/4950 cal BC	Late Neolithic

22. Promachon, Serres, Greece

The **Promachon-Topolinca** settlement is situated on the southeastern slope of the mountain Kerkini, close to the western bank of the Strymon river on a natural pass at the beginning of the Middle Strymon valley. This Neolithic settlement, which lies across the borderline of Greece and Bulgaria has been jointly investigated by a Greek-Bulgarian archeological project. Three phases of occupation have been defined on the basis of ^{14}C : Phase 1 (5320-5070 Cal BC) and Phase 2 (5070-4700 Cal BC), which belong to the early stage of the Late Neolithic (LN1), and Phase 3 (4460-4250 Cal BC), which belongs to the late stage of the Late Neolithic (LN2) (84, 85). The main structural feature during the first phase of occupation are pits dug in the natural soil, while the subsequent phases are characterized by the presence of timber-framed structures with interior hearths. Of particular interest, however, is the presence of a large circular pit with a diameter of more than 12 m and a depth of more than 7 m, which belongs to the first phase of occupation. Its deposits yielded large quantities of material culture objects (vases, figurines, tools, fragments of jewellery *etc.*), animal bones and bucrania. The large number of storage and “table” vases, stone querns and animal bones which were found in the successive layers of this large pit, are serious indicators of activities involving consumption of animal carcasses (and possibly other stimulants) by a large number of participants.

The single petrous bone used here for analysis, derives from the use surfaces of the first phase of occupation and belongs to domestic cattle (*Bos taurus*) on the basis of its size (*cf.* (86)). During this phase, cattle are represented with the highest frequencies (in terms of the number of fragments) among the main domesticates (87). The predominance of cattle during the first phase of occupation, along with evidence

from the material culture and the structural features, suggests that the site was “culturally” linked to the Late and Final Neolithic communities of the northern regions of the Balkan peninsula.

Pro1 Γ, 6, #14 676-8/130-3 78,90 *Phase I / Late Neolithic I* 5320-5070 Cal. BC

23. Sarakenos Cave, Boeotia, Greece

The **Sarakenos cave** is located in the eastern part of the former lake Kopais (Boeotia, Greece) at an altitude of c. 180 m above sea level. The exceptional stratigraphic data and a series ¹⁴C dates suggest an occupation from the Middle/Upper Palaeolithic to the Middle Helladic (2nd millennium BC) (88–90). The archaeological finds indicate a sporadic occupation of the site by human groups during the Final Palaeolithic (c. 13000/12000 BC), followed by more frequent visits in the Mesolithic (c. 8500-7000 BC) and Early Neolithic (c. 6600-6200 BC) periods (90). Among the finds (e.g. pottery, lithics, figurines) were numerous *ovis*, *capra*, *bos taurus*, small mustelid, rodent and avian bones (91–93). The single bovine petrous bone used in this study has been recovered from trench F (layer 22, square 46) that is dated to c. 5750-5600 BC.

Sar38 F, 22, 46 *Middle Neolithic* 5750-5600 BC

24. Stubline, Serbia

Stubline is a Late Neolithic Vinča culture site built around 4850/4800 BC on small elevation, 40 km to the southwest of Belgrade, Serbia. The site covers an area around 16.5 ha. The Stubline site lies in a small micro-region, with several contemporary Late Neolithic Vinča settlements in the immediate vicinity. The first excavations at the site were carried out in the late 1960s, while systematic excavations were renewed in 2006 and are still in progress (94–96). A well-preserved settlement was discovered with more than 200 above-ground houses arranged in rows, with linear communications, open spaces, and circular ditches surrounding the settlement. Preliminary results of the archaeozoological analysis (83) indicate that domestic cattle is the most common and most important species, followed by caprines (sheep and goat together), domestic pig, and red deer. Remains of wild boar, dog, roe deer, aurochs, beaver, bear, and hare were also identified. One domestic cattle (*Bos taurus*) specimen from the site was analysed in this study, deriving from Feature 30.

Stu1 S 14/3/5 Feature 30 Late Neolithic

25. Suberde and Erbaba, Turkey

Suberde Höyük represents the remains of an Aceramic Neolithic village settlement located in the SW Turkey (Beyşehir-Suğla basin) (97). Radiocarbon dating and artifact parallels firmly place the main prehistoric occupation of the site to the second half of the eighth millennium BC (7500-7000 cal BC) (98).

The faunal assemblage is dominated by morphologically wild, but likely managed, sheep (*Ovis orientalis*) and goats (*Capra aegarus*) (c.80%), as well as wild (hunted) boar (*Sus scrofa*) (c. 12%) as well as smaller quantities (<5%) of wild cattle (*Bos primigenius*) and Red deer (*Cervus elephus*) (99). Due to its curation history (98) the Suberde faunal assemblage likely includes some specimens from the nearby Pottery Neolithic site (6500-6000 cal BC) of Erbaba Höyük (also located in the Beyşehir-Suğla basin of SW Turkey). Both Erbaba and Suberde were excavated by Jacques Bordaz as part of the Beyşehir-Suğla Project between 1964 and 1977 and the faunas from both sites were initially studied by and curated under Dexter Perkins. The faunal assemblage from Erbaba Höyük represents a more mature pastoral economy dominated by the remains of domestic sheep (*Ovis aries*) and goats (*Capra hircus*) (79% of the mammalian fauna) as well as domestic cattle (*Bos taurus*) (6%). However, pig remains (9% of the faunal assemblage) from the site represent wild boar (*Sus scrofa*) rather than domestic swine (100).

Specimen *Sub1* (Unique bone number: S0005) represents a fragment of a petrous bone identified as *Bos* sp. A direct radiocarbon date on the specimen (UBA-29052: 7247+/-51bp) produced a date of 6020-6140 cal BC. This date strongly suggests that specimen S0005 derives from Erbaba rather than Suberde and therefore represents domestic cattle. The cattle from Erbaba represent the earliest morphologically domestic cattle in central Anatolia where their appearance is quite late compared to neighboring regions (101). This may suggest that domestic cattle were imported into central Anatolia in the late seventh millennium BC following several millennia of hunting local aurochs. Moreover, specimen S0005 is associated with a label for excavation unit 254. Unfortunately a list of Suberde excavation units is not currently available. An excavation unit 254 is listed for the Erbaba excavation, further supporting the interpretation that specimen S0005 derives from Erbaba Höyük, and therefore represents domestic cattle from the central Anatolian Pottery Neolithic.

Sub1 *S0005* 6221-6024 cal. BC *Neolithic*

26. *Taghit Haddouch, Morocco*

The small cave site of **Taghit Haddouch** is located near the current village of Dar Driouch (commune of Ain Zohra, Province of Nador) in north-eastern Morocco. Excavations were conducted in 1997 and 1998 by a team of researchers from the *Institut National des Sciences de l'Archeologie et du Patrimoine* (INSAP), Rabat under the direction of Abdesalam Mikdad. They revealed early to mid-Holocene anthropogenic deposits, with radiocarbon dates ranging from around 9.700 to 4.900 calBP. According to the radiocarbon ages the shelter was occupied during the Epipalaeolithic, Early and Late Neolithic period. As main occupation the Epipalaeolithic and Late Neolithic period can be considered. The site is characterised by a very good preservation state of the faunal remains and frequent occurrence of gastropod shells, carved ostrich eggshells, stone and bone artefacts and ornaments.

The Epipalaeolithic deposit provides a rich lithic assemblage produced predominantly by unipolar bladelet technology and shows the whole spectrum of tools such as backed bladelets, microliths and notched pieces

as they are typical for the continental Mediterranean Epipalaeolithic of this region (102). The main lithic raw materials used come from the Ain Zora region in the west and the gravels of the Moulouya River east of the site. The Late Neolithic assemblage is rich in pottery including the so-called herring bone pottery, typical for the Late Neolithic of North-western Africa.

The final study and publication of the material is still ongoing. Of particular interest is the study of the numerous remains of land snails. On one hand the species distribution indicates dramatic environmental shifts during the transition from the early to the middle Holocene. On the other hand Taghit Haddouch is one of the first sites of the Eastern Rif where systematic manipulations on the snail shells were detected, indication clearly that land snails were an essential part of the diet at that time (103).

Th7

7051-6801 cal. BC

Epipaleolithic

27. *Tappeh-Sang-e-Chakhmaq, Iran*

Tappeh Sang-e Chakhmaq is located at 1400 m ASL, near the town of Shahroud in the Semnan province. It is a unique Neolithic site that provides the earliest evidence for agricultural and herding in the North East of Iran and the spread of the Neolithic way of life in Central Asia. During the early 70s a Japanese team supervised by Seichii Masuda exposed several trenches on the East and West mounds (104, 105). Recent soundings on these mounds led by K. Roustaei allowed a better contextualisation of the material culture and its chronological framework (106). The West mound is a pre-pottery site dating to late 8th to the beginning of 7th Mil. BC, while the East mound has pottery levels occupied from the late 7th to mid 6th Mil BC (106, 107). Cattle remains were studied and sampled in Tsukuba, Japan. The individual Sac3 belongs to the East Mound, pottery Neolithic, and absolutely dated to 5373 Cal. BC. Wild species are very numerous in the faunal remains and the small herbivores (sheep and goat and gazelle) are the most exploited taxa. Domestic goat is present from the earliest stages of the occupation(106, 108).

Sac3

SAC3

5373 cal BC

Late Neolithic (PN)

28. *Tel Ashqelon, Israel*

Tel Ashkelon (Ashqelon) is located on the Mediterranean coast ca. 30km south of the city of Tel Aviv. It was one of the most important ancient cities in Israel with peak occupation in the Middle Bronze Age (2000-1550 BC), when it was a Canaanite city and in the Iron Age, when it served as one of the Philistine Decapolis (ca. 1175-604 BC). It was also a thriving city in Classical era (Persian, Hellenistic, Roman) as well as in the Crusader and Islamic periods (109, 110). The single *Bos* sample used in this study derives from an early Iron I context.

<i>Tsa1</i>	<i>Permit:10/7/2013; Area F; Square 28A; Locus 16F28A08; Basket 16F28A033; Height 203.09-203.00</i>	<i>925-720 BC</i>	<i>Iron Age II- 9th Century</i>
<i>Tsa2</i>	<i>Permit 2009; Area A3; Locus 123017; Basket 1230068; Height 175.97</i>	<i>1200-1000BC</i>	<i>Iron Age I</i>
<i>Tsa3</i>	<i>Area D; Square 94C; Locus D15AQ07; Basket D15AQ49; Height 127.73-127.36</i>	<i>925-720 BC</i>	<i>Iron Age II - 9th century</i>

32. Tel-Hreiz, Israel

Tel Hreiz is one of several submerged late Pottery Neolithic (5100-4300 BC) sites located off the Carmel coast of northern Israel. The settlement, which currently lies at a depth of 0-5m below sea level, was inundated due to a mid-Holocene rise in sea levels (*116, 117*). A single domestic *Bos* sample was analysed from this site.

<i>Thr1</i>	<i>Permit 53/95; Basket Dive 9;</i>	<i>7100-6300 yrs. BP (uncalibrated C14)</i>	<i>Late Pottery Neolithic</i>
-------------	-------------------------------------	---	-------------------------------

33. Tel Masos, Israel

Tel Masos (Hirbet el-Msas) is a small mound located some 12 km east of the city of Beersheva in the northern Negev (Israel). The main occupation of the tel dates to the Chalcolithic and Iron Age I periods. The sites location relates to the ancient east-west route, passing from the Judean hills through to the central Negev and Arava (*118*). A single sample of domestic cattle, dating to the Iron Age I (ca. 1200-1000 BC), was analysed in this study.

<i>Mas1</i>	<i>Locus 83; Basket 281</i>	<i>1200-1000 BC</i>	<i>Iron Age I</i>
-------------	-----------------------------	---------------------	-------------------

34. Tel Migne-Ekron, Israel

Tel Miqne-Ekron is located on the Israeli coastal plain (Shephelah), ca. 35 km south-west of Jerusalem. Periods represented span the Chalcolithic to Islamic periods with peak occupation in the Late Bronze Age II through Iron Age (ca. late 16th-15th centuries to 7th/6th centuries BC), when it was a Philistine city (119–123). *Bos* samples analysed in this study derive from domestic animals; one sample from the Late Bronze IIA (14th/13th century BC), one from the Late Bronze/Iron Age I interface, and two from the Iron Age I A (1st third of 12th century BC).

<i>Tmq1</i>	<i>Square INW; Locus 3.108; Basket 3033;</i>	<i>1200-1150 BC</i>	<i>Iron Age IA-1st third of 12 century</i>
<i>Tmq2</i>	<i>Square INE; Locus 7.127;</i>	<i>1200-1150 BC</i>	<i>Iron Age IA-1st third of 12 century</i>
<i>Tmq3</i>	<i>Square INE; Locus 6.198</i>	<i>1000-925 BC</i>	<i>Late Bronze IIA - 14th/13th century</i>
<i>Tmq4</i>	<i>Square INW; Locus 3.5</i>	<i>1400-1200 BC</i>	<i>Late Bronze-Iron Age unclear attribution</i>

35. Tel Yoqneam, Israel

The multi-period settlement of **Tel Yoqne'am** is located ca. 30 km south-east of the city of Haifa and has yielded archaeological remains spanning from the Early Bronze Age to the Ottoman period. The site relates to a complex of ancient trade routes that connected the Mediterranean coast from Tyre (Lebanon) and the route through Wadi Milek to the Jordan Valley and beyond (124, 125). The single domestic *Bos* sample analysed here derives from the Hellenistic period.

<i>Tyq1</i>	<i>Area A-B; Locus 2270; Basket 6619</i>	<i>332-167 BC</i>	<i>Early Hellenistic</i>
-------------	--	-------------------	--------------------------

36. Tel Zahara, Israel

Tel Zahara is a small mound located ca. 5km west of the town of Bet Shean in the central Jordan valley (Israel). It was a short-lived site with deposits dating to the late Persian, Hellenistic and Roman periods. The site probably served as the rural hinterland that supplied the nearby town of Tel Bet Shean. In addition, with several pits, cisterns and other fills containing remains from the Islamic-Ottoman periods were found (126). The domestic cattle petrous bone analysed here derives from these Islamic period deposits.

<i>Zah1</i>	<i>Permit 2008; Square B3; Basket 20</i>	<i>c. 63 BC to 330 AD</i>	<i>Islamic</i>
-------------	--	---------------------------	----------------

37. *Tel-Dalit, Israel*

Tel Dalit is a small Early Bronze Age settlement located in the foothills of the Samarian hill country in central Israel. The occupations of the site represent unwalled villages, beginning in the Early Bronze IB with the final settlement in the Early Bronze III. The peak occupation was in the Early Bronze Age II (ca. 3050 BC) from which the single domestic *Bos* sample analysed in this study derives (127).

Tdal *Permit 78; Area A2; 3050 BC Early Bronze Age II*
Locus 72; Basket 1380

38. *Tepe Shizar, Qazvin, Iran*

Tepe Shizar, in Takestan a town in Qazvin Province, is a 19 metres high mound with cultural sequence from the Chalcolithic to the Iron Age. Two trenches were excavated in 2006 under the supervision of H. Valipour. The cattle sample from Tepe Shizar (QAZ1, #108/MMTCH24), belongs to the Middle Bronze Age (128). Faunal remains were studied by H. Davoudi under the supervision of M. Mashkour at the Archaeozoology section, Archaeometry Laboratory of the University of Tehran and not yet published. This study complements, in particular for the third millennium, previous studies on the Qazvin Plain subsistence economy (129–131). Domesticates (sheep, goat, cattle) are the most abundant species followed by wild and domestic equids. Game species are gazelle, a steppe-adapted animal. Wild sheep and goat, deer and boar that indicate a mosaic of environments around the site. and the presence of rich pastures at the junction of Alborz and Zagros piedmonts.

Qaz1 *#108/MMTCH24; Excavated: 2006; 2882-2636 cal. BC Early Bronze Age*
Trench I; Context 1042;

39. *Tilla Bulak, Uzbekistan*

The small hilltop settlement of **Tilla Bulak** is located near the current village of Pashkurt at the foothills of the Kugitang mountain range close to the borders to Afghanistan and Turkmenistan in South Uzbekistan. The Late Bronze Age site of Sapalli Culture dates to the beginning of the 2nd millennium cal. BC (132). Preliminary analysis of the faunal record from the excavations in 2008 revealed that it is dominated by domesticates, especially by sheep and goat (79%). Cattle and wild species only played a minor role with 8 and 9%, respectively.

40. Yerqurqan (Erkurgan), Uzbekistan:

The petrosa sample 29,3 was recovered at **Yerqurqan** (also referred to as **Erkurgan**), the Achaemenid Xenippa/Nikhshapaya later named Nakhshab, located 10 km north of Qarshi in Kashka Darya Valley (Uzbekistan). It was first settled during the second half of the 2nd millennium BC, then continuously occupied until the Sasanian period and destroyed by the Turks during the 6th century AD before being abandoned without significant reoccupation after the 8th-9th centuries in favor of the current Qarshi site (133). The original urban area lies within two lines of ramparts, the first of which, in the form of an irregular 35-hectare pentagon reinforced by rectangular towers, was erected in the 5th century BC and the second between the 1st and 3rd centuries AD on an area of 150 ha. The excavations revealed the presence of a large palace located within a citadel, as well as temples: a first one whose columns were painted in bright colors and a mausoleum on a podium, identified by archaeologists as a Zoroastrian “dakhma” (for the exhibition of the deceased’s bones), thus showing the political and religious influence of this city (134). Moreover, excavated blacksmith tools and a pottery production center suggest that this site was once a major hub for trade.

*Yer1**23,29,30,NISP-1**Late 1st BC/ Early AD**Achaemenid/Sasanid****DNA Extraction, whole genome sequencing and SNP chip genotyping of modern samples***

A classic phenol/chloroform extraction protocol was used to extract DNA from variable volumes of blood for all the modern samples. A minimum of 200 ng (4 µl of 50 ng/µl) of genomic DNA per sample was sent to a commercial company, “Weatherbys Ireland Laboratory”, to be genotyped with the “Bovine High Density SNP Chip 770K”. About 1 µg of genomic DNA was sent to a commercial company (Macrogen, Inc , 1002, 254 Beotkkot-ro, Geumcheon-gu, Seoul, 153-781, Republic of Korea) to sequence the whole genome (coverage >10x) of selected modern animals using the HiSeqX Illumina platform.

DNA Extraction and Sequencing of ancient samples

All samples except Ch22 and Th7 were processed in a designated clean and separate laboratory at Trinity College Dublin (TCD). Samples Ch22 and Th7 were processed in the dedicated ancient DNA facilities of Johannes Gutenberg-University Mainz.

Trinity College Dublin

Bone sampling

Samples were exposed under UV light for 20 minutes on each side of the bone in a clean flow hood before cleaning; and for 15 minutes on each side after the surface of the bone was cleaned. For each sample, new and clean conditions/materials were used as is typical for best practice guidelines for ancient DNA (135). Cleaning and cutting of the surface of the bone was done using a drill bit with the Maxima Micro-Drill. Bone piece(s) were powdered using a mixer mill (MM400, Retsch) and 100mg-150mg of bone powder was typically used for extraction. Water and air controls were always included and sequenced for contamination control.

DNA extraction

DNA extraction from bone powder was carried out as described in (136), based on (137) and modified by (138), with other minor modifications which are described. The mixture of bone powder and extraction buffer (0.5M EDTA pH8, 1 M Tris-HCl, 2% sodium dodecyl sulphate, and 100 µg/mL proteinase K) was briefly vortexed and incubated for 24 hours at 37°C, with gentle mixing in an Eppendorf ThermoMixer®. After incubation, samples were spun at 10,000 rpm for 10 minutes and the supernatant was removed. Fresh extraction buffer was added to the bone pellets and these were re-suspended by brief vortexing and subsequently incubated for a further 24 hours in the conditions described above. 24 hour incubations were normally done 2 times for 100-120 mg or of 3 times for ≥150mg of bone powder. A Tris-EDTA wash was performed by transferring 1 mL of supernatant to Amicon® Ultra 4 mL filter (Merck Millipore) and adding 3 mL of 1X Tris-EDTA. Each sample was then centrifuged at 2500 rpm until the final volume was reduced to 100µl. The final step of DNA purification was carried out using the “QIAQuick minElute purification kit” (Qiagen) and eluted in 40 µL of EB buffer + Tween® 20 (Sigma-Aldrich). Extraction controls were always included and sequenced for contamination control.

UDG-treatment

Following extraction, each 16.25 µl of purified DNA was used for treatment with 5 µl (1U/1uL) USER™ enzyme (New England BioLabs®, Inc.) and incubated for 3 hours at 37°C followed by immediate freezing or a Blunt End Repair step as described in (103). All samples processed at Trinity College Dublin were USER-treated with the exception of Bub1.

Library Preparation

DNA libraries were prepared using 16.25 µL of purified DNA by following the Meyer and Kircher’s protocol for Illumina® sequencing (139) with some reagents substitutions and slight modifications which included the substitution of Solid Phase Reversible Immobilization (SPRI) purification with the Qiagen

MinElute Purification, and the modification of adding a heat-inactivation of *Bst* polymerase (20 minutes at 80°C) instead of another purification step as described in (136). Indexing PCR was performed on a total volume of 25 µL which contained 20.5 µL of AccuPrime Pfx Polymerase (Invitrogen®), 0.5 µL of 10 µM Primer IS4, 1 µL of 5 µM indexing adapter (to allow multiplexing) and 3 µL of DNA library. PCR reactions were done in a designated separate room, specifically and exclusively for ancient DNA, with the following reaction conditions: 95°C for 5 minutes, followed by 10-13 cycles of 95°C for 15 seconds, 60°C for 30 seconds, 68°C for 30 seconds; and 68°C at 5 minutes. PCR products were purified using Qiagen MinElute purification spin columns and eluted in 8-10 µL of EB buffer. Library and PCR controls were always included for contamination control.

Screening of ancient DNA libraries

Ancient DNA libraries were quantified either by using the Agilent 2100 Bioanalyzer High Sensitivity DNA kit or the Agilent TapeStation 2200 D1000 kit. Samples were pooled in equimolar concentrations and the pool was quantified again using the same methods plus a Qubit™ dsDNA HS Assay kit (Invitrogen™). Screening for endogenous DNA content was done by 50 bp single-end sequencing (run for 65 cycles) on an Illumina Miseq at TrinSeq, the Trinity Genome Sequencing Laboratory, located in the Institute of Molecular Medicine (IMM). A PhiX genome library (1% concentration) was added as a sequencing control for each run. Controls from all the steps mentioned above were also sequenced for contamination control purposes.

Johannes Gutenberg-University Mainz

Sample preparation including documentation, drilling and milling of samples Ch22 and Th7 was conducted in dedicated ancient DNA facilities of Johannes Gutenberg-University Mainz under strict rules for contamination prevention as described in (140). Sample preparation, DNA extraction and library preparation was performed as described for sample CTC in (141) with slight modifications given below and as specified in Table S4.

Sample Ch22

For sample Ch22, modifications include washing steps of the bone powder with EDTA, transformation of two independent extracts into five sequencing libraries, four including USER-treatment. Each of these five libraries was amplified three times whereby double indexing was performed according to (142) using the index sequences given therein and from Illumina's NexteraXT Kit v2. The library from the non-USER-treated DNA extract was sequenced on a Miseq, 50 bp single end at StarSEQ GmbH (Mainz, Germany) to determine endogenous DNA content and damage patterns prior to deeper sequencing.

Sample Th7

For sample Th7, modifications include washing or pre-lysis steps of four independent DNA extracts with either EDTA or full extraction buffer, four independent DNA extractions of which six sequencing libraries were created, four including USER-treatment. Each of these six libraries were amplified three times whereby double indexing was performed according to Kircher et al. 2012 using the index sequences given therein and from Illumina's NexteraXT Kit v2. One library from non-USER-treated DNA extract was sequenced on a Miseq, 50 bp single end at StarSEQ GmbH (Mainz, Germany) to determine endogenous DNA content and damage patterns prior to deeper sequencing. Prior to sequencing, all libraries were purified using either Stratec MSB® Spin PCRapace kit (Stratec Biomedical AG) or Agencourt®

AMPure® XP beads (Beckmann Coulter) whereby all three amplifications per library were eluted together in 12 µl of EB. The resulting pools were quantified with both, Qubit™ Fluorometric quantitation (dsDNA HS assay, Invitrogen™) and Agilent 2100 Bioanalyzer (HS, Agilent Technologies) and re-purified with beads in case of visible primer dimers in the Bioanalyzer measurement. Blank controls were carried along both, DNA extractions and library preparations and were always quantified with Qubit™ and at random with Bioanalyzer and sequenced on a Miseq at StarSEQ GmbH (Mainz, Germany), never showing any appreciable sign of contamination.

Genome sequencing

All libraries were sequenced (100 bp SE) on either an Illumina Hiseq 2000 or 2500 at Macrogen, Inc (1002, 254 Beotkkot-ro, Geumcheon-gu, Seoul, 153-781, Republic of Korea).

Sequencing strategy

Our ancient dataset comprised of samples that ranged from 0.1 to 62% endogenous DNA content (Table S1), with ~39% of samples being below 10%. Both mitochondrial (3, 143, 144) and autosomal (10, 145) markers give estimates for the divergence of *Bos taurus* and *Bos indicus* in the order of ~200,000 years ago. This divergence facilitates informative SNP sampling by shotgun sequencing and therefore we chose to include poorly preserved samples in our sequencing. This increased our dataset significantly.

Mitochondrial capture

Given that mitochondrial genome coverages retrieved from whole genome shotgun sequencing were sometimes too low for robust phylogenetic placement, some samples have been subsequently captured in order to increase mtDNA coverage (Table S3). Mitochondrial capture involved indexing PCR prior to pooling; and enrichment was performed using a commercial custom design RNA capture (MYcroarray, 5692 Plymouth Road, Ann Arbor, MI 48105) and used as per manufacturer's instructions. The capture design included a large number of diverse domesticated mtDNAs as described in (146). A final PCR amplification step followed the enrichment with 16 cycles. Captured mitochondrial sequences were then sequenced on an Illumina® MiSeq at TrinSeq (50 cycles SE run for 65 cycles), the Trinity Genome Sequencing Laboratory, located in the Institute of Molecular Medicine (IMM).

Radiocarbon Dating

Samples that were key to our analyses and dataset were radiocarbon dated by sampling of approximately 2.0g of fresh bone. Radiocarbon dating was done at Beta Analytic (<http://www.radiocarbon.com/>), at 14CHRONO at Queen's University Belfast (<http://www.chrono.qub.ac.uk/>) or at Klaus Tschira Archaeometry Centre at Heidelberg University (based in Mannheim, http://www.cez-archaeometrie.de/?page_id=226). Conventional radiocarbon dates, calibrated dates and curves produced by OxCal v.4.3.2 and IntCal13 atmospheric curve (147, 148) are shown in Fig. S6.

Genome data processing

Quality control of NGS data

All raw fastq files were put through FastQC (v. 0.10.1) (149) for quality control of high throughput sequencing data obtained from both Illumina Miseq and Hiseq sequencing platforms.

Alignment of Ancient Specimen NGS reads to cattle reference genome

All raw reads were processed through a standardized pipeline adapted for all ancient samples. Adapters were removed using cutadapt (v. 1.1) (150) (-a AGATCGGAAGAGCACACGTCTGAACTCCAGTCAC option) and with a minimum overlap length of 1 bp between read and the adapter sequence, reducing the number of bases that are trimmed only due to short random adapter matches (-o 1 option); and reads shorter than 30 base pairs in length were discarded (-m 30 option). Samples were aligned to the BosTau6 reference genome (UCSC UMD3.1) with the addition of the Y chromosome from BosTau7 and the mitochondrial reference sequence (GenBank Acc.No. V00654.1). Alignments were performed using the Burrows-Wheeler Alignment Tool (v. BWA 0.7.5a-r405) (151) with the sub-command aln, with seeding disabled -l 1024, and the sub-command samse with the option -r for defining read groups and to produce unfiltered SAM files, which were subsequently converted to BAM files using the command *samtools view -Sb*. BAM files were also sorted using SAMtools (v. 0.1.19) (152) and subsequently filtered for removal of PCR duplicates (rmdup -s). BAM files were merged using picard-tools (v.1.129) and indel realignment was performed using the Genome Analysis ToolKit (GATK; v. 3.3-0-g37228af) (153). For samples Th7 and Ch22, duplicates were removed using picard-tools (v. 1.128) (MarkDuplicates REMOVE_DUPLICATES=true) prior to Indel Realignment. Samples were filtered using SAMtools for removal of unaligned reads (view -F4) and for mapping quality of Q25 (view -q25). To further minimize the effect of deamination in analyses, which was still present after USER treatment, soft clipping was performed for 6 base pairs at the ends of reads for USER treated samples and 8 base pairs at the ends of reads for Non-USER samples and for all libraries of samples Ch22 and Th7. Quality control of alignment sequencing data and coverage statistics were calculated using Qualimap (v. 2.2), and are described in Table S1 (154).

Alignment of Ancient specimen NGS reads to Water Buffalo genome

Fastq reads, post adapter trimmed, were aligned to the Water Buffalo (*Bubalus bubalis*) reference genome (UOA_WB_1). Alignments were performed using the Burrows-Wheeler Alignment Tool (v. BWA 0.7.5a-r405) (151) utilising the sub-command aln with the seed disabled (-l 1024), the edit distance set to 0.01 to allow for more substitutions (-n 0.01) and the number of gaps allowed increased to 2 (-o 2). The BWA sub command samse was run with the option -r for defining read groups and to produce unfiltered SAM files, which were subsequently converted to BAM files using the command *samtools view -Sb*. BAM files were also sorted using SAMtools (v. 0.1.19) (152) and subsequently filtered for removal of PCR duplicates (rmdup -s). BAM files were merged using picard-tools (v.1.129). BAM files were filtered using SAMtools for removal of unaligned reads (view -F4) and for mapping quality of Q25 (view -q25). To further minimize the effect of deamination in analyses, which was still present after USER treatment, soft clipping

was performed for 6 base pairs at the ends of reads for USER treated samples and 8 base pairs at the ends of reads for Non-USER samples.

Alignment of Modern specimen NGS reads to Water Buffalo genome

Paired-end alignment for Gaur and Tharaparkar was performed using BWA mem (0.7.5), followed by fixmate using SAMtools (v 1.4) (152) indel realignment performed using the Genome Analysis ToolKit (GATK; v. 3.3) (153), duplicate removal using picard tools (v. 1.129) (MarkDuplicates) and mapping quality of Q25 with SAMtools (v 1.4) (152) (view -q25).

Mitochondrial alignment

Adapters were removed using cutadapt (v. 1.1) (150) with a minimum overlap length of 1 bp between read and the adapter sequence, reducing the number of bases that are trimmed only due to short random adapter matches (-o 1 option); and reads shorter than 30 base pairs in length were discarded (-m 30 option). Reads were aligned using BWA (v. 0.7.5a-r405) (151) to the *Bos taurus* mitochondrial reference genome (V00654.1) (155). To improve alignment to the circularised genome 30bp of sequence from the end of the mtDNA was attached to the beginning. Reads were subsequently filtered for PCR duplicates and a mapping quality of 30 using SAMtools (v. 0.1.19) (152). Additionally reads were filtered for uniqueness (XT flag) and the removal of suboptimal hits (X1). mtDNA coverages were calculated by Qualimap (154).

Modern cattle SNP Dataset curation (770K)

The Illumina 770K SNP chip dataset comprised a mix of in-house genotyping and the WIDDE dataset (Table S5) (156). SNP data recovered from the WIDDE database was flipped to forward strand orientation and merged with the TCD dataset using PLINK 1.07 (157). The merged TCD+WIDDE dataset was filtered by: including only autosomal sites, excluding A/T and G/C SNPs, excluding sites with less than 90% genotyping rate and excluding previously problematic SNPs. Individuals with more than 10% missingness were also excluded. The final dataset comprised a total of 665,252 SNPs, from 824 individuals from 45 cattle breeds and two outgroup *Bos* species: Yak (*Bos grunniens*) and Gaur (*Bos gaurus*).

Modern cattle SNP position set (1000 bulls)

Ancient genome comparisons for f_4 statistics were carried out using a predefined set of SNP positions. These were defined using a filtered dataset of variant calls generated from Run6 of the 1K Bull imputation run (<http://www.1000bullgenomes.com/>) which were further filtered using PLINK (v. 1.9) (157) for autosomal biallelic sites with a posterior probability of 0.99, removal of individuals with a missingness greater than 10%, removal of one animal from a pair with a relatedness greater than 0.3 Pihat and a maximum number of individuals per breed of 10. Sites with a genotyping rate less than 99% and a minor

allele frequency less than 1% were then removed. After filtering the position catalogue comprised 13,452,190 SNPs. The modern animal dataset used here comprised only individual genomes which are publicly available or which were sequenced in this study. Table S6 summarizes the information for these individuals.

Ancient DNA damage patterns

To authenticate ancient DNA sequences based on typical ancient DNA damage patterns mapDamage2 was used (158) and results are shown in Fig. S7-9.

Population Genomics analyses

Procrustes Projection Principal Components Analysis

We use LASER (v. 2.4) to perform procrustes projection PCA (159, 160). The 770K Bovine reference dataset was formatted to the LASER input format and the LASER pipeline for producing a procrustes projection PCA was followed. Pileup files were generated for each individual ancient sample, using SAMtools mpileup with a minimum mapping quality of 30 (-q30), a minimum base quality of 20 (-Q20) and with the base alignment quality computation probabilistic realignment disabled (-B). Input files for LASER were then generated using the pileup2seq.py python script (available with the software package). LASER was run with the final SNP dataset of 665,252 SNPs and 825 modern individuals. The 67 ancient individuals were projected onto the modern reference and LASER was run 100 times with the parameter REPS (-r) in order to provide account for variance between individual runs. The plotted values were the mean coordinates averaged across the multiple runs. PCA plots were produced using the ggplot2 package in R (161) (Fig. S10 and S11)

SNP calling

Autosome only SNPs were called on filtered BAM files using the Genome Analysis ToolKit (GATK) Pileup (153). Ancient genomes were pseudo-diploidized and pileup files were converted to PLINK format using an in-house script (available at: <https://github.com/teasdalm/pileupTools>) that converts to ped format by calling consensus calls (randomly picking a base in case of a tie), filters for minimum base quality score of 30 and excludes tri-allelic SNPs. PLINK format files for ancient samples and the modern dataset were merged with PLINK. This method was used to compute input for the f_4 -ratio estimation, ADMIXTURE, and qpGraph calculations.

ABBA-BABA test (D statistics)

Patterson's D -statistic compares four genomes, where a test population's relative genetic closeness is compared to two other reference populations (162). If no gene flow has happened then we would expect the D -statistic to be zero (Null hypothesis). In the case of gene flow, a deviation from zero is observed where a higher number of derived alleles (B) are shared between one of the reference populations and test, producing either ABBA or BABA trees. Standard error is obtained by a block JackKnife approach and Z-scores giving statistical significance, typically if $|Z| > 3$ (163, 164).

Formally testing zebu introgression using whole genome D-statistics

D statistics (165) provide a test for ancient admixture that remains sensitive under alternative demographic scenarios (166). We used ANGSD -doAbbababa 1 on whole genome data from the autosomes to test for zebu (*Bos indicus*) admixture (167). This allowed us to use all available genomic data, especially for low coverage samples, instead of being restricted to previously-ascertained sites. ANGSD samples a randomly chosen single base at each position of the genome (167), decreasing the potential effect of reference bias.

We computed D statistics with a filtering of minimum base quality 20 (-minQ 20), minimum mapping quality 25 (-minMapQ 25) and -rmTrans 1 to remove transitions.

The test $D(((\text{Sub1}, \text{Test}), \text{Bos indicus}), \text{Gaur})$ was repeated using different *Bos indicus* individuals: Nelore, Tharparkar, Gir, Haryana and Sahiwal. Sub1 was used as a representative non-admixed individual (previously tested) and Test represents every ancient individual in turn. The median D statistics obtained from using these five alternate modern *Bos indicus* genomes were taken for each test individual with the corresponding SE. The D -statistic was considered significant if all Z scores were above 3 and non significant if at least one Z score was below 3. Tests where the total number of ABBA+BABA sites were below 200 were excluded from plotting and these comprised: Abu1, Abu2, Dan1, Gil1, Nah1, Pro1, Sar38. Results are shown in Table S7.

Formally testing aurochs introgression using whole genome D -statistics

We also used the ABBA-BABA test to interrogate clade integrity of ancient population pairs and testing aurochs introgression on whole genome data from the autosomes. The $D(\text{gaur}, \text{aurochs}; \text{ancient group1}, \text{ancient group2})$ was computed by ANGSD where ancient group is each Near Eastern population in turn (Table S8), aurochs is each *Bos primigenius* sample in turn and Gaur (*Bos gaurus*) as the outgroup. ANGSD was run with the multipopulation option -doAbbababa2 1 (167, 168), with a filtering of minimum base quality 20 (-minQ 20), minimum mapping quality 25 (-minMapQ 25) and -rmTrans 1 to remove transitions. Results are shown in Table S9. The Abbababa2 is an improved D -statistic that has been demonstrated to be suitable for low and variable coverage data, using all the available bases (168).

f_4 -ratio estimation

f_4 -ratio estimation of individual genome components resulting from *Bos indicus* ancestry was done using the AdmixTools package and the qpF4ratio program for ancient individuals using the test $f_4(\text{Gaur}, \text{Bos indicus-Haryana}; \text{Test}, \text{Sub1})/(\text{Gaur}, \text{Bos indicus-Haryana}; \text{Bos indicus-Sahiwal}, \text{Sub1})$ (162, 163). SNP positions called were as detailed above, using the 1K Bulls SNP dataset. In order to remove any bias caused by deamination we also removed transitions from our f_4 -ratio estimation. Results are shown in Table S2 and plotted in Fig. S12.

Ancestry estimation with model-based clustering -ADMIXTURE

We used the 770K Bovine SNP data to estimate individual ancestries using ADMIXTURE (v. 1.23) (169). A missingness filter was applied for ≥ 0.05 using PLINK (157) leaving 413,809 variants from a total of 665,252 SNPs. In order to account for linkage disequilibrium (LD) the dataset was pruned in PLINK (v. 1.90b2m) (157) with the command --indep-pairwise 50 5 0.5 to account for linkage disequilibrium between markers, leaving a total of 178,059 variants. Admixture was run for $K=3$ as it is the common practice for cattle to distinguish between Indicine, African *Bos taurus* and European *Bos taurus* clusters (6, 23). We grouped samples into below 1x coverage and above 1x coverage. Samples with mean coverage above 1x were merged and run together with the modern dataset. For samples with mean coverage lower than 1x, ADMIXTURE was run individually for each sample, together with the modern dataset. In all

cases, 40 ADMIXTURE replicates were performed with different random seeds each time, the replicate with the highest log likelihood was used for plotting (Fig. S1).

Mitochondria analyses

For samples with $90\% \leq$ of the mtDNA genome covered at $3x \leq$, pileup files were produced by GATK (v. 3.3-0-g37228af) (153) using the mpileup option with default settings. The resulting files were filtered using a custom script for a minimum base quality of 20, a minimum depth of coverage of $3x$, and calling the consensus allele. Where necessary ties were symbolised by the character N and checked by eye. All generated fasta files were visually inspected against visualized BAM files, and where necessary altered using SEAVIEW (170).

Multiple sequence alignment of the fasta files was performed using the MUSCLE algorithm in SEAVIEW (170). In addition to the samples sequences, previously published sequences of known haplogroups were added into the multiple alignment.

The Multiple Sequence Alignment file was uploaded onto the PhyML 3.0 online execution platform (171) and maximum likelihood trees drawn using the following options:

- Automatic substitution model selection using the AIC (Akaike Information Criterion) (172). The model selected was the GTR substitution model with a gamma-distributed rate of variation among sites (+G) (ie. GTR +G model).
- Starting tree with BioNJ, using NNI for tree topology search.
- Branch support was calculated by 100 bootstrap replications.

The tree was then visualized and altered using FigTree (173).

For samples with $> 90\%$ of the mtDNA genome covered at $3x \leq$, filtered BAM files were visually inspected for previously published haplogroup defining SNPs (174–176). See Table S3 for haplogroup assignments.

The maximum likelihood tree places the aurochs that do not originate from the Near East (CPC98, Gyu2, Th7) as outgroups to domestic cattle haplogroups, in line with previous publications (3, 177–179). Additionally, the haplogroup assignment of R for the Moroccan aurochs, Th7, sheds light on the origin of the rare R haplogroup; previously attributed to a local aurochs domestication in Italy (180). In contrast the aurochs from the greater Near East belong to haplogroups associated with domestic animals (Fig S4 and Table S3). The majority of the domestic ancient samples cluster in groups equivalent to the modern taurine haplogroups of Q, T1, T2 & T3. While T3 predominates in modern European cattle, the ancient mitogenomes show somewhat greater diversity of haplogroup assignment, previously identified in the Near East and Balkans regions by studies of modern and ancient partial mitogenomes (3, 5). Intriguingly, the T1 haplogroup, which is associated with modern African cattle or cattle of African origin, is identified in samples from the Levant (10 out of 21 samples) (Fig S4 and Table S3). While many of these sample are low coverage, the proliferation of T1 (or likely T1) is not present in any other geographical areas studied here. Only two samples assigned domestic status belong to non-aurine domestic mtDNA haplogroups. Kok1 an Iron Age sample from Uzbekistan belongs to haplogroup P which is associated with wild European aurochs (177, 178), while the Iranian sample Kho1 is the only ancient sample to belong to an indicine haplogroup.

Admixture Graph construction

To better elucidate the population history of the aurochsen populations and taurine and zebu cattle, admixture graphs were fitted using *qpGraph* v.6450 included in the ADMIXTOOLS package (181) which uses *f*-statistics based on allele frequency correlations between samples to assess whether a fitted admixture graph of population history is consistent with the data. *qpGraph* was run using default settings with a *Z* score=3 as a cutoff for outlier *f*-statistics. The option “useallsnps” was set to YES because of the low coverage of some of the samples which precluded consideration of a shared set of SNPs across the whole dataset. Only transversions were used in this analysis. We focused our attention on reconstructing the relationships between the aurochsen populations, *Bos indicus* and ancient taurine cattle groups. For each we used higher genome coverage individuals as single representatives where available and joined genomes as populations for lower coverage groups (table S10). Gaur (*Bos gaurus*) was used as an outgroup and fits in the graph as suggested by previous analyses.

To construct an initial framework of *Bos*, we constructed a graph include Near East aurochsen (Gyu2) and Neolithic domestic cattle (Sub1), *Bos indicus*-admixed Iraqi cattle (Bes2), and modern *Bos indicus* (Fig. S2A). This graph fit with no *f*₄ outliers and placed indicine cattle as an outgroup to all other genomes, but with some contributions from taurine populations (see below). Neolithic Anatolian cattle (Sub1) were modeled as a sister clade to Armenian auroch (Gyu2). To this, we fit Th7 as sister lineage to Gyu2, with some gene flow between the aurochsen genomes resulting in the population ancestral to Neolithic cattle (Figure S2B). In addition, Neolithic Levantine cattle were modelled as a mixture between the Moroccan aurochsen and taurine domestic lineages. This graph fit with no *f*₄ outliers. The next graph iteration (Figure S2C) included the British auroch CPC98, which we fit with three *f*₄ outliers as an outgroup to all non-indicine genomes. The largest of these *f*₄ outliers was (Sub1, Neolithic Levant; Bes2, CPC98) with *Z* = -3.09, suggesting unresolved affinity between Sub1 and Bes2 or Neolithic Levant and CPC98; the two remaining outliers also suggested additional affinity between Neolithic Levantine cattle and European aurochsen as represented by CPC98. Gene flow between the CPC98 and Sub2 ancestral populations suggests a complex population structure within *Bos primigenius*, which we resolve as admixture events.

In the final graph, we added the Neolithic Balkan cattle and were able to place all individuals in a single graph (Fig. S3) without any *f*₂ outliers but with 11 *F*₄ outliers, with the highest |*Z*score| giving 4.886. The graph suggests a high level of population structure among the aurochs. All auroch samples are not modelled as stemming from a single deme and they do require input from different ancestral populations. The admixed Near Eastern sample (Bes2) requires a majority contribution (68%) from an ancestral *Bos indicus* population in agreement with the results from the *f*₄ analysis (70%, Table S2). The earlier unadmixed Neolithic Anatolian taurine sample (Sub1) contributes to several ancestral taurine populations including those ones in the Levant and Balkans. We also recovered a minor contribution of Sub1 into modern *Bos indicus* (Sahiwal) in agreement with previous studies (182) which most probably represents a secondary admixture event. We also found a contribution from a source resembling the British aurochs (CPC98) into the ancestral *Bos taurus* population in the Balkans. Finally, a source similar to the Moroccan aurochs (Th7) contributed to the ancestral population of the Levantine ancient domestic samples.

Directionality of introgression

In order to test the directionality of introgression within the later ancient Near Eastern cattle we followed a method similar to that in Cahill et al. (2018)(183), presented in Fig S13. In this we survey the two higher coverage ancient Near Eastern admixed genomes (Bes1 and Bes2) in 1 Mb windows calculating *Fst* between these and both modern *Bos taurus* (comprised of three genomes, Highland, Alentejana and Wagyu) and modern *Bos indicus* (Sahiwal, Tharparkar and Hariana). These two tests are plotted along with the equivalent values calculated for the high coverage Ancient Near Eastern *Bos taurus* genome (Sub1). *Fst* was calculated for 3 populations using realSFS from the ANGSD toolkit (v 0.920)(167). A pronounced lower genomewide divergence from *Bos indicus* is visible in the admixed samples compared to the earlier unadmixed genome as expected under our model of zebu introgression into later Near Eastern Cattle.

Reference bias

Reference bias, where allele calls are biased toward the genome used for alignment may be a particular problem for ancient DNA study because of lower genome coverage achieved with short sequence reads (Cahill et al 2018). To test if our results were robust to this we replicated our key analyses following the outgroup approach in the original D-statistic inference of Neanderthal introgression(165). Water buffalo, *Bubalus bubalus*, is a secure outgroup to cattle and other Bovini, is ~4 Myr divergent and is not interfertile with cattle. We realigned our modern and ancient genome data to a recently published high quality *Bubalus* genome(184) using the Burrows-Wheeler Alignment Tool (v. BWA 0.7.5a-r405) (151) utilising the sub-command aln with the seed disabled (-l 1024), the edit distance set to 0.01 to allow for more substitutions (-n 0.01) and the number of gaps allowed increased to 2 (-o 2) and recalculated *D* statistics implying differential aurochs input into ancient populations and those inferring a temporal pattern in *Bos indicus* introgression. Table S11 shows the recalculated aurochs statistics $D(\text{gaur, aurochs; ancient group1, ancient group2})$ computed by ANGSD using the multipopulation option -doAbbababa2 1, where ancient group is each Near Eastern population in turn (Table S8). Importantly, the key finding that ancient Levantine cattle hold significantly less Near Eastern (Armenian) and European (British) aurochs ancestry than the other ancient populations, remains highly significant. Figure S14 shows a plot of recalculated zebu introgression D-statistic tests using BAM files aligned to water buffalo. The test $D(\text{Sub1, Test, Tharparkar, Gaur})$ was run ANGSD -doAbbababa 1 on whole genome data from the autosomes to test for zebu (*Bos indicus*) admixture. *D* statistics Vs Years BP are plotted and the core finding of a sharp increase in *Bos indicus* genetic influx beginning ~4,000 BP remains.

Testing of clade integrity within the Near East

The results in table S9, displayed in Fig 3 invite a further test of whether ancient domestic populations form a true clade with the Near Eastern aurochs, Gyu2. The test $D(\text{gaur, aurochs; ancient group, Gyu2})$ was computed to test for unbalanced allele sharing between each of the domesticated ancient regional groups in a clade with Gyu2 compared to either the British aurochs (CPC) or the Moroccan aurochs (Th7).

We performed this alternately using *Bos taurus* (table S12) and *Bubalus bubalus* (table S13) as reference sequences for aligning sequence reads. Conservatively we only consider statistics which hold as significant under both. The test returned two such combinations indicating imbalance and which replicate the finding of secondary aurochs input. First, the British aurochs shares more alleles with the Balkan Neolithic population than with the Armenian aurochs. This supports the assertion of local introgression into European cattle. Second, the British and Armenian aurochs have an excess sharing of alleles relative to Levantine domesticates which is consistent with a different wild source having had input into the latter group.

Bos indicus admixture and drought adaptation.

Bos indicus cattle and their hybrids are known to show markedly enhanced production in arid and thermally stressed environments compared to *Bos taurus*. This knowledge has been widely and practically applied in animal production. Particularly, it has been implemented in the introduction of *Bos indicus* (e.g. Brahman, Nellore) and hybrids (such as the Droughtmaster breed) in millions during the 20th Century to tropical environments with aridity challenges that preclude the ranching of *Bos taurus*. These introductions cope better with water deprivation, show good reproductive performance in challenging ecological conditions, have heat tolerance and can survive on limited and poor quality food resources (185–191). Examples of successful introduction are semi-arid ranching in Australia (e.g. Northern Queensland)(192, 193) and the north-east of Brazil, where although there is a substantial tropical rainy season, for a substantial portion of each year animals have to survive drought. The results of a premodern dispersal of *Bos indicus* across the Sahel in North Africa are also supportive(194, 195); *Bos indicus* predominate in village conditions in arid regions, whereas native *Bos taurus* breeds are confined to the humid regions in the south. Here one geographical exception is instructive; Kuri *Bos taurus* cattle have persisted in N. Nigeria, Niger and Chad but are here confined to the well-watered environs of the Lake Chad and are surrounded on all sides by zebu populations which can survive on the poorer quality dry grass in semi arid conditions inland (196). An adaptive advantage to hot and dry conditions is assumed in cattle breeding; Davis RJ et al. (section 5.2.2 figure 4) record that average daily water intakes of zebu are less than *Bos taurus*, with hybrids giving intermediate performance(197). Reasons are not clear but include higher surface area to weight ratio, higher tissue conductance capacity, lower sweating rate under hot conditions, higher red blood cell count resulting in lower respiration rate, lower thyroid activity suggesting a lower basal metabolic rate under elevated temperatures.

Supplementary Figures

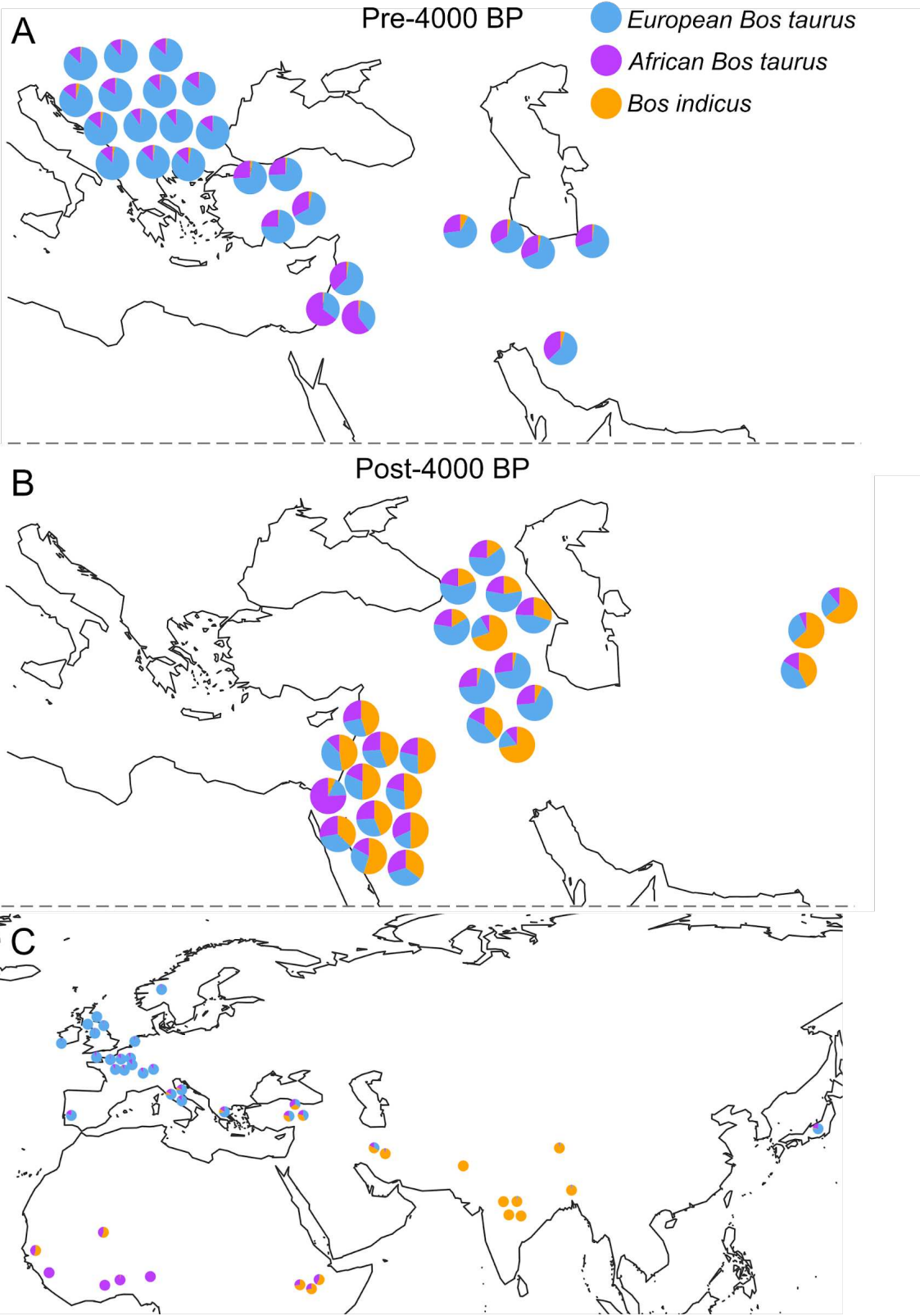


Fig. S1. Model based estimates of ancestral coefficients for (A) pre- and (B) post-4,000 BP ancient domestics. ADMIXTURE analysis based on SNPs from the 770K bovine array. This models three components which distinguish shared ancestry with modern African (purple), European (blue) and indicine (orange) populations. These are geographically distributed among ancients - the indicine component arrives after 4,000 BP and shows a greater concentration in Central Asian and southern Fertile Crescent samples. The European component predominates in early Anatolians, Balkans and North Iran genomes. Notably, the African component predominates in the early southern Levant genomes. Geographical locations are approximate. Samples with less than 1000 SNPs have been excluded. (C) Model based estimates of ancestral coefficients for modern day cattle populations. Modern cattle breeds from the 770K dataset are shown, where each pie chart corresponds to the median value for each component, across a group of individuals belonging to the same breed. Admixture components are represented by colours: European taurine (blue), African taurine (purple), Indicine (orange). Individuals are plotted by approximate geographical location to allow for better display of data.

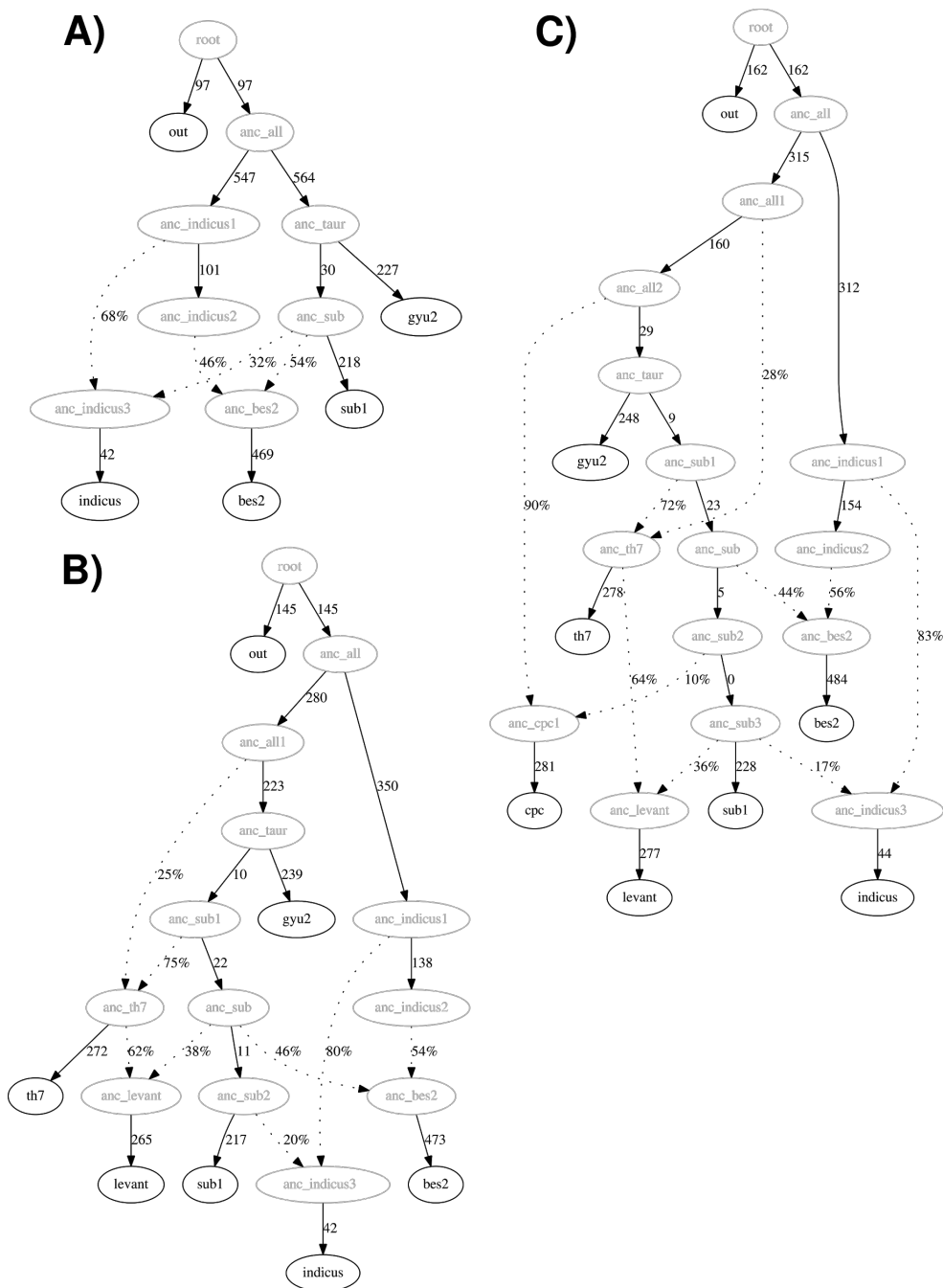


Fig. S2. Iterative building of admixture graphs using Admixtools - qpGraph. Intermediate, theoretical populations are in grey while samples included in the dataset are shown in black. Edge drift values = $F_{st} \times 1000$. Node labels area as follows: out=outgroup (Gaur), gyu2=Armenian aurochs, th7=Moroccan aurochs, cpc=British aurochs, balk=Balkans population, sub1=Anatolia unadmixed, bes2=Near Eastern admixed, indicus=*Bos indicus* (Sahiwal).

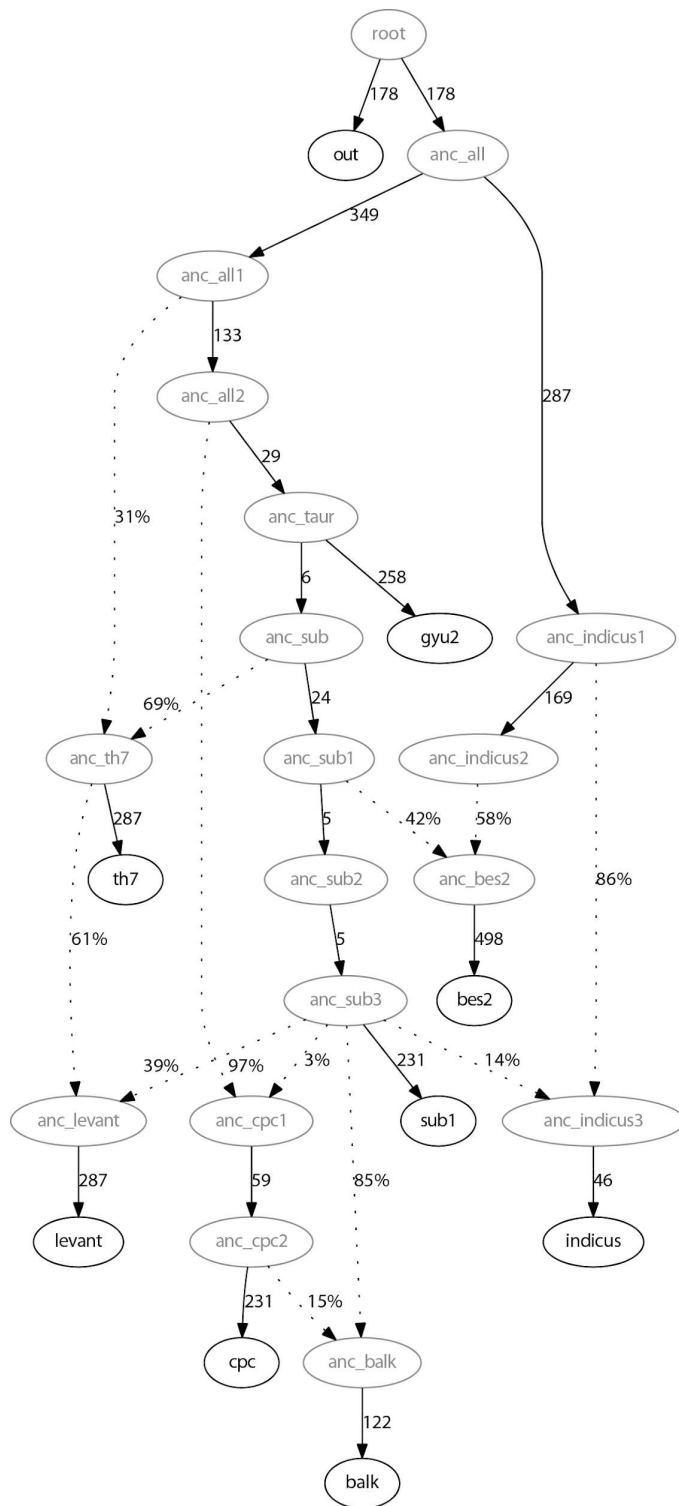


Fig. S3. Final admixture graph model using Admixtools - qpGraph. Intermediate, theoretical populations are denoted in grey while samples included in the dataset are shown in black. Edge drift values = $F_{st} \times 1000$. Node labels area as follows: out=outgroup (Gaur), gyu2=Armenian aurochs, th7=Moroccan aurochs, cpc=British aurochs, balk=Balkans population, sub1=Anatolia unadmixed, bes2=Near Eastern admixed, indicus=*Bos indicus* (Sahiwal).

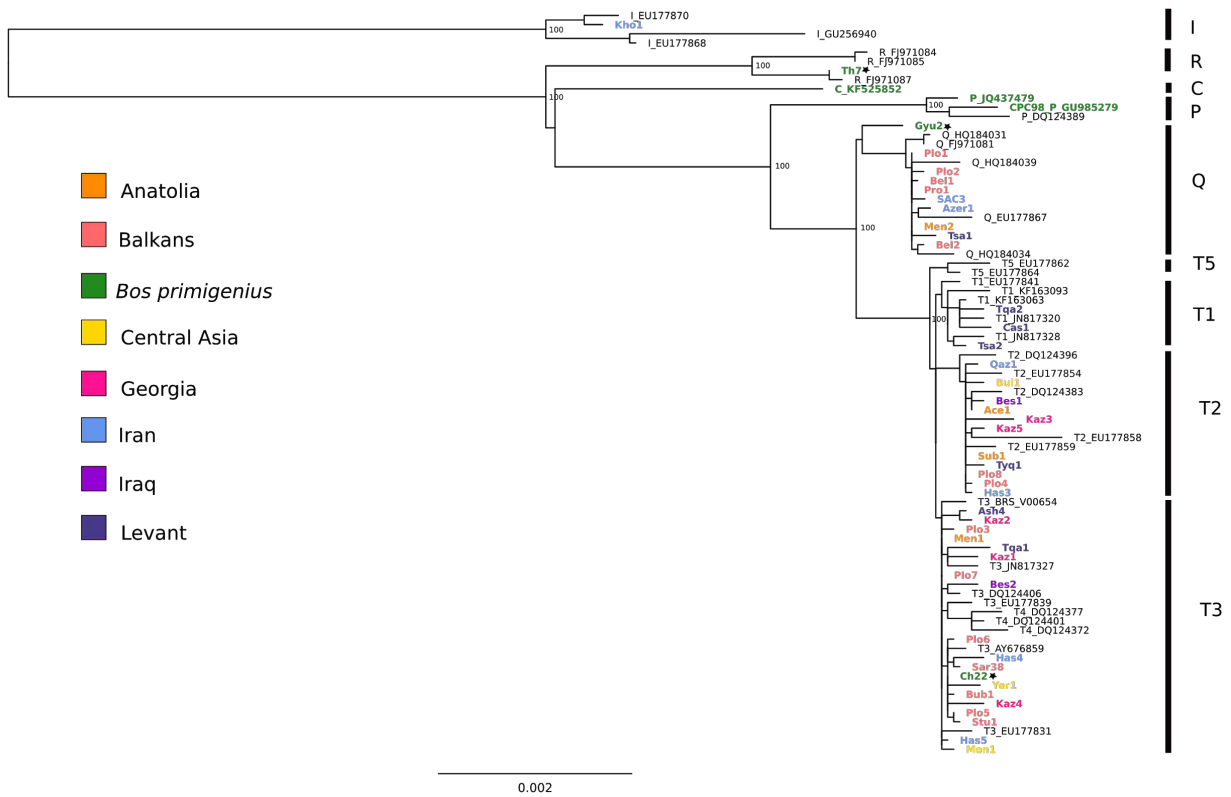


Fig. S4. mtDNA Maximum Likelihood Tree. Ancient domestic samples are coloured by geographical location. *Bos primigenius* samples are coloured in green, aurochs sequenced in this study are marked with a star, three others were published (179, 198, 199). mtDNA haplogroups are labelled on the right hand side. Previously published samples are denoted by haplogroup followed by GenBank ID. Samples were included in this tree if $90\% \leq$ of the mtDNA genome was covered at $3x \leq$. The *Bos primigenius* samples originating from outside the Near East are placed as outgroups to the domestic haplogroup of Q and the macro-haplogroup of T. The only ancient domestic sample that clusters within the indicine variation is the Iranian sample Kho1, from Nishapur Qohandez (Khorasan) in Iran (300 BC-1300 AD).



Fig. S5. Aurochs skull No. 11138 in the Zoological Institute, Russian Academy of Sciences, St Petersburg. Petrous bone sample *Gyu2* was sampled from this specimen. The ruler scale is 40 cm.

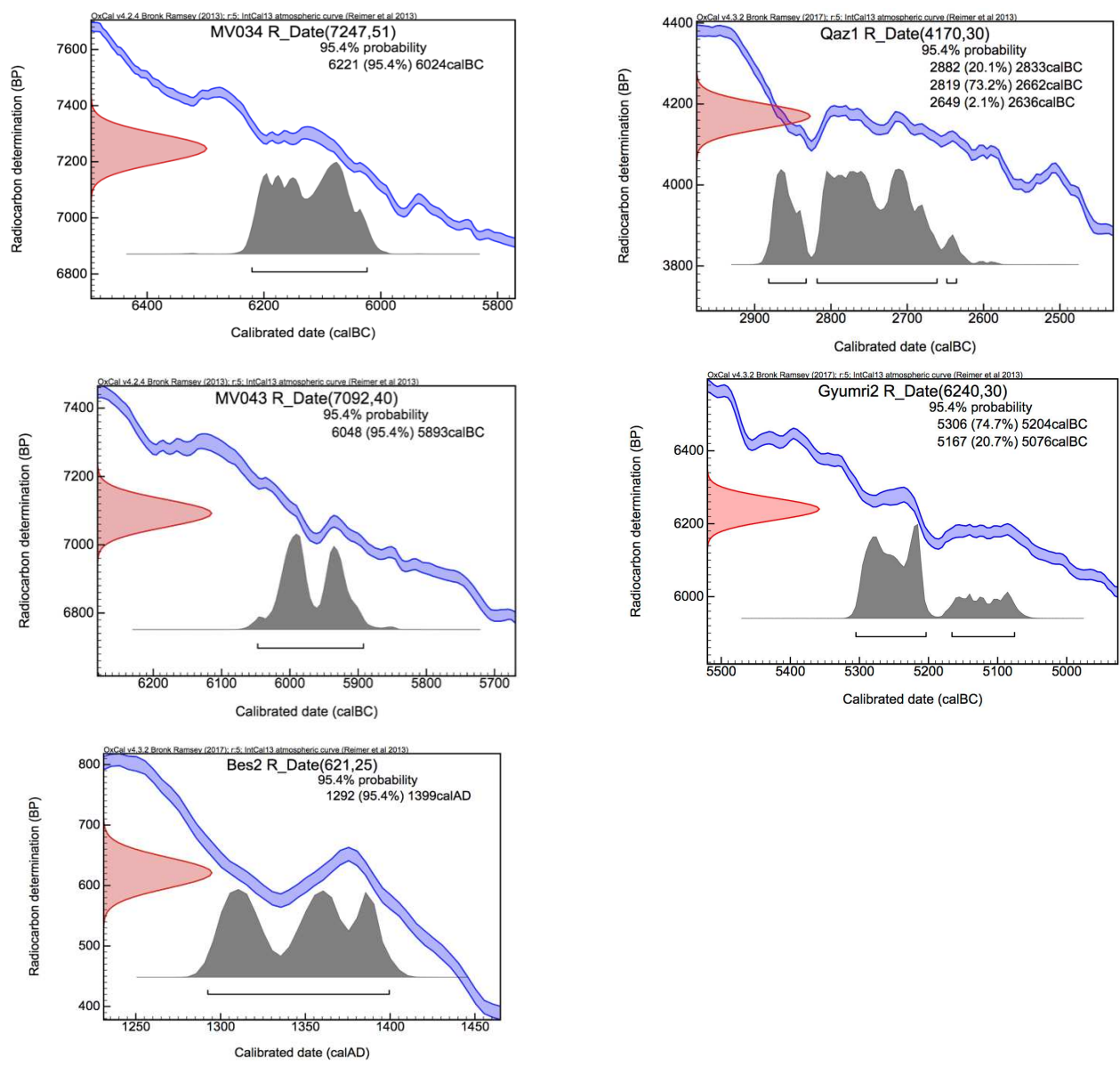


Fig. S6. Radiocarbon calibration curves for samples: Sub1 (MV034), Men2 (MV043), Bes2, Qaz1 and Gyu2 (Gyumri2).

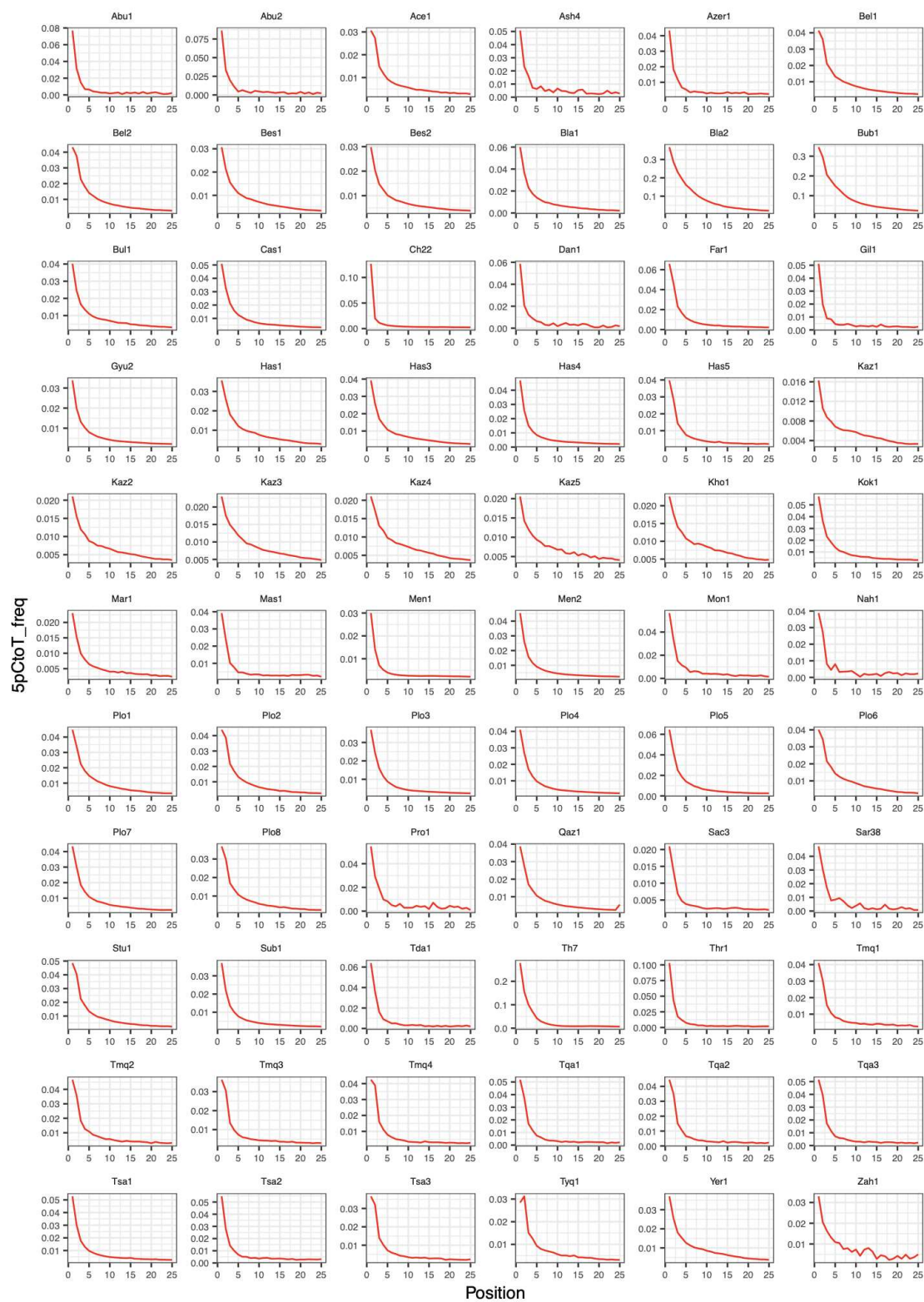


Fig. S7. mapDamage deamination patterns for each ancient individual at the 5' end of reads. Analysis for the UK aurochs CPC98 is not included and is published in Park *et al.* (2015)(6).

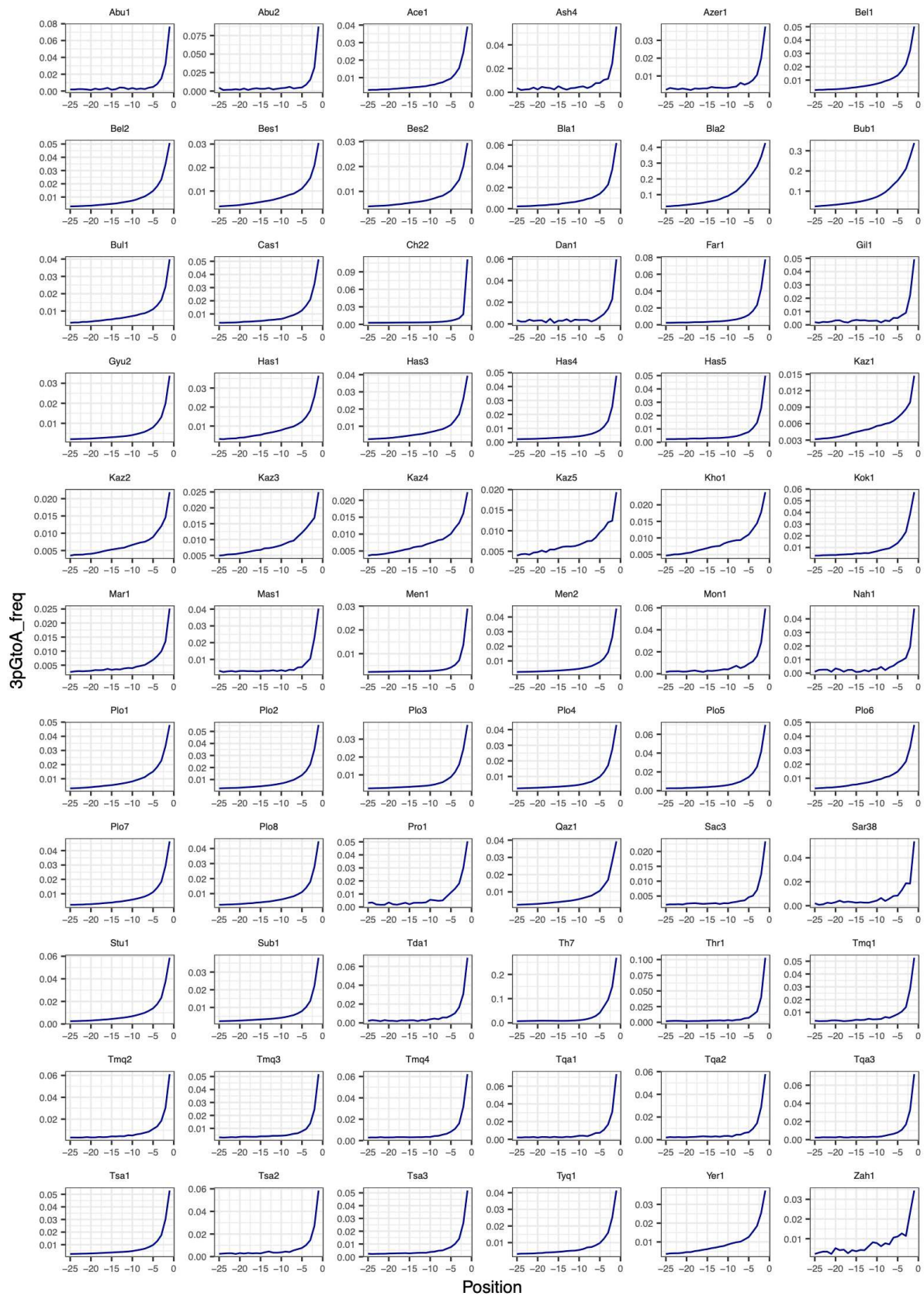


Fig. S8. mapDamage deamination patterns for each ancient individual at the 3' end of reads.



Fig. S9. mapDamage read length distributions for each ancient individual.

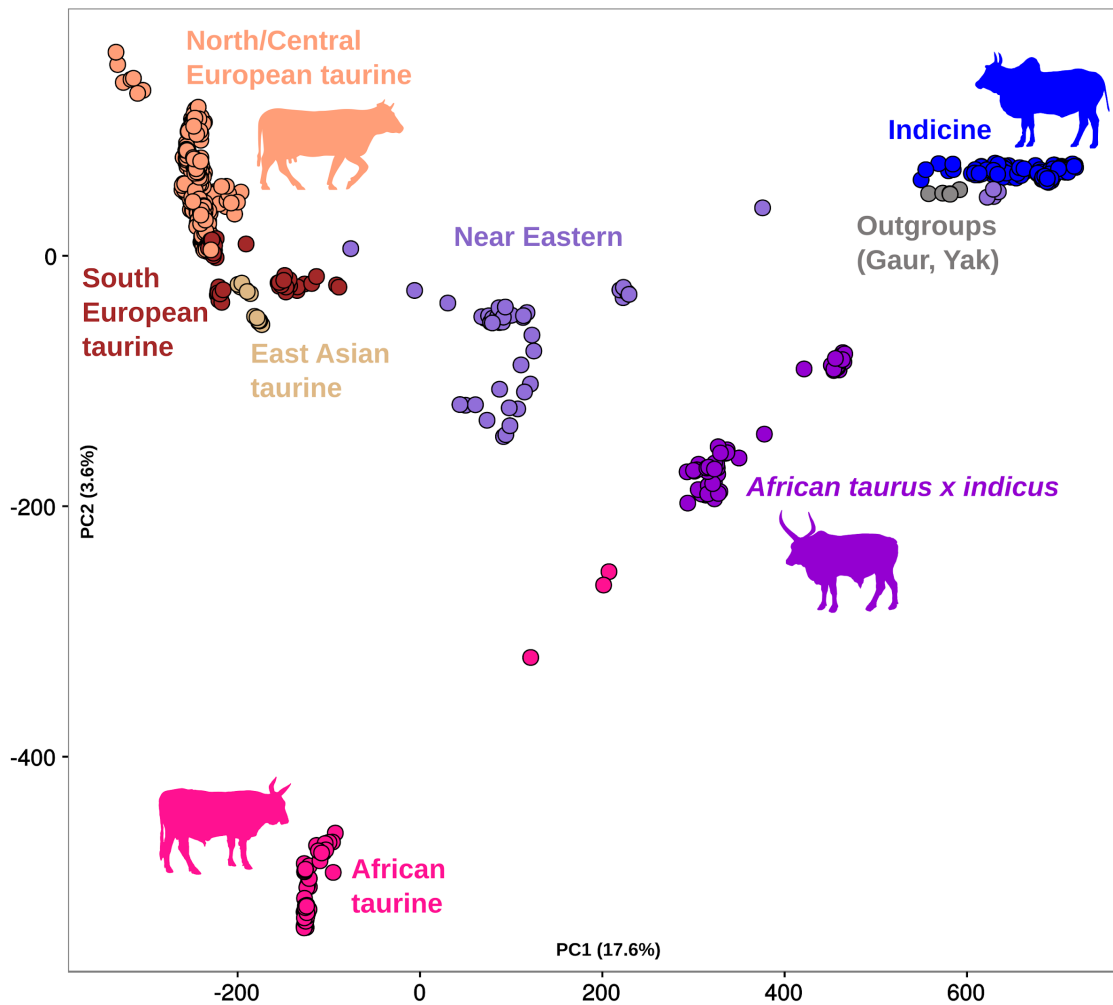


Fig. S10. Principal components analysis on 665,252 SNPs from the Illumina Bovine HD 770K SNP chip dataset on modern individuals only. Taxa or geographical origin are defined by colours.

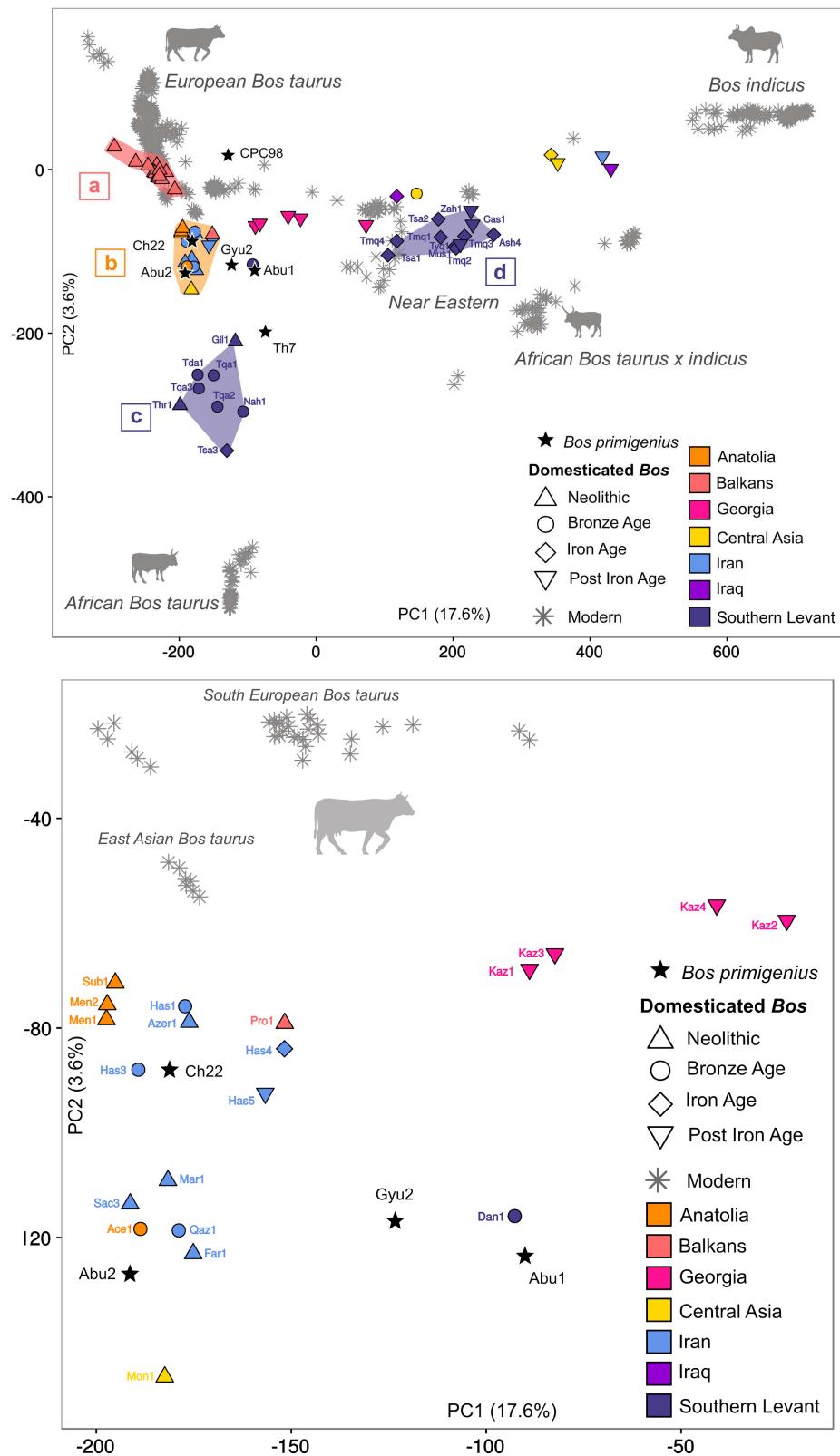


Fig. S11. Projection Procrustes PCA of ancient cattle (full plot and below, zoom). Ancient animals are projected on the modern reference 770K Bovine SNP dataset shown as asterisks. Colours denominate place of origin and symbol the time periods for ancient data. *Bos primigenius* samples are shown as stars.

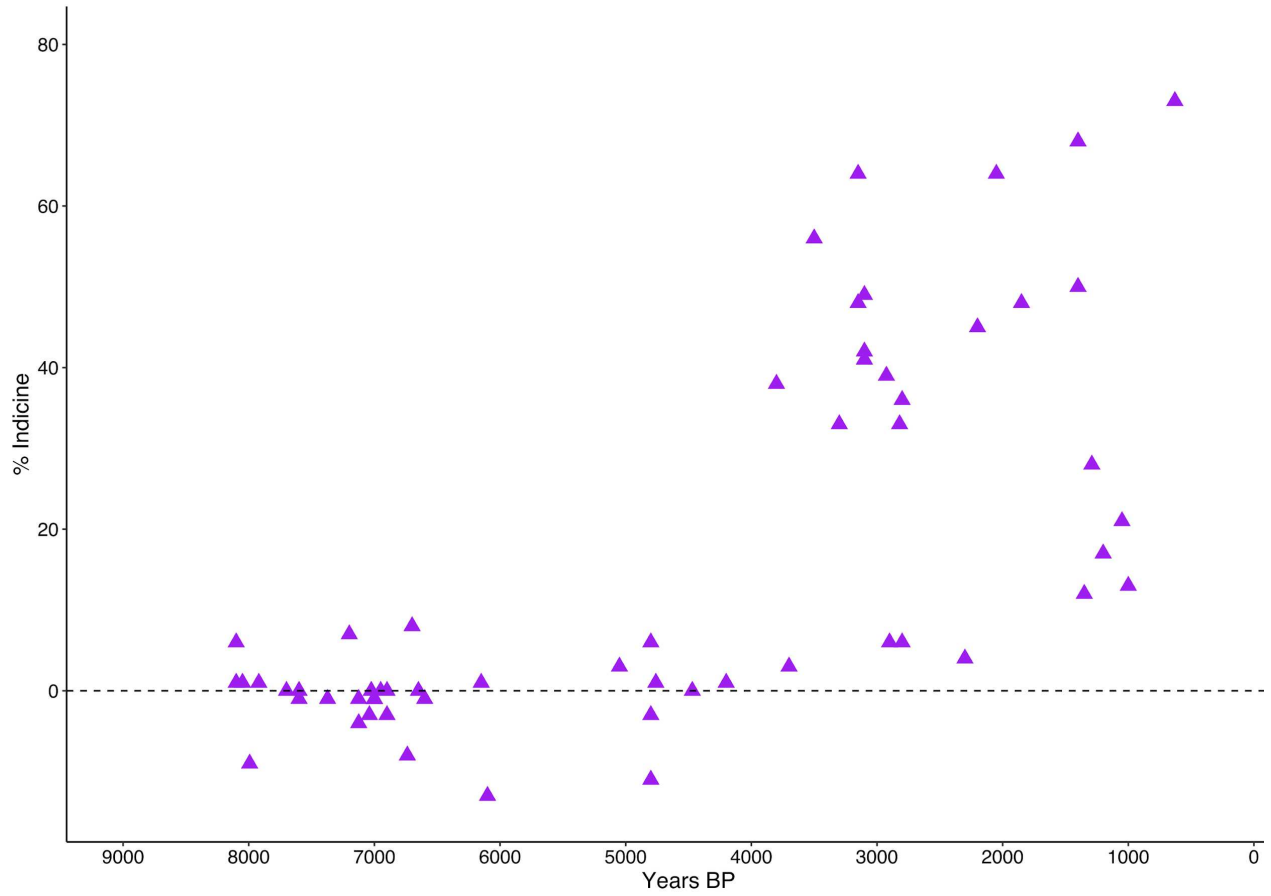


Fig. S12 Plot of *Bos indicus* admixture in Near Eastern cattle through time; data from table S2. These estimates are calculated using the statistic $f_4(\text{Gaur}, \text{Bos indicus-Hariana}; \text{Test}, \text{Sub1}) / (\text{Gaur}, \text{Bos indicus-Hariana}; \text{Bos indicus-Sahiwal}, \text{Sub1})$.

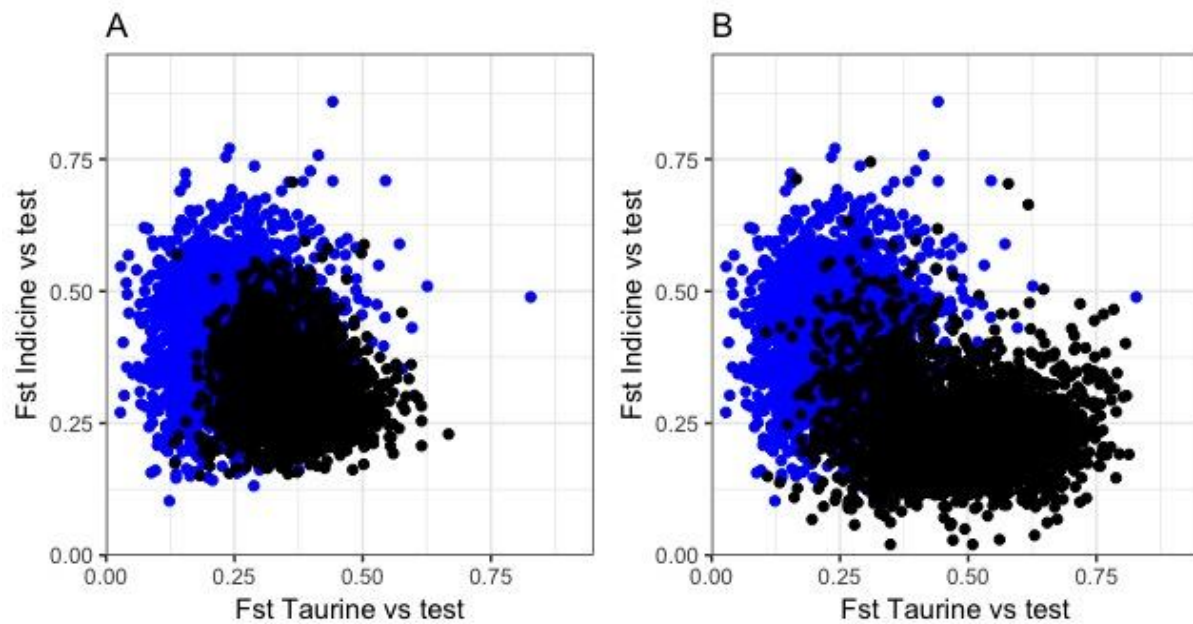


Fig S13. Plot of genome wide 1 Mb sliding windows measuring F_{st} between modern *Bos taurus* and test vs F_{st} between modern *Bos indicus* and test. A) Test represents Sub1 (blue) and Bes1 (black). Sub1 is an unadmixed ancient Anatolian Neolithic *Bos taurus*, while Bes1 is a later Near Eastern ancient admixed individual (f_4 ratio estimate of 36% indicine). B) Test represents again Sub1 (blue) and Bes2 (black), a Near Eastern ancient admixed individual (f_4 ratio estimate of 70% indicine).

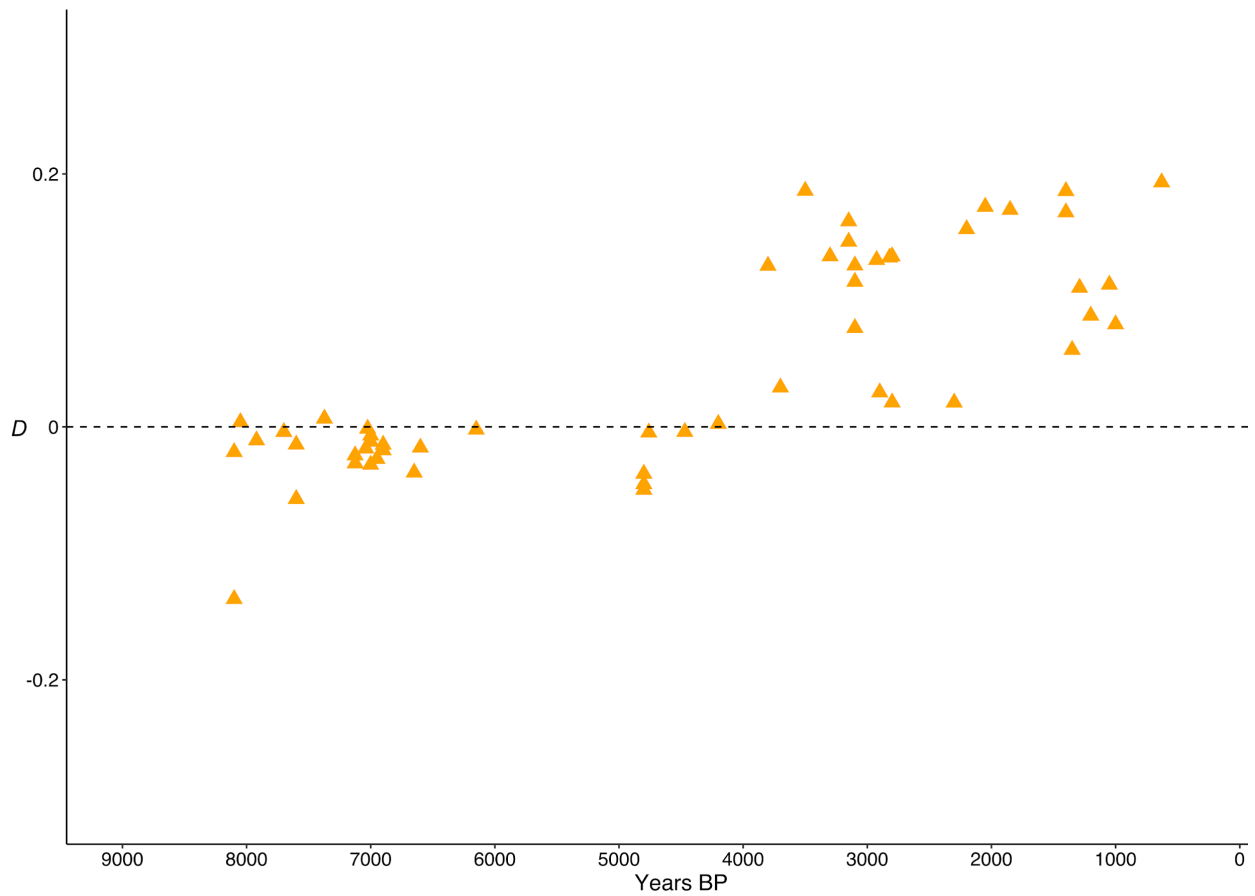


Fig. S14. Plot of D statistic: $D(B. gaurus, Tharparkar B. indicus; Sub1, Test)$ applied to Near Eastern ancient cattle genomes aligned to the water buffalo genome. Positive values are indicative of zebu ancestry and appear, as with the cattle genome-aligned data (Fig. 2), after 4,000 BP in our sample. Calculations were performed using ANGSD and statistics with less than 250 ABBA+BABA sites for analysis were discarded.

Supplementary Tables

Table S1. Table summarizing the Total trimmed reads, mapped reads, mapped after duplicate removal, mapped after Q25 to the *Bos taurus* genome reference (BostTau6), as well as percentage of endogenous DNA for each individual and genome coverage calculated using Qualimap (154) after removal of duplicates and a filtering of minimum mapping quality of 25. Sample CPC98 has previously been published (6) and we use 237M reads giving 3.63X coverage.

ID	# total reads	# mapped reads	#Q25 reads	Coverage Qualimap Q25	%endogenous DNA	USER treated
Abu1	6555630	24576	14998	0.0002	0.2288	Yes
Abu2	14499285	22202	14543	0.0002	0.1003	Yes
Ace1	21951434	10537799	6427935	0.11	29.3	Yes
Ash4	25675479	1379088	577651	0.0096	2.2	Yes
Azer1	20482966	140323	58414	0.0012	0.2852	Yes
Bell1	43031338	17114143	5577498	0.087	13.0	Yes
Bel2	48011799	22211886	8109337	0.13	16.9	Yes
Bes1	428155168	221828481	114960182	2.12	26.9	Yes
Bes2	2440131518	1503284527	673189179	14	27.6	Yes
Bla1	8173395	1979134	1164612	0.0185	14.2	Yes
Bla2	13457520	495338	283923	0.0046	2.1	Yes
Bub1	64755274	43073564	21965306	0.43	33.9	No
Bul1	12997139	5859371	2683077	0.0486	20.6	Yes
Cas1	10139456	6889547	3867269	0.068	38.1	Yes
Ch22	479280742	39424571	15960454	0.3	8.2	Yes
Dan1	22252637	72623	25451	0.0002	0.1144	Yes
Far1	27947179	4195932	1980741	0.03	7.1	Yes
Gil1	50199816	4268555	45085	0.0007	0.0898	Yes
Gyu2	433243538	103784163	98168995	2	22.7	Yes
Has1	47018020	20072551	1902700	0.033	4.0	Yes
Has3	367942264	198402283	71241792	1.2	19.4	Yes
Has4	668888962	279102412	84530672	1.4	12.6	Yes
Has5	16706200	3560738	2098236	0.03	12.6	Yes
Kaz1	228093405	196187349	129742608	3.12	56.9	Yes
Kaz2	26196338	22446389	13253716	0.289	50.6	Yes
Kaz3	35925135	32922054	22366765	0.46	62.3	Yes
Kaz4	40817162	33323516	21521150	0.47	52.7	Yes

Kaz5	3111550	1471698	954553	0.02	30.7	Yes
Kho1	20615027	17727212	10587157	0.2	51.4	Yes
Kok1	10366617	1182517	676894	0.01	6.5	Yes
Mar1	71777368	4547299	1709108	0.0373	2.4	Yes
Mas1	31912430	790056	192398	0.0032	0.6	Yes
Men1	1214058437	314877626	152322795	2.97	12.5	Yes
Men2	816487427	305535871	118879128	1.88	14.6	Yes
Mon1	879467	108472	61932	0.001	7.0	Yes
Nah1	50911900	45796	24099	0.0004	0.0473	Yes
Plo1	20478277	14541646	7960201	0.13	38.9	Yes
Plo2	69364893	42716804	22097133	0.3497	31.9	Yes
Plo3	271999027	232951801	151785549	2.66	55.8	Yes
Plo4	304983701	256156124	156805063	2.74	51.4	Yes
Plo5	19220499	9326701	5534543	0.08	28.8	Yes
Plo6	57708577	26028197	7668035	0.12	13.3	Yes
Plo7	24158707	12661995	6879081	0.11	28.5	Yes
Plo8	61804181	30871028	11836624	0.2	19.2	Yes
Pro1	67411	21369	13564	0.0002	20.1	Yes
Qaz1	359828392	295959815	99931128	1.7	27.8	Yes
Sac3	52371068	1622199	882633	0.02	1.7	Yes
Sar38	48417	16890	11071	0.0002	22.9	Yes
Stu1	47503349	27767021	9155701	0.1497	19.3	Yes
Sub1	2575506641	1792490389	809972714	13.5	31.4	Yes
Tda1	62715982	138932	69851	0.0011	0.1114	Yes
Th7	533144837	22924042	5114650	0.07	4.3	Partial
Thr1	51519905	212834	90062	0.0013	0.1748	Yes
Tmq1	67153487	578403	200531	0.003	0.2986	Yes
Tmq2	52254086	563825	239805	0.0037	0.4589	Yes
Tmq3	21652921	2638665	1255947	0.02	5.8	Yes
Tmq4	7800276	2283447	1422889	0.02	18.2	Yes
Tqa1	33820159	305365	190111	0.0027	0.6	Yes
Tqa2	7403198	487358	325996	0.0051	4.4	Yes
Tqa3	14531237	421840	220873	0.0035	1.5	Yes
Tsa1	186097692	124333521	57907001	0.97	31.1	Yes

Tsa2	31243357	220934	125010	0.002	0.4001	Yes
Tsa3	33731764	2468991	1084536	0.017	3.2	Yes
Tyq1	10461250	5322776	2976163	0.055	28.4	Yes
Yer1	7345134	5929627	3329619	0.06	45.3	Yes
Zah1	7644700	2504570	1557667	0.03	20.4	Yes

Table S2. f_4 ratio estimating *Bos indicus* ancestry: $f_4(\text{Gaur, Haryana; ancient test, Sub1})/(\text{Gaur, Haryana; Sahiwal, Sub1})$ calculated using AdmixTools and the 1000 bulls SNP positions.

Test ID	alpha	% indicine	SE	Z score	Country/Region	Approximate Date BP	% DNA	Coverage Qualimap q25
Ace1	0.00	0	0.01	0.49	Turkey	4200	29	0.11
Ash4	0.40	40	0.04	9.20	Israel	3100	2.3	0.0096
Azer1	-0.03	-3	0.09	-0.33	Iran	6100	0.29	0.0012
Bel1	-0.02	-2	0.01	-1.83	Serbia	6900	21	0.087
Bel2	-0.01	-1	0.01	-0.99	Serbia	6900	28	0.13
Bes1	0.36	36	0.02	24.01	Iraq	2800	35	2.12
Bes2	0.70	70	0.02	38.67	Iraq	629	39	14
Bla1	0.00	0	0.02	0.04	Serbia	8100	13.5	0.0185
Bla2	0.06	6	0.04	1.55	Serbia	8100	17	0.0046
Bub1	-0.01	-1	0.01	-2.02	Serbia	7600	38	0.43
Bul1	0.35	35	0.02	14.45	Uzbekistan	3800	24	0.0486
Cas1	0.50	49	0.02	23.97	Israel	1400	38.14	0.068
Ch22	-0.01	-1	0.01	-1.84	Turkey	7600	3.17	0.3
CPC98	-0.09	-9	0.01	-11.03	U.K.	6738	21	3.63
Far1	0.01	1	0.02	0.82	Iran	7700	7.5	0.03
Gyu2	-0.03	-3	0.01	-5.06	Armenia	7040	25	2
Has1	0.04	4	0.02	2.30	Iran	3700	22	0.033
Has3	0.00	0	0.01	-0.77	Iran	4470	43	1.2
Has4	0.06	6	0.01	6.11	Iran	2900	24	1.4
Has5	0.04	4	0.02	2.70	Iran	2300	13	0.03
Kaz1	0.13	13	0.01	12.30	Georgia	1000	58	3.12
Kaz2	0.22	22	0.01	15.99	Georgia	1050	57	0.289
Kaz3	0.11	11	0.01	9.45	Georgia	1350	62	0.46

Kaz4	0.17	17	0.01	14.06	Georgia	1200	54	0.47
Kaz5	0.31	31	0.03	10.74	Georgia	1290	9	0.02
Kho1	0.69	69	0.02	38.33	Iran	1400	51	0.2
Kok1	0.54	54	0.04	13.76	Uzbekistan	3500	6	0.01
Mar1	0.01	1	0.01	0.37	Iran	6150	3.2	0.0373
Mas1	0.38	38	0.09	4.43	Israel	3100	2	0.0032
Men1	0.00	0	0.01	-0.09	Turkey	8050	13	2.97
Men2	0.00	0	0.01	0.20	Turkey	7920	20	1.88
Mon1	0.00	0	0.08	0.05	Turkmenistan	7200	8	0.001
Plo1	-0.03	-3	0.01	-3.49	Serbia	7125	44	0.13
Plo2	-0.01	-1	0.01	-1.29	Serbia	6950	36	0.3497
Plo3	-0.01	-1	0.01	-1.75	Serbia	7025	57	2.66
Plo4	-0.01	-1	0.01	-1.66	Serbia	7000	54	2.74
Plo5	-0.02	-2	0.01	-1.82	Serbia	6650	31	0.08
Plo6	-0.01	-1	0.01	-1.02	Serbia	7126	26	0.12
Plo7	0.00	0	0.01	0.02	Serbia	7000	32	0.11
Plo8	-0.02	-2	0.01	-2.23	Serbia	7001	29	0.2
Qaz1	0.01	0	0.01	0.87	Iran	4760	48	1.7
Sac3	-0.03	-3	0.02	-1.38	Iran	7373	4.4	0.02
Stu1	-0.01	-1	0.01	-0.98	Serbia	6600	33	0.1497
Tda1	-0.01	-1	0.08	-0.11	Israel	5050	0.32	0.0011
Th7	-0.09	-9	0.02	-6.17	Morocco	7993	0.81	0.07
Thr1	0.04	4	0.06	0.69	Israel	6700	0.25	0.0013
Tmq1	0.71	71	0.08	8.53	Israel	3150	0.48	0.003
Tmq2	0.41	41	0.06	6.94	Israel	3150	0.68	0.0037
Tmq3	0.42	42	0.04	11.90	Israel	2925	6.65	0.02

Tmq4	0.34	34	0.03	11.69	Israel	3300	17	0.02
Tqa1	0.00	0	0.05	-0.01	Israel	4800	0.58	0.0027
Tqa2	-0.01	0	0.04	-0.13	Israel	4800	3.84	0.0051
Tqa3	-0.04	-4	0.05	-0.92	Israel	4800	3.5	0.0035
Tsa1	0.32	32	0.02	20.47	Israel	2820	38	0.97
Tsa2	0.32	31	0.10	3.10	Israel	3100	0.3	0.002
Tsa3	0.03	3	0.02	1.33	Israel	2800	3.7	0.017
Tyq1	0.45	45	0.02	19.98	Israel	2200	29	0.055
Yer1	0.61	61	0.02	28.11	Uzbekistan	2050	46	0.06
Zah1	0.48	47	0.03	17.08	Israel	1850	20.35	0.03

Table S3. mtDNA coverage and assignment for all the ancient samples. Haplogroup assignment denoted with * indicates probable assignment by eye using diagnostic positions as samples were not included in the maximum likelihood tree (Fig S4) due to low coverage. The macro-haplogroup of T is given where assignment to a specific T haplogroup was not possible. *Bos primigenius* samples are indicated with †.

Sample ID	Shotgun	Capture	Average mtDNA Coverage	% of Genome Covered \geq 3X	mtDNA haplotype	Maximum Likelihood Tree
Abu1†	X	X	5.85	84.73	T1*	
Abu2†	X	X	1.90	30.01	NA	
Ace1	X		22.37	99.80	T2	X
Ash4	X	X	12.54	96.40	T3	X
Azer1	X	X	35.38	99.86	Q	X
Bel1	X		13.82	99.82	Q	X
Bel2	X		28.68	99.91	Q	X
Bes1	X		160.41	99.99	T2	X
Bes2	X		626.78	100.00	T3	X
Bla1	X		4.60	78.91	T3*	
Bla2	X		1.16	12.56	Q*	
Bub1	X		52.15	99.97	T3	X
Bul1	X		14.80	99.71	T2	X
Cas1	X		10.55	96.77	T1	X
Ch22†	X		52.56	99.98	T3	X
Dan1	X	X	4.08	67.58	T*	
Far1	X		5.34	82.12	T*	
Gil1	X	X	2.04	31.93	T3*	
Gyu2†	X		479.45	100.00	Q outgroup	X
Has1	X		5.72	89.00	Q*	
Has3	X		109.96	99.96	T2	X
Has4	X		163.38	99.99	T3	X
Has5	X		13.48	99.47	T3	X
Kaz1	X		125.59	99.99	T3	X
Kaz2	X		29.99	99.93	T3	X
Kaz3	X		39.27	99.94	T2	X
Kaz4	X		30.04	99.95	T3	X
Kaz5	X		7.45	96.41	T2	X

Kho1	X		22.45	98.41	I	X
Kok1	X		2.08	34.45	P*	
Mar1			2.24	80.25	Q*	
Mas1	X		2.45	45.22	T1*	
Men1	X		353.44	99.99	T3	X
Men2	X		130.16	99.99	Q	X
Mon1	X	X	23.66	99.86	T3	X
Nah1	X	X	5.71	84.86	T1*	
Plo1	X		11.49	99.79	Q	X
Plo2	X		40.44	99.92	Q	X
Plo3	X		163.44	99.99	T3	X
Plo4	X		182.95	99.99	T2	X
Plo5	X		14.69	99.82	T3	X
Plo6	X		9.00	98.58	T3	X
Plo7	X		20.96	99.85	T3	X
Plo8	X		26.35	99.96	T2	X
Pro1	X	X	7.58	94.90	Q	X
Qaz1	X		206.83	99.99	T2	X
Sac3	X		6.50	91.59	Q	X
Sar38	X	X	101.04	99.99	T3	X
Stu1	X		22.04	99.90	T3	X
Sub1	X		1514.00	100.00	T2	X
Tda1	X	X	3.19	54.49	T1*	
Th7†	X		9.69	95.12	R	X
Thr1	X	X	3.17	52.40	T1*	
Tmq1	X		1.78	28.11	T2*	
Tmq2	X	X	6.25	87.55	T*	
Tmq3	X		2.82	51.44	T3*	
Tmq4	X		3.53	66.70	T1*	
Tqa1	X	X	14.78	99.38	T3	X
Tqa2	X	X	35.05	99.96	T1	X
Tqa3	X		3.56	62.72	T1*	
Tsa1	X		169.19	99.99	Q	X
Tsa2	X	X	35.61	99.98	T1	X

Tsa3	X		3.27	60.22	T1*	
Tyq1	X		11.56	98.56	T2	X
Yer1	X		7.77	92.56	T3	X
Zah1	X		3.88	72.13	T3*	

Table S4. Experimental modifications for samples Ch22 and Th7.

Sample	Extraction	Powder (g)	Washing/pre-lysis (ml); incubation conditions	EDTA in buffer (ml)	Library (from extractions)	Extract + USER (μ l); incubation conditions	PCR cycles
Ch22	C18	1	3 x 1 EDTA, 30 min at RT	10	C30 (C18)	50 + 5; 3h at 37°C	12
	C23	0.86	3 x 1 EDTA, 30 min at RT	15	C31 (C18)	50 + 10; 3h at 37°C	14
					C39a (C23)	25 + 12; 3h at 37°C	12
					C39b (C23)	20 + 12; 3h at 37°C	12
Th7	C16	1	1 x buffer*, 1h at 37°C, 2 x buffer**, 30 min at 37°C	10	C24 (C16)	no USER	16
	C21	1	3 x 2 EDTA, 30 min at RT	10	C29 (C16)	no USER	12
	C18	1	3 x 1 EDTA, 30 min at RT	10	C31 (C16)	50 + 10; 3h at 37°C	12
	C19	1	3 x 1 EDTA, 30 min at RT	10	C34 (C21)	38 + 12; 3h at 37°C	12
					C35a (C16)	20 + 12; 3h at 37°C	12
					C37a (C18+C19)	38 + 12; 3h at 37°C	12

* 1 x 1 ml of EDTA (0.5 M, pH8; Ambion®, Applied Biosystems), 250 μ l of N-Laurylsarcosine (0.5 %, Merck) and 30 μ l of Proteinase K (18 U, Roche)

** 2 x 2 ml of EDTA (0.5 M, pH8; Ambion®, Applied Biosystems), 250 μ l of N-Laurylsarcosine (0.5 %, Merck) and 30 μ l of Proteinase K (18 U, Roche)

Table S5. Summary of 770K modern Bovine dataset used for analyses. Showing breed code, cattle breed, number of animals per breed and source reference.

Breed Code	Breed	Number of Animals	Source
ALE	Alentejana	9	This Study
ANB	Anatolian Black	13	This Study
ANG	Angus	42	WIDDE (156)
BLO	Blonde d'Aquitaine	5	WIDDE (156)
BMA	Beef Master	23	WIDDE (156)
BRG	Brangus	12	WIDDE (156)
BRM	Brahman	46	WIDDE (156)
BSW	Brown Swiss	22	WIDDE (156)
BUT	Butana	7	This Study -
CHL	Charolais (UK)	37	WIDDE (156)
EAR	East Anatolian Red	12	This Study
GAL	Galloway	9	This Study
GIR	Gir (WIDDE)	27	WIDDE (156)
GIR	Gir (TCD)	2	This Study
GNS	Guernsey	21	WIDDE (156)
GOB	Gobra	10	This Study
HAR	Hariana	10	This Study
HFD	Hereford	35	WIDDE (156)
HIG	Highland	8	This Study
HOL	Holstein (FR)	60	WIDDE (156)
JER	Jersey (FR)	38	WIDDE (156)

KEN	Kenana	10	This Study
KER	Kerry	9	This Study
LAG	Lagune	5	WIDDE (156)
LMS	Limousin	50	WIDDE (156)
MAR	Maremmana	4	This Study
MAU	Maure	10	This Study
MON	Montbeliarde	5	WIDDE (156)
MUR	Murutu	11	This Study
NDA	N'Dama (WIDDE) (G)	23	WIDDE (156)
NDA	N'Dama (TCD) (T)	9	This Study
NEL	Nelore	31	WIDDE (156)
NOR	Normande	5	WIDDE (156)
NRC	Norwegian Red Cattle	17	WIDDE (156)
OGR	Gaur (WIDDE)	2	WIDDE (156)
OGR	Gaur (TCD)	1	This Study
OYK	Yak	2	WIDDE (156)
PMT	Piedmontese	21	WIDDE (156)
RGU	Red Angus	10	WIDDE (156)
RMG	Romagnola	21	WIDDE (156)
SAH	Sahiwal	10	This Study
SAR	South Anatolian Red	13	This Study
SEN	Senepol	12	WIDDE (156)
SGT	Santa Gertrudis	32	WIDDE (156)

SHK	Sheko	16	WIDDE (156)
SIK	Sikia	5	This Study
SIM	Simmental	10	WIDDE (156)
SIS	Sistani	5	This Study
SOM	Somba	10	This Study
TAL	Taleshi	5	This Study
WAG	Wagyu	13	WIDDE (156)

Table S6. Table summarizes information for the individual modern genomes used. Publication and Accession number are indicated where available.

Breed	Code	Publication	Accession number	Coverage
Alentejana	ALNPRTM000000000012	This study		31
Ankole	AnkoleAN001	(200)	PRJNA312138	9
Ankole	AnkoleAN030	(200)	PRJNA312138	7
Boran	Boran_BO130	(200)	PRJNA312138	9
Boran	Boran_BO672	(200)	PRJNA312138	6
Fleckvieh	SIMDEUM000910950070	(201)	PRJNA238491	9
Fleckvieh	SIMDEUM000913892370	(201)	PRJNA238491	10
Hariana	HARINDF000000000003	This study		35
Holstein	HOLUSAM000002030882	(201)	PRJNA238491	12
Kenana	Kenana_11	(200)	PRJNA312138	9
Lagune	LAGUNKM000000000040	This study		24
Ndama	NDamaND064	(200)	PRJNA312138	10
Ndama	NDamaND118	(200)	PRJNA312138	9
Ogaden	Ogaden_OgD5	(200)	PRJNA312138	9
Ogaden	Ogaden_OgS1	(200)	PRJNA312138	8
ScottishHighland	HLAGBRM0000000008059	This study		38
Sahiwal	Sha_3b	(25)	PRJNA379859	21
Sikias	SIKUNKU000000000005	This study		20
Somba	SOMTGOF000000003437	This study		35
SouthAnatolianRed	SARTURM000000000001	This study		18
Tharparkar	Thar1	(25)	PRJNA379859	16
Wagyu	WAGIRLM000000000001	This study		18
Gaur	OGRUNKF000000000005	This study		29

Table S7. Whole genome *D*-statistic test for zebu/indicine introgression using ANGSD. Showing reduced ancient dataset with ancient individuals only with 200 or more ABBA+BABA sites for analyses. Median value for each ancient test is shown, where five different *Bos indicus* individuals from five different breeds were rotated. Test was classified as significant if all Z-scores were equal or more than 3; and classified as non-significant if at least one test was below a Z-score of 3.

Test ID	Place	Time (BP)	D_Median	SE	Significant
Ace1	Anatolia	4200	0.013	0.007	No
Ash4	Israel	3100	0.169	0.016	Yes
Azer1	Iran	6100	0.004	0.059	No
Bel1	Serbia	6900	-0.007	0.008	No
Bel2	Serbia	6900	-0.001	0.008	No
Bes1	Iraq-Kurdistan	2800	0.164	0.007	Yes
Bes2	Iraq-Kurdistan	629	0.211	0.008	Yes
Bla1	Serbia	8100	0.005	0.016	No
Bla2	Serbia	8100	0.011	0.032	No
Bub1	Serbia	7600	-0.010	0.005	No
Bul1	Central Asia	3800	0.159	0.010	Yes
Cas1	Israel	1400	0.211	0.009	Yes
Ch22	<i>Bos primigenius</i>	7600	-0.012	0.006	No
Far1	Iran	7700	0.041	0.014	No
Gyu2	<i>Bos primigenius</i>	7040	-0.007	0.004	No
Has1	Iran	3700	0.057	0.012	Yes
Has3	Iran	4470	0.013	0.005	No
Has4	Iran	2900	0.057	0.006	Yes
Has5	Iran	2300	0.058	0.012	Yes
Kaz1	Georgia	1000	0.090	0.006	Yes
Kaz2	Georgia	1050	0.130	0.007	Yes
Kaz3	Georgia	1350	0.089	0.007	Yes

Kaz4	Georgia	1200	0.113	0.007	Yes
Kaz5	Georgia	1290	0.141	0.013	Yes
Kho1	Iran	1400	0.235	0.008	Yes
Kok1	Central Asia	3500	0.228	0.014	Yes
Mar1	Iran	6150	-0.028	0.011	No
Mas1	Israel	3100	0.221	0.026	Yes
Men1	Anatolia	8050	-0.014	0.004	No
Men2	Anatolia	7920	0.009	0.004	No
Plo1	Serbia	7125	-0.014	0.007	No
Plo2	Serbia	6950	0.001	0.006	No
Plo3	Serbia	7025	0.002	0.005	No
Plo4	Serbia	7000	0.000	0.005	No
Plo5	Serbia	6650	0.000	0.008	No
Plo6	Serbia	7126	-0.006	0.008	No
Plo7	Serbia	7000	0.003	0.007	No
Plo8	Serbia	7001	-0.009	0.006	No
Qaz1	Iran	4760	0.009	0.005	No
Sac3	Iran	7373	-0.012	0.015	No
Stu1	Serbia	6600	-0.003	0.007	No
Tda1	Israel	5050	-0.011	0.063	No
Thr1	Israel	6700	0.000	0.057	No
Tmq1	Israel	3150	0.213	0.025	Yes
Tmq2	Israel	3150	0.192	0.024	Yes
Tmq3	Israel	2925	0.178	0.012	Yes
Tmq4	Israel	3300	0.153	0.012	Yes
Tqa1	Israel	4800	0.020	0.039	No
Tqa2	Israel	4800	0.012	0.028	No

Tqa3	Israel	4800	-0.006	0.036	No
Tsa1	Israel	2820	0.160	0.007	Yes
Tsa2	Israel	3100	0.086	0.034	No
Tsa3	Israel	2800	0.025	0.015	No
Tyq1	Israel	2200	0.174	0.009	Yes
Yer1	Central Asia	2050	0.213	0.009	Yes
Zah1	Israel	1850	0.189	0.011	Yes

Table S8. Populations used in computation of ANGSD *D* statistics displayed in Figure 3 and Tables S8, S11.

ID	Population for Dstats ANGSD
Sub1	Anatolia
Men1	Anatolia
Men2	Anatolia
Plo1	Balkans
Plo2	Balkans
Plo3	Balkans
Plo4	Balkans
Plo5	Balkans
Plo6	Balkans
Plo7	Balkans
Plo8	Balkans
Bel1	Balkans
Bel2	Balkans
Bla1	Balkans
Bla2	Balkans
Gil1	Levant
Tda1	Levant
Tqa1	Levant
Tqa2	Levant
Tqa3	Levant
Nah1	Levant
Tsa3	Levant
Thr1	Levant
Azer1	Iran
Has1	Iran
Has3	Iran
Mar1	Iran
Far1	Iran
Sac3	Iran

Qaz1	Iran
------	------

Table S9. Whole genome *D*-statistic to test clade integrity of ancient population pairs with respect to aurochs introgression. The test $D(\text{gaur, aurochs; ancient group1, ancient group2})$ was computed and two standard errors are shown. Results shown here are displayed in Figure 3.

(Ancient group 1, Ancient group 2)	Aurochs	D	2SE	Z	pvalue	nABBA	nBABA
(Levant, Anatolia)	Gyu2	0.059	0.019	6.070	0.000	4469	3975
(Levant, Iran)	Gyu2	0.063	0.022	5.806	0.000	3961	3494
(Levant, Balkans)	Gyu2	0.054	0.019	5.669	0.000	4492	4036
(Anatolia, Balkans)	Gyu2	-0.006	0.007	-1.787	0.074	143053	144913
(Iran, Balkans)	Gyu2	-0.009	0.007	-2.599	0.009	127336	129702
(Anatolia, Iran)	Gyu2	0.003	0.008	0.802	0.423	130901	130086
(Levant, Anatolia)	CPC98	0.068	0.018	7.608	0.023	5254	4587
(Levant, Iran)	CPC98	0.074	0.020	7.267	0.014	4541	3918
(Levant, Balkans)	CPC98	0.103	0.018	11.477	0.000	5496	4473
(Anatolia, Balkans)	CPC98	0.042	0.007	11.467	0.000	168913	155360
(Iran, Balkans)	CPC98	0.038	0.007	10.790	0.000	147133	136436
(Anatolia, Iran)	CPC98	0.001	0.007	0.376	0.319	142235	141839
(Levant, Anatolia)	Th7	-0.068	0.049	-2.783	0.005	489	513
(Levant, Iran)	Th7	-0.038	0.057	-1.351	0.177	389	420
(Levant, Balkans)	Th7	-0.036	0.049	-1.457	0.145	475	503
(Anatolia, Balkans)	Th7	0.000	0.010	-0.034	0.973	10538	10542
(Iran, Balkans)	Th7	-0.008	0.012	-1.393	0.164	9415	9571
(Anatolia, Iran)	Th7	0.007	0.012	1.140	0.254	9616	9484

Table S10. Populations used for the admixture graph reconstruction (*qpGraph*).

ID	Population for <i>qpGraph</i>
Sub1	Anatolia unadmixed
Plo1	Balkans
Plo3	Balkans
Plo4	Balkans
Gil1	Levant
Tda1	Levant
Tqa1	Levant
Tqa2	Levant
Tqa3	Levant
Nah1	Levant
Tsa3	Levant
Thr1	Levant
Gyu2	Armenian aurochs
Th7	Moroccan aurochs
CPC98	British aurochs
Gaur	outgroup
Bes2	Near Eastern admixed
Sahiwal	<i>Bos indicus</i>

Table S11. Whole genome *D*-statistic to test clade integrity of ancient population pairs with respect to aurochs introgression calculated from alignments to the *Bubalus bubalus* reference genome. The test $D(\text{gaur, aurochs; ancient group1, ancient group2})$ was computed and two standard errors are shown.

(Ancient group 1, Ancient group 2)	Aurochs	D	2SE	Z	pvalue	nABBA	nBABA
(Levant, Anatolia)	Gyu2	0.073	0.019	7.471	0.000	3959	3423
(Levant, Iran)	Gyu2	0.067	0.021	6.233	0.000	3502	3063
(Levant, Balkans)	Gyu2	0.062	0.020	6.181	0.000	3920	3465
(Anatolia, Balkans)	Gyu2	-0.015	0.006	-4.878	0.000	145389	149684
(Iran, Balkans)	Gyu2	-0.013	0.006	-4.138	0.000	126503	129767
(Anatolia, Iran)	Gyu2	0.000	0.006	0.020	0.984	134692	134675
(Levant, Anatolia)	CPC98	0.067	0.017	7.751	0.000	4896	4278
(Levant, Iran)	CPC98	0.073	0.020	7.244	0.000	4215	3640
(Levant, Balkans)	CPC98	0.090	0.018	9.909	0.000	4973	4153
(Anatolia, Balkans)	CPC98	0.021	0.006	6.925	0.000	185635	178108
(Iran, Balkans)	CPC98	0.026	0.006	8.297	0.000	156261	148315
(Anatolia, Iran)	CPC98	-0.004	0.006	-1.458	0.145	157865	159271
(Levant, Anatolia)	Th7	-0.028	0.053	-1.038	0.299	384	406
(Levant, Iran)	Th7	-0.008	0.060	-0.284	0.776	357	363
(Levant, Balkans)	Th7	-0.032	0.055	-1.163	0.245	387	413
(Anatolia, Balkans)	Th7	-0.007	0.009	-1.555	0.120	10402	10556
(Iran, Balkans)	Th7	-0.006	0.012	-0.967	0.334	9200	9308
(Anatolia, Iran)	Th7	-0.002	0.011	-0.399	0.690	9510	9553

Table S12. Whole genome *D*-statistic to test clade integrity of ancient population pairings with the Near Eastern aurochs Gyu2, using a *Bos taurus* reference genome. This tests for unbalanced allele sharing with the British aurochs (CPC) and the Moroccan aurochs (Th7). The test $D(\text{gaur, aurochs; ancient group, Gyu2})$ was computed and two standard errors are shown. This calculation was performed in using ANGSD with *Bos taurus* reference sequence aligned reads.

Ancient group	Aurochs	D	2SE	Z	pvalue	nABBA	nBABA
Anatolia	CPC	-0.002	0.009	-0.545	0.586	129192	129823
Balkans	CPC	-0.039	0.008	-9.494	0.000	124368	134401
Levant	CPC	0.064	0.023	5.482	0.000	4016	3532
Iran	CPC	-0.003	0.008	-0.731	0.465	113013	113723
Anatolia	Th7	-0.020	0.014	-2.884	0.004	8376	8725
Balkans	Th7	-0.022	0.014	-3.261	0.001	8354	8734
Levant	Th7	-0.080	0.063	-2.529	0.011	351	411
Iran	Th7	-0.032	0.015	-4.225	0.000	7464	7955

Table S13. Whole genome *D*-statistic to test clade integrity of ancient population pairings with the Near Eastern aurochs Gyu2, using a *Bubalus bubalus* reference genome. This tests for unbalanced allele sharing with the British aurochs (CPC) and the Moroccan aurochs (Th7). The test $D(\text{gaur, aurochs; ancient group, Gyu2})$ was computed and two standard errors are shown. This calculation was performed in using ANGSD with *Bubalus bubalus* reference sequence aligned reads.

Ancient group	Aurochs	D	2SE	Z	pvalue	nABBA	nBABA
Anatolia	CPC	-0.006	0.008	-1.521	0.128	130966	132542
Balkans	CPC	-0.024	0.007	-6.348	0.000	124105	130211
Levant	CPC	0.068	0.024	5.640	0.000	3503	3056
Iran	CPC	0.002	0.008	0.633	0.527	113537	112979
Anatolia	Th7	-0.017	0.014	-2.437	0.015	7787	8061
Balkans	Th7	-0.011	0.015	-1.464	0.143	7677	7843
Levant	Th7	-0.060	0.067	-1.788	0.074	297	335
Iran	Th7	-0.020	0.015	-2.683	0.007	6977	7259