The Multilayered Prehistory of Wild Aurochs and Domestic Cattle

An Ancient Genomics Perspective

Marta Alexandra Pereira da Silva Verdugo



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This thesis and work is dedicated to my late grandad Fernando Joffre Baltazar Pereira and to my mum Maria Manuela Furtado Pereira

"Valeu a pena? Tudo vale a pena

Se a alma não é pequena.

Quem quer passar além do Bojador

Tem que passar além da dor.

Deus ao mar o perigo e o abismo deu,

Mas nele é que espelhou o céu."

Fernando Pessoa

Thesis Ancient Dataset

Sample data marked with (**) has been provided by Amelie Scheu; and sample data marked with (***) has been provided by Victoria Mullin; Sample marked with (*) has been previously published (Edwards *et al.* 2010; Park *et al.* 2015)

ID	bone	Country	Site	Archaeological Context	Date	Species	% DNA	Coverage	Mitochondria	Sex
Ace1	petrous	Turkey	Acemhöyük	Early Bronze Age	c. 2200 BC	*Bos taurus*	29	0.1	21	Female
Ash4	petrous	Israel	Tel Ashqelon	Early Iron I	1200–1000 BC	*Bos*	2	0.01	1	Male
Azer1	petrous	Iran	Kültəpə	Late Chalcolithic	4260-4050 cal. BC	*Bos*	0.3	0.001	0.36	Female
Baikal1	petrous	Russia	Barguzin River	Neolithic	10431-10029 cal. BC	*Bos primigenius*	70	3.6	493	Male
Bed3**	petrous	Germany	Bedburg-Königshoven	Early Mesolithic	9608 ± 151 cal. BC	*Bos primigenius*	30	18.5	3521	Female
Bed4**	petrous	Germany	Bedburg-Königshoven	early Mesolithic	9758 ± 191 cal. BC	*Bos primigenius*	17	2.13	657	Female
Bel1	petrous	Serbia	Belovode-Veliko	Late Neolithic	5050/4925-4900/4800 cal. BC	*Bos taurus*	21	0.09	12	Female
Bel2	petrous	Serbia	Belovode-Veliko	Late Neolithic	5050/4925-4900/4800 cal. BC	*Bos taurus*	28	0.1	25	Male
Belorus1	petrous	Belorus	No Info	Unknown	N/A	*Bos primigenius*	22	2	325	Male
Bes1	petrous	Iraq-Kurdistan	Bestanşur	Iron age	911–609 BC	*Bos taurus*	35	2	149	Female
Bes2	petrous	Iraq-Kurdistan	Bestanşur	Medieval	1292-1399 cal. AD	*Bos taurus*	39	14	609	Male
Bir1	tooth	Moldova	Birnova/Byrnova Luka	Cucuteni-Trypillian	c.5200 - 3500 BC	*Bos taurus*	0.3	0.002	1	Female

Bir2	astralagus	Moldova	Birnova/Byrnova Luka	Cucuteni-Trypillian	c.5200 - 3500 BC	*Bos taurus*	0.05	0.001	4	Female
Bir3	astralagus	Moldova	Birnova/Byrnova Luka	Cucuteni-Trypillian	c. 5200 - 3500 BC	*Bos taurus*	1	0.004	2	Female
Bla1	petrous	Serbia	Blagotin	Early Neolithic Starčevo	6200-6000 cal BC	*Bos taurus*	14	0.018	4	Male
Bla2	petrous	Serbia	Blagotin	Early Neolithic Starčevo	6200-6000 cal BC	*Bos taurus*	17	0.005	1	Male
Bri1	petrous	Netherlands	Britsum	Roman	257-421 cal. AD	*Bos primigenius*	56	3	207	Male
Bub1	petrous	Serbia	Bubanj	Neolithic	c.6000-5600 BC	*Bos taurus*	38	0.4	53	Female
Bul1	petrous	Uzbekistan	Tilla Bulak	Late Bronze Age	2000-1700 cal. BC	*Bos taurus*	24	0.05	14	Male
Bun1	petrous	Netherlands	Odjik	Middle Iron	500-250 BC	*Bos taurus*	41	2	242	Female
Bun2	petrous	Netherlands	Odjik	Middle Iron	500-250 BC	*Bos taurus*	50	2	253	Female
CA317	non petrous	Georgia	Tamara Fort	Medieval	AD 651-766	*Bos primigenius?*	9	0.02	7	Male
Cas1	petrous	Israel	Horvat Castra	Byzantine	AD 324-638	*Bos*	38	0.07	10	Female
Ch22**	Scapula	Turkey	Çatalhöyük	Neolithic	c.7500 BC to 5700 BC	*Bos primigenius?*	3	0.31	45	Male
Cla1***	petrous	UK	Cladh Hallan	Late Bronze	1054-826 BC	*Bos taurus*	59	15	679	Female
Cla2***	petrous	UK	Cladh Hallan	Late Bronze	1118-924 BC	*Bos taurus*	51	2	187	Male
CPC98*	humerus	UK	Carsington Pasture Cave	Mesolithic	4788 cal. BC	*Bos primigenius*	21	4	10	Male
Dan1	petrous	Israel	Tel Dan	Pottery Neolithic/ Early Bronze	3500-3000 BC	*Bos taurus*	0.1	0.0002	0.04	Female
Dav1	petrous	Israel	Jerusalem	Middle Bronze	1929-1753 cal. BC	*Bos taurus*	16	5	946	Female

Dav3	petrous	Israel	Jerusalem	Middle Bronze	2200-2000 BC	*Bos taurus*	7	0.01	3.6	Female
Dav4	petrous	Israel	Jerusalem	Middle Bronze	2200-2000 BC	*Bos taurus*	6	0.01	12	Male
Dav5	petrous	Israel	Jerusalem	Early Hellenistic	332-167 BC	*Bos*	0.22	0.004	1	Female
Dro1	petrous	Netherlands	Dronrijp-zuid	Middle Roman	AD 100-300	*Bos taurus*	53	3	318	Male
Dub1**	petrous	Ireland	Dublin	Medieval	AD 900-1000	*Bos taurus*	32	2	153	Female
Dyr1**	petrous	Germany	Dyrotz 25	late slavic	9th-13th century	*Bos taurus*	68	2	103	Female
Dzh1**	petrous	Bulgaria	Dzulhunitsa	Early Neolithic	5831 ± 51 - 6049 ± 25 cal. BC	*Bos taurus*	58	10	2043	Male
Dzh2**	petrous	Bulgaria	Dzulhunitsa	Early Neolithic	5605 ± 33 cal. BC	*Bos taurus*	26	4	976	Female
Els1	petrous	Netherlands	Elst	Roman	AD 1-70	*Bos taurus*	55	2	179	Male
Fal7**	?	Germany	Falkenwalde	Early Slavic	1100-1250 AD	*Bos primigenius*	30	2	189	Male
Far1	petrous	Iran	Miyanroud	Late Neolithic	waiting for Azadeh to answer	*Bos*	8	0.03	5	Female
Fir1	petrous	Netherlands	Firdgum	Early Medieval	AD 450-1050	*Bos taurus*	60	3	185	Female
Gil1	petrous	Israel	Gilat	Chalcolithic	c.4300–3300 BC	*Bos*	0.2	0.0007	0.16	Female
Gyumri1	petrous	Armenia	Gyumri	Mesolithic	11842-11622 cal. BC	*Bos primigenius*	53	2	226	Male
Gyumri2	petrous	Armenia	Gyumri	Neolithic	5036-5076 cal. BC	*Bos primigenius*	25	2	477	Male
Has1	petrous	Iran	Hasanlu	Middle Bronze	1900-1600 BC	*Bos*	22	0.03	5	Male
Has3	petrous	Iran	Hasanlu	Early Bronze II	2470 cal. BC	*Bos*	43	1	174	Male
Has4	petrous	Iran	Hasanlu	Iron II	1050-800 BC	*Bos*	24	1	150	Male

Has5	petrous	Iran	Hasanlu	Achaemenid/Seleuco-Parthian	550-275 BC	*Bos*	13	0.03	13	Female
Hou1	petrous	Netherlands	Houten-Loerik	Medieval	AD 450-1500	*Bos taurus*	59	3	202	Male
Hou2	petrous	Netherlands	Houten-Hoogdijk	Medieval	AD 1100-1199	*Bos taurus*	57	3	195	Female
Hxh1**	petrous	Germany	Herxheim	early Neolithic (LBK)	c.5000 BC	*Bos taurus*	33	8	980	Female
Hxh2**	petrous	Germany	Herxheim	Early Neolithic (LBK)	around 5000	*Bos primigenius*	53	23	2209	Female
Kalisz1	petrous	Poland	Kalisz	No info	No info	*Bos primigenius*	0.2	0.0006	1.35	Male
Kalisz2	petrous	Poland	Kalisz	No info	No info	*Bos primigenius*	35	3	417	Male
Kalisz3	petrous	Poland	Kalisz	No info	No info	*Bos primigenius*	6	0.01	11	Male
Kaz1	petrous	Georgia	Tamara Fort	Medieval	AD c.950	*Bos*	58	3	157	Female
Kaz2	petrous	Georgia	Tamara Fort	Medieval	AD c.900	*Bos*	57	0.3	28	Female
Kaz3	petrous	Georgia	Tamara Fort	Medieval	AD c.900	*Bos*	62	0.5	37	Female
Kaz4	petrous	Georgia	Darialiti Fort	Medieval	AD c.910	*Bos*	54	0.5	29	Female
Kho1	petrous	Iran	Nishapur Qohandez	Parthes-Islamic	300 BC- AD 1300	*Bos*	51	0.2	21	Female
Kie1	petrous	Poland	Kierzkowo	Late Neolithic	c.3000 BC	*Bos taurus*	14	0.04	5	Male
Kie2	petrous	Poland	Kierzkowo	Late Neolithic	c.3000 BC	*Bos taurus*	46	0.21	13	Male
Kir4**	petrous	Germany	Kirschbaumhöhle	Late Neolithic	2794 ± 78 cal. BC	*Bos taurus*	54	15	813	Female
Kok1	petrous	Uzbekistan	Kok Teppe	Iron Age	1500-3000 BC	*Bos*	6	0.01	2	Male
Kor1	?	Turkey	Körtik Tepe	PPNA	~7950 BC	*Bos*	1	0.002	12	Female
Lud1	petrous	Poland	Ludwinowo	Early Neolithic	c. 5500 BC	*Bos taurus*	34	0.1	10	Female
Lud2	petrous	Poland	Ludwinowo	Early Neolithic	c. 5500 BC	*Bos taurus*	49	0.4	29	Female
Lud3	petrous	Poland	Ludwinowo	Early Neolithic	c. 5500 BC	*Bos taurus*	53	0.3	31	Male

Lud4	petrous	Poland	Ludwinowo	Early Neolithic	c. 5500 BC	*Bos taurus*	35	0.2	16	Female
Mar1	scapula	Iran	Maral Tappeh	Neolithic	c.5000 BC	*Bos taurus*	3.2	0.04	4	Male
Mar1	scapula	Iran	Maral Tappeh	Chalcolithic/Bronze Age	c.5000 BC	*Bos primigenius?*	3	0.04	4	Male
Men1	astragalus	Turkey	Mentese	Neolithic	c.6000-5500 BC	*Bos*	13	3	334	Male
Men2	petrous	Turkey	Mentese	Neolithic	6048-5893 cal. BC	*Bos*	20	2	88	Female
Mon1	petrous	Turkmenistan	Monjukli Depe	Chalcolithic	5100-4500 cal. BC	*Bos taurus*	8	0.001	0.1	Female
Mus1	petrous	Israel	Tel Masos	Iron Age I	1200-1000 BC	*Bos*	2	0.003	2	Female
Nah1	petrous	Israel	Nahal Tillah	Early Bronze I	3300-3050 BC	*Bos*	0.3	0.0004	0.2	Male
New1* **	petrous	Ireland	Newgrange	Neolithic	2795-2580 BC	*Bos taurus*	55	17	778	Male
New2* **	petrous	Ireland	Newgrange	Late Iron	AD 321-425	*Bos taurus*	36	4	194	Male
New3* **	petrous	Ireland	Newgrange	Neolithic	c.2800 BC	*Bos taurus*	49	5	346	Male
New4* **	petrous	Ireland	Newgrange	Neolithic	c.2800 BC	*Bos taurus*	43	4	244	Female
New5* **	petrous	Ireland	Newgrange	Neolithic	3024-2894 BC	*Bos taurus*	51	5	322	Male
Otb1	petrous	Netherlands	Oosterbierum	Middle Roman	AD 100-300	*Bos taurus*	57	3	167	Male
Plo1	petrous	Serbia	Pločnik	Neolithic	5275/5125-5100/5000 cal. BC	*Bos taurus*	44	0.1	10	Female
Plo2	petrous	Serbia	Pločnik	Neolithic	5025/4950-4850-4650 cal. BC	*Bos taurus*	36	0.4	36	Female
Plo3	petrous	Serbia	Pločnik	Neolithic	5100/5000-5025/4950 cal. BC	*Bos taurus*	57	3	153	Male

Plo4	petrous	Serbia	Pločnik	Neolithic	5100/5000-5025/4950 cal. BC	*Bos taurus*	54	3	154	Male
Plo5	petrous	Serbia	Pločnik	Neolithic	4850/4650-4600/4500 cal. BC	*Bos taurus*	31	0.08	13	Male
Plo6	petrous	Serbia	Pločnik	Neolithic	5275/5125-5100/5000 cal. BC	*Bos taurus*	26	0.1	8	Male
Plo7	petrous	Serbia	Pločnik	Neolithic	5100/5000-5025/4950 cal. BC	*Bos taurus*	32	0.1	19	Female
Plo8	petrous	Serbia	Pločnik	Neolithic	5100/5000-5025/4950 cal. BC	*Bos taurus*	29	0.2	14	Female
Qaz1	petrous	Iran	Tepe Shizar	Middle Bronze Age	2880-2830 cal. BC	*Bos*	48	2	193	Female
Sac3	non petrous	Iran	Tapeh-Sang-e-Caxmaq	Late Neolithic	5373 cal. BC	*Bos*	4	0.02	3	Female
Sch1	petrous	Netherlands	Schipluiden	Mid-Neolithic	3500-2850 BC	*Bos taurus*	47	2	159	Female
Ste1	petrous	Netherlands	Stevenshofjespolder	Iron/Roman	800BC- AD 400	*Bos taurus*	42	1	257	Female
Stu1	petrous	Serbia	Stubline	Neolithic	4800-4500 cal. BC	*Bos taurus*	33	0.1	10	Male
Sub1	petrous	Turkey	Suberde	Neolithic	6221-6024 cal. BC	*Bos*	40	14	1344	Male
Tango1	petrous	No Info	No Info	Unknown	N/A	*Bos primigenius*	45	2	339	Male
Tango2	petrous	No Info	No Info	Unknown	2470-2297 cal. BC	*Bos primigenius*	49	2	295	Male

Tda1	petrous	Israel	Tel-Dalit	Early Bronze Age II	3050 BC	*Bos*	0.3	0.001	0.3	Male
Th7**	Phalanx 2	Morocco	Taghit Haddouch	Epipalaeolithic	6933 cal. BC	*Bos primigenius*	0.81	0.07	8.4	Female
Thr1	petrous	Israel	Tel Hreiz	Pottery Neolithic	5100-4300 BC	*Bos*	0.3	0.001	0.2	Male
Tmq1	petrous	Israel	Tel Miqne-Ekron	Iron Age IA	1200-1150 BC	*Bos*	0.5	0.003	2	Female
Tmq2	petrous	Israel	Tel Miqne-Ekron	Iron Age IA	1200-1150 BC	*Bos*	0.7	0.004	1	Female
Tmq3	petrous	Israel	Tel Miqne-Ekron	Late Bronze IIA	1000-925 BC	*Bos*	7	0.02	3	Female
Tmq4	petrous	Israel	Tel Miqne-Ekron	Late Bronze/Iron Age	1400-1200 BC	*Bos*	17	0.02	3	Female
Tqa1	petrous	Israel	Tel es-Qashish	Early Bronze Age 3	3150-2200 BC	*Bos*	0.6	0.003	0.8	Male
Tqa2	petrous	Israel	Tel es-Qashish	Early Bronze Age 3	3150-2200 BC	*Bos*	4	0.005	0.6	Female
Tqa3	petrous	Israel	Tel es-Qashish	Early Bronze Age 3	3150-2200 BC	*Bos*	4	0.004	3	Female
Tri1**	metatarsus	Germany	Trier-Brüderkrankenhaus	Mesolithic	8116 cal. BC	*Bos primigenius*	24	2	822	Male
Tsa1	petrous	Israel	Tel es-Safi	Iron Age II	925-720 BC	*Bos*	38	1	160	Female
Tsa2	petrous	Israel	Tel es-Safi	Iron Age I	1200-1000 BC	*Bos*	0.3	0.002	1	Female
Tsa3	petrous	Israel	Tel es-Safi	Iron Age II	925-720 BC	*Bos*	4	0.02	3	Female
Tyq1	petrous	Israel	Tel Yoqneam	Early Hellenistic	332-167 BC	*Bos*	29	0.05	11	Male
Viz1	petrous	Netherlands	Zijderveld	Bronze	1500-1300 BC	*Bos taurus*	33	0.7	574	Male
Viz2	petrous	Netherlands	Zijderveld	Bronze	1500-1300 BC	*Bos taurus*	43	2	251	Male
Win1	petrous	Netherlands	Winsum	Roman	AD 100-300	*Bos taurus*	63	19	856	Female
Yer1	petrous	Uzbekistan	Yerqorqan	Achaemenid	c.50 BC	*Bos*	46	0.02	7	Female
Yor1***	petrous	UK	York	Roman	AD 110	*Bos taurus*	58	8	603	Female
Yor2***	petrous	UK	York	Viking	AD 801-901	*Bos taurus*	41	4	213	Male
Yor3***	petrous	UK	York	Norman	AD 1350	*Bos taurus*	48	2	201	Male
Yor4***	petrous	UK	York	Viking	AD 950	*Bos taurus*	46	3	242	Female

Zah1* **	petrous	Israel	Tel Zahara	Islamic	c. 63 BC - AD 330	*Bos*	20	0.03	3	Male

Abbreviations

A: Adenine
ANGSD: Analysis of next generation Sequencing Data
BC: Before Christ (corresponding to -1950 (~2000) years BP)
BCE: Before Christian Era, Before Common Era
BGI: Beijing Genomics Institute
BP: Before Present (corresponding to +1950 (~2000) years BC)
C: Cytosine
Cal. BC: calibrated date in BC years
Cal. BP: calibrated date in BP years
DNA: Deoxyribonucleic acid
G: Guanine
GATK: Genome Analysis Toolkit
IBS: Identity by state
KYA: thousand years ago
LASER: Locating Ancestry from SEquence Reads
LBK: Linearbandkeramik culture (Linear Pottery culture), ~5000 BC Neolithic culture from Central Europe
NGS: Next generation sequencing
LD: Linkage Disequilibrium
MDS: Multidimensional Scaling
MSY: Male specific region of the Y chromosome
mtDNA: mitochondrial DNA
MYA: Million Years Ago
NJ: Neighbour Joining
PCA: Principal Component Analysis
PPNA: Pre-Pottery Neolithic A
PPNB: Pre-Pottery Neolithic B
SNP: Single Nucleotide Polymorphism
T: Thymine
U: Uracil
USER: Uracil-Specific Excision Reagent
VCF: Variant Call Format

Summary

250 bone specimens were sampled, and a total of 122 ancient genomes are presented that were generated using Next Generation Sequencing. Each chapter will comprise a subset of that ancient depending on the questions being discussed.

Chapter 4 looks at the population genetics of ancient taurine domestics from their centre of domestication in the Near East to dispersal into Europe. It also delves into *Bos primigenius* introgression in Europe, which was confirmed to have happened from about 1000 years after the arrival of domestics into Europe. Mitochondrial DNA diversity revealed two new haplogroups and supported previous studies of an origin of T and Q haplotypes in the Near East.

Chapter 5 presents 18 *Bos primigenius* samples from Asia, North Africa and Europe and explores the relationship between these. Analysis on whole nuclear genome data, mitochondrial genomes and Y chromosomes reveal a genetic homogeneity in the European population, whereas Near Eastern aurochs reveal a greater diversity at centre of taurine cattle domestication. A North African aurochs refutes previous hypothesis on the origins of the R mtDNA lineage and also reveals a strong influence in the ancient Southern Levant. A Y chromosome phylogeny based on 160 SNPs, including ancients and moderns, reveals a possible novel Y chromosome haplogroup in Upper Paleolithic Asian aurochs.

Chapter 6 investigates admixture between *Bos taurus* and *Bos indicus* in the Near East, analysing 67 ancient individuals across Western Asia, in a temporal context of 8000 years. PCA, ADMIXTURE analysis, *D*-statistics and *F*-statistics have confirmed admixture between *Bos taurus* and *Bos indicus* with a likely introduction of the latter during the Bronze Age, with continued admixture from then on, with the highest proportion of indicine in this dataset found in Medieval Iraq. Furthermore, it is demonstrated the power of whole nuclear genome data in detecting gene flow in comparison to haploid loci as well as the use of low coverage data to answer key questions of past population events.

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Firstly, I would like to thank my supervisor Dan Bradley, for allowing me to be part of his lab and part of this project. I am truly grateful for the opportunities to grow as a young scientist and for the guidance and support over the years.

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1. Introduction

1.1. Setting the stage for farming and animal husbandry

In the Late Pleistocene the Near East was inhabited by hunter-gatherers. Ancient Anatolia and Iran were mostly occupied by mobile hunter-gatherers, whereas the Tigris-Euphrates and the Nile regions were occupied by semi-sedentary groups (Bar-Yosef 1998). The Mediterranean Levant was an important region in the period that preceded the Agricultural Revolution - the transition from hunting to farming. In this region, a variety of landscapes were present, from mountains (southern side of the Taurus Mountains in Turkey) to the sea coast of the Mediterranean. Furthermore, this region was rich in game like gazelle, wild cattle, fallow deer and wild boar (Bar-Yosef 1998). Climate changes in the area also played a crucial role in human lifestyle. The cold and dry conditions of the end of Last Glacial Maximum around ~13,000 cal. BC (calibrated years BC) were followed by higher precipitation levels and the subsequent colder Younger Dryas period (~11,000-9,600 cal. BC) (Arbuckle 2012a). The latter was a colder and drier interval in which forests that had expanded with the increasing rainfall give way to wild grass. This, in addition to increase in sea level and higher precipitation levels, were the perfect environmental catalysts for the transition into an agricultural lifestyle (Bar-Yosef 1998; Zeder 2011; Cunliffe 2015).

1.2. The first farmers

With the change in climate, came changes in hunting strategies and also a more sedentary lifeway. The Late Epipalaeolithic in the Levant is described as the Natufian culture: sedentary hunter-gatherers that practiced some control of wild animals. The Natufian period was followed by two Aceramic or Pre-pottery periods. The first, Pre-Pottery Neolithic A (PPNA) (~9,500-8,700 cal. BC) was characterised by sedentary

communities that were cultivators of wild cereals and legumes. These communities were larger than the Natufians and had more complex societies (Vigne 2011; Arbuckle 2012a). The Pre-Pottery Neolithic B (PPNB) (~8,700 cal. BC) was characterised by the domestication of plants and of intensive livestock management (Arbuckle 2012a). In fact, animals such as cattle, sheep, goats, pigs and fallow deer were already being transported to the Island of Cyprus as early as ~8,500 BC, which demonstrates the already advanced knowledge of these populations on how to manage and transport these animals (Vigne 2011; Zeder 2011).

1.3. Domestication of animals

Animal domestication is still a highly debated topic. This includes: its definition, the key regions of where it might have happened, the time it took and the characterisation of a domesticated animal, whether genetical and/or morphological. It is agreed, however, that the path to domestication was a slow and complex process that was not always successful and that typically started with some control of wild animal populations, slowly progressing into capturing animals and controlling them in captivity, followed by extensive and intensive breeding (Vigne 2011). Moreover, domestication is a process that can have profound effects on the evolutionary paths of both the domesticated and the domesticator (Zeder 2015). A definition of domestication has been proposed by Zeder (2015): "*Domestication is a sustained multigenerational, mutualistic relationship in which one organism assumes a significant degree of influence over the reproduction and care of another organism in order to secure a more predictable supply of a resource of interest, and through which the partner organism gains advantage over individuals that remain outside this relationship, thereby benefitting and often increasing the fitness of both the domesticator and the target domesticate*."

There are many fields dedicated to the study of animal domestication and signals of domestication of animals and plants come from many sources. Changes in diet and the

use of secondary products from domestic animals is evident from organic residues preserved in pottery or from isotope analysis of human and animal remains (Vigne & Helmer 2007; Evershed *et al.* 2008). For example, evidence for milk consumption in the Near East and southeastern Europe has been shown from lipid residues preserved in pottery vessels (Evershed *et al.* 2008).

Archaeozoology is the field of archaeology that looks at animal skeletal remains and it has been essential to the study of animal domestication. The direct analysis of animal remains is perhaps the most widely used approach to look for evidence of domestication, by which zooarchaeologists are able to distinguish wild from domestic species based on bone morphology; for example, using the assumption that there is a rapid reduction in body size from wild to domestic. However, this has been subject to much debate; it might be hard to morphologically distinguish between wild and early domestic populations (Helmer *et al.* 2005; Zeder 2008). Furthermore, morphometric analysis of skeletons are able to inform on size, sex and age of death, which can be a reflection of human practices (Vigne 2011).

1.4. The importance of cattle

Domestic cattle have played important and extensive roles in human life for thousands of years and across continents. From being a source of animal products (dairy, meat, leather), to being a source of traction for plowing and pulling. They have also been described as symbols of wealth and elites, as well as being considered sacred beings in Hindu culture, for example (Arbuckle 2014). In the ancient world, in Mesopotamia, they were highly associated with gods and were heavily represented in iconography, as well as represented in elite burials. In the Roman period both domestic bulls and wild aurochs were used in rituals, serving as trophies, specifically skulls and the horns (Grant & Sauer 2006). Today, they are part of one of the biggest industries in the world and are still central to many world economies and play an important role in society. For example, in

Africa, cattle are not only a source of food and force, but are also highly associated with social status (Kim *et al.* 2017). In addition, their genetic development is now highly associated with technological advances; they have been replaced by tractors and their draught purpose in agriculture has been reduced in importance relative to milk and beef production. Advances in genetic methods have also enabled farmers to select for specific traits, using molecular approaches. On the other hand, this has also led to cattle breeders focusing on highly productive breeds, which are typically less genetically diverse relative to landraces, which are less productive but of generally higher genetic diversity (Felius *et al.* 2014).

1.5. The "ancient" world of Genomics

A lot has changed in the ancient DNA (aDNA) field in the more than three decades since the first ancient DNA research paper was published (Higuchi *et al.* 1984). Dramatic changes have included not only in DNA extraction techniques, but also the type of starting bone material favoured (Gamba *et al.* 2014), the target genetic material (from mitochondria to full genomes) and the molecular approaches for obtaining such material (from PCR-based to ultra high throughput shotgun and capture-facilitated sequencing). Moreover, the dramatic decrease of sequencing costs associated with an increase in output data has enabled an unprecedented accumulation of sequencing data belonging to ancient organisms (Mardis 2011; Leonardi *et al.* 2017). This growth has put a strain on computational resources and bioinformatic approaches and aDNA has entered the realm of statistical genomics. For the field of ancient DNA this meant developing software or bioinformatic tools to better deal with the specific nature of ancient DNA. Such tools include adapted pipelines and programs for ancient DNA and low coverage data like PALEOMIX (Schubert *et al.* 2014) and ANGSD (Korneliussen *et al.* 2014), DNA damage pattern detection tools such as mapDamage (Ginolhac *et al.* 2011) and, more recently, programs that not only recognize post mortem damage but which also take it into

consideration for downstream analysis and variant calling, giving higher confidence in the resulting inference (Kousathanas *et al.* 2017).

Post-mortem, DNA is no longer subject to repair mechanisms present in a cell and therefore it will tend to accumulate damage in its structure and its chemical composition. Typically, ancient DNA is characterized by being fragmented due to the combined action of nucleases and microorganisms, resulting in fragment sizes of on average between 50-70 base pairs in length (Pääbo *et al.* 2004; Stoneking & Krause 2011). This, however, is an advantage when it comes to high throughput sequencing methods, which require short fragments as a starting material for sequencing libraries. Moreover, by neglecting the artificial shearing of DNA we are less likely to sequence modern contaminants as they will be comprised of longer fragments.

Additionally, the amount of DNA from the target organism (endogenous) is present at much lower quantities, and in many cases exogenous DNA (microbial, environmental and any other contaminating sources *post-mortem*) constitutes the majority of DNA content in an archaeological sample (Stoneking & Krause 2011). Another common and important damage characteristic of aDNA is cytosine deamination, in which cytosine residues are turned into uracils caused by a loss of an amino group; consequently resulting in the incorporation of an incorrect base during DNA synthesis (C->T, G->A substitutions). Oxidative damage and DNA crosslinking have also been described as other types of damage common to ancient DNA (Pääbo *et al.* 2004).

Together, advances in laboratory methods for ancient DNA and bioinformatic/statistical approaches have led to an increase in the number of available whole genomes, comprising both whole mitochondrial genomes and more recently complete nuclear genomes at relatively high coverage. Furthermore, even though archaic hominins and humans remain the main focus of ancient DNA studies (Green *et al.* 2010; Reich *et al.* 2010; Meyer *et al.* 2012; Fu *et al.* 2014; Gamba *et al.* 2014; Jones *et al.* 2015; Martiniano *et al.* 2016), considerable effort and interest in ancient animals, plants and

pathogens have resulted in sequencing many organisms that one way or another have had a high impact on human life and vice-versa (Orlando *et al.* 2013; Giguet-Covex *et al.* 2014; Skoglund *et al.* 2015; Park *et al.* 2015; Frantz *et al.* 2016; Bos *et al.* 2016).

1.5.1. Bone as a source for ancient DNA

Bone, just like any living tissue, contains cells and blood supply, making it possible for it to grow in size, to be modified and to be repaired. The bone matrix comprises two main parts: organic and inorganic. The inorganic part of the bone is mainly constituted by hydroxyapatite; while the organic part of the bone is mainly made up of Type I collagen. It has been proposed that adhesion of DNA to the mineral fraction (hydroxyapatite) is possible and that DNA can also equally bind to the organic fraction (collagen). Nonetheless, how DNA is preserved in the bone is still debated and the amount of DNA that can be recovered from any given ancient sample is highly variable. Nevertheless, there are certain conditions known to influence DNA preservation in ancient bones. For example, temperature, proximity to free water or oxygen, the characteristics of the soil (pH, salt) and exposure to radiation. It is also generally accepted that samples originating from higher latitudes or permafrost often contain higher percentages of endogenous DNA, in comparison to temperate and tropical climates (O'Connor 2008; Campos *et al.* 2012).

Furthermore, the type of bone being sampled has also been shown to be a major determinant in preservation of endogenous DNA, the *Pars petrosa ossis temporalis* or the petrous part of the temporal bone (Gray 1918). This bone, one of the densest bones in the mammalian body, has been shown to be extremely good in preserving ancient DNA, even out-performing skeletal elements like teeth, which have also been regarded as good reservoirs for ancient DNA (Gamba *et al.* 2014; Hansen *et al.* 2017).

1.6. Cattle Genetic Diversity

1.6.1. The domestication of Bos taurus and Bos indicus

Modern cattle were domesticated from aurochs (*Bos primigenius*), which were widespread, consisting of three different races/subspecies: *Bos primigenius primigenius* (Eurasia), *Bos primigenius namadicus* (South Asia) and *Bos primigenius mauretanicus* (North Africa) (Grigson 1980). It is generally accepted that there were two main centres of domestication for cattle, the Near East and Southern Asia, giving rise to the two taxa of domestic cattle of today: taurine cattle (*Bos taurus*) and indicine cattle (*Bos indicus*), respectively (Loftus, MacHugh, Bradley, *et al.* 1994). These domestication events have not only been supported by archaeology but have also been supported by genetic studies on modern and ancient cattle (Troy *et al.* 2001; Zeder 2008; Chen *et al.* 2010). Archaeological evidence points the domestication of *Bos taurus* to the Taurus Mountains around 8,500 BC with the movement of domestic animals into Europe by migrating farmers at around 5,000 BC mainly via two routes: a Danubian route and a Mediterranean route (Zeder 2008). The Indus Valley is generally accepted as the centre for *Bos indicus* domestication in Baluchistan from the local *Bos primigenius namadicus* around 6,500 BC after the introduction of domesticated crops from Western Asia about a millennium earlier (Grigson 1980; Loftus, MacHugh, Bradley, *et al.* 1994; Meadow 1993; Fuller 2006).

One of the most pressing questions with regards to the diffusion of the Neolithic culture through Europe is how this dispersal actually took place. One view contends that this diffusion occurred due to migrating farmers from the Near East who would have introduced this culture to European hunter-gatherers. Another contrasting view is the domestication of animals and plants and the adoption of animal husbandry and cultivation by the local hunter-gatherers (Tresset & Vigne 2011). Understanding the genetic history of extant and ancient cattle will play a role in understanding such questions. A single domestication event in the Near East would be consistent with the

first view, however, more than one domestication centres across Europe and other parts of the world, would be consistent with the second.

1.6.2. Genetic evidence for a dual domestication

The origin of these two subspecies has been debated over many years, although most support appears to be for dual domestication events from two different genetically distinct aurochs populations. A Near Eastern aurochs gave rise to the *Bos taurus* taxa (humpless taurine cattle), in Anatolia; and a South Asian aurochs gave rise to the *Bos indicus* (zebu/humped cattle) subspecies in the Indus Valley. This dual domestication has been consecutively supported by genetic evidence on mitochondrial DNA (Loftus, MacHugh, Bradley, *et al.* 1994; Bradley *et al.* 1996; Troy *et al.* 2001; Bollongino *et al.* 2006; Edwards, Bollongino, *et al.* 2007; Magee *et al.* 2007; Achilli *et al.* 2008; Achilli *et al.* 2009; Bonfiglio *et al.* 2010; Chen *et al.* 2010), Y chromosome (Bradley *et al.* 1994; Teale *et al.* 1995; Bradley *et al.* 1996; Hanotte *et al.* 1997; Hanotte *et al.* 2000; Edwards, Baird, *et al.* 2007; Pérez-Pardal, Royo, Beja-Pereira, Chen, *et al.* 2010), autosomal markers (MacHugh *et al.* 1997; Loftus *et al.* 1999; Murray *et al.* 2010) and high-density SNP data (Bovine HapMap Consortium *et al.* 2009; Porto-Neto *et al.* 2013; Decker *et al.* 2014; Upadhyay *et al.* 2017).

1.6.3. Mitochondrial DNA variation in cattle

A deep bifurcation in the mitochondrial phylogeny in cattle was described as the first evidence for two independent domestication events. Two highly divergent lineages were described for taurine and indicine cattle: T and I. These are estimated to have diverged over 300,000 years ago (Loftus, MacHugh, Bradley, *et al.* 1994; Achilli *et al.* 2009).

The T haplogroup in *Bos taurus* can be divided into five previously described sub-haplogroups: T1, T2, T3, T4 and T5 (Troy *et al.* 2001; Achilli *et al.* 2009) and although they represent the major haplogroup in taurine cattle, others have also been described.

For example haplogroups Q, R have been observed in modern Italian and Egyptian breeds and ancient Southeastern Europe cattle (Achilli *et al.* 2008; Achilli *et al.* 2009; Olivieri *et al.* 2015; Scheu *et al.* 2015) and haplogroup C has been reported in an ancient Chinese *Bos primigenius* individual as well as in aurochs divination bones (Zhang *et al.* 2013; Brunson *et al.* 2016). The most common sub-haplogroup in European cattle is by a large margin T3, which is also present in the Near East. It is generally accepted that this, together with the higher variability of mitotypes in the Near East, supports the Near East as a centre for domestication of *Bos taurus*, with subsequent loss of diversity as animals moved into Europe. Moreover, starlike phylogenies from reduced median network analysis are consistent with a past population expansion (Troy *et al.* 2001).

The African continent shows T1 as the predominant haplogroup, which is very rare elsewhere, including the Fertile Crescent. This has been previously described as possible evidence for a separate domestication event in Africa (Bradley *et al.* 1996). Furthermore, the identification of T1 outside of Africa, in Southern Europe (Italy and the Iberian Peninsula) could reflect a later migration of cattle from Africa, corresponding to historical events like the Moorish occupation of the Iberian Peninsula, for example (Cymbron *et al.* 1999; Troy *et al.* 2001). However, this African domestication event has been challenged by complete mitochondrial sequence data, in which the coalescence times and poor sequence variation of haplogroup T1 supports a single Near Eastern origin for the all T mitochondria (Achilli *et al.* 2008; Achilli *et al.* 2009; Bonfiglio *et al.* 2010; Bonfiglio *et al.* 2012).

In addition, the haplogroup T4, has also been suggested as another possible centre of domestication in East Asia in that it is found in Chinese, Korean, Siberian and Japanese breeds but not in western Asia or the European continent (Mannen *et al.* 2004; Lai *et al.* 2006; Kim *et al.* 2016). However, the possibility of a domestication in East Asia has been proposed to be highly unlikely by further studies on ancient and domestic mitochondrial DNA from East Asian cattle, which suggest that East Asian cattle are an import from the

Near East and could have possibly have been introduced into domestic lineages by aurochs hybridization upon the Eastern migration (Mannen *et al.* 1998; Decker *et al.* 2009; Kantanen *et al.* 2009; Cai *et al.* 2014).

Mitochondrial DNA diversity has also revealed a predominance of haplogroup P in Eurasian aurochs (Troy *et al.* 2001; Edwards, Bollongino, *et al.* 2007; Edwards *et al.* 2010). However, this was not exclusive and an unusually robust German aurochs has been shown, based on partial mitochondrial DNA sequence, to belong the novel haplogroup E, which indicates greater genetic variability during the Pleistocene (Edwards, Bollongino, *et al.* 2007). Furthermore, and surprisingly, T mitochondrial DNA sequences have been found in aurochs from Italy, which challenge the view of a single Near Eastern-domestication event for European cattle and arguably local domestication events have been proposed to have occurred in the peninsula (Troy *et al.* 2001; Beja-Pereira *et al.* 2006).

Effort has been put into sequencing whole mitochondrial genomes from both ancient taurine cattle (Achilli *et al.* 2008; Achilli *et al.* 2009) and wild aurochs (Edwards *et al.* 2010). These have revealed previously unknown mitochondrial DNA haplogroups, such as haplogroup Q and haplogroup R (Achilli *et al.* 2008; Achilli *et al.* 2009). The Q haplogroup has been proposed as having a Near Eastern origin and it has been found in modern Italian and Egyptian breeds (Achilli *et al.* 2008; Achilli *et al.* 2009; Bonfiglio *et al.* 2010; Olivieri *et al.* 2015) as well as Near Eastern ancient domestics (Scheu *et al.* 2015); whereas the origin R haplogroup remains debatable (Bonfiglio *et al.* 2010).

For *Bos indicus*, the majority of mtDNA sequences belong to the I haplogroup and two sub-haplogroups have been described: I1 and I2 (Chen *et al.* 2010). Higher genetic diversity in the Indus Valley has shown support for this as the centre of domestication, in resemblance to the Near East and taurine mtDNA (Troy *et al.* 2001; Magee *et al.* 2007; Chen *et al.* 2010). Furthermore, the presence of only two very closely related haplogroups would mean that very little variation has been accumulated through time and that the ancestral matriline that was domesticated had very little genetic diversity (Magee *et al.* 2014).

1.6.4. The Y chromosome

There has not been extensive research focusing on producing complete sequences on the other uni-parentally inherited chromosome: the Y chromosome. The Y chromosome is more difficult to retrieve from ancient samples given that it is part of the nuclear genome, in addition to being present in only half of samples. Therefore, studies have mainly focused on a few key single nucleotide polymorphisms or microsatellites (Bradley *et al.* 1994; Hanotte *et al.* 2000; Hanotte *et al.* 1997; Anderung *et al.* 2007; Ginja *et al.* 2009; Ginja *et al.* 2010; Edwards *et al.* 2011; Li *et al.* 2013). Three Y chromosome haplogroups have been described: Y1, Y2, Y3. The latter, Y3, being the only haplogroup found in the Indian subcontinent and well represented in African cattle - likely reflecting male-mediated past admixture events (Bradley *et al.* 1994; Teale *et al.* 1995; Bradley *et al.* 1996; Hanotte *et al.* 1997; Hanotte *et al.* 2000; Gotherstrom *et al.* 2005; Edwards, Baird, *et al.* 2007; Bollongino *et al.* 2008; Pérez-Pardal, Royo, Beja-Pereira, Chen, *et al.* 2010). Whereas, Y1 and Y2 are typically found in taurine animals: Y1 at higher frequencies in Northern Europe and Y2 at higher frequencies Central, Mediterranean and Iberian breeds (Gotherstrom *et al.* 2005; Edwards *et al.* 2011).

1.6.5. Autosomal markers and high-density SNP

Autosomal microsatellite markers have supported the divergence times for *Bos taurus* and *Bos indicus*, albeit with some slight differences in estimates that can be accounted for by error estimates or different evolutionary dynamics (MacHugh *et al.* 1997). Moreover, modelling demographic history from autosomal sequences from 17 genes in extant cattle from Eurasia and Africa has supported the divergence time for *taurus* and *indicus* wild ancestors at around 280,000 years ago (Murray *et al.* 2010); and high-density SNP data has also been able to demonstrate this divergence and to elucidate on patterns of admixture between the two taxa (Decker *et al.* 2014; Karimi *et al.* 2016).

1.6.6. Improvement of modern cattle datasets and the 1000 Bulls Genomes Project

Finally, the scale of available modern cattle whole genome sequence data has also been rapidly increasing. One important project has been the 1000 bull genomes project which is compiling a sequence variance database from modern cattle breeds in order to pinpoint genetic changes that might influence animal health and production. The whole genomes of 234 bulls have been released and with them the mapping of the recessive mutation for embryonic lethality and dominant mutation causing lethal chondrodysplasia, clearly demonstrating the potential of such genome projects (Daetwyler *et al*. 2014).

2. Materials and Methods

2.1. Archaeological samples

For this project a total of 250 bone samples have been drilled, DNA extracted and sequenced for preliminary endogenous DNA content estimation. A table summarizing these can be found in the Appendix Table 9.1.7. For each chapter a subsection of these with sufficient endogenous DNA content is presented. Most bones sampled were petrosal bones, which are part of the temporal bone and that have been shown to yield significantly higher endogenous DNA content than any other bone (Gamba *et al*. 2014). Some other bone types have also been sampled, mainly astragalus and teeth.

2.2. Sampling bones

All samples were dealt with in a designated clean and separate laboratory at Trinity College Dublin. Upon arrival, samples were photographed and given a Lab ID for easier handling in the subsequent molecular approaches. After that samples were exposed under UV light for 20 minutes on each side of the bone in a clean flow hood. Times for UV exposure are specified in Table 2.1 for the different types of samples. Following UV exposure samples were either kept in the fridge in clean and labelled bags or were processed immediately. For each sample, new and clean conditions/material were used as is typical for good ancient DNA practice. Clean conditions were maintained by cleaning surfaces and material with bleach, DNA-exit plus and ethanol, in that order, followed by a UV exposure of material for 30 minutes on each side, before being stored in clear, new and labelled plastic bags.

Firstly, cleaning of the surface of the bone was done using a drill bit with the Maxima Micro-Drill. After, mechanical cleaning the bone was again exposed to UV light for a further 5-10 minutes on each side (Table 2.1). Secondly, a sample of the bone was cut

using a saw with a Maxima Micro-Drill; bone piece(s) were powdered using a mixer mill (MM400, Retsch) and bone powder kept in new and labelled 2ml Eppendorf® tubes for extraction (0.120-0.150g) and spare. For each drilling session/day water and air controls were taken and put through the molecular protocol for sequencing.

Table 2.1 - UV times. UV times for different types of starting material, before and after cleaning the surface.

Sample type	UV exposure before drilling (minutes/side)	UV exposure after cleaning (minutes/side)
Long bone (non petrous)	20-25	15-20
Petrous bone	20-25	5-10
Tooth	20-25	5-10

2.3. Radiocarbon Dating

Sampling of approximately 2.0g of fresh bone and dating was done at Beta Analytic (http://www.radiocarbon.com/) or at ^{14}CHRONO at Queen's University Belfast (http://www.chrono.qub.ac.uk/). Calibration curve plots produced by OxCal (Ramsey 2009).

2.4. Bone powder DNA extraction

DNA extraction was carried out as described in Gamba *et al.* 2014, with minor modifications for better yield of endogenous content, which will be described. A 1 mL extraction buffer comprised of 0.5M EDTA pH8, 1 M Tris-HCl, 2% sodium dodecyl sulphate, and 100 μg/mL proteinase K was used to dissolve bone powder. Extraction buffer was exposed to UV light for 30 minutes before adding proteinase K. The mixture of bone powder and extraction buffer was briefly vortexed and incubated for 24 hours at 37°C, with gentle mixing in an Eppendorf ThermoMixer®.

Following the incubation period, samples were spun at 10,000 rpm (except in the final step at 13,300 rpm) for 10 minutes and the supernatant was kept in new 2mL Eppendorf® tubes in the freezer unless DNA purification was done immediately. After the first 24 hours, 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. These 24 hour incubations were done 2 times for 0.100-0.120g or 3 times for ≥0.150g of bone powder, the last supernatant being the highest in endogenous DNA content. A Tris-EDTA wash was done by transferring 1 mL of supernatant to Amicon® Ultra 4 mL filter (Merk Millipore) and adding 3 mL of 1X Tris-EDTA (previously exposed to UV light for 30 minutes). Each sample was then centrifuged at 2500 rpm until reaching the the filter's 250 μL mark, when a further 3 mL of 1X Tris-EDTA was added to the column, followed by another centrifugation at 2500 rpm until the 100 μL mark was reached. 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).

2.4.1. USER™ treatment

Following extraction, each 16.25 μl of purified DNA was used for treatment with 5 μl USER™ enzyme (New England BioLabs®, Inc.) and incubated for 3 hours at 37°C followed by immediate freezing or a Blunt End Repair step. The USER™ enzyme mix is a mixture of Uracil DNA-Glycosylase (UDG) and DNA glycosylase-lyase Endonuclease VIII. Its application to ancient DNA is that UDG will remove the uracils, typically at higher frequency at the overhangs ends of molecules (5′ and 3′). This first enzyme creates abasic sites but leaving the phosphodiester backbone of the DNA molecule intact, while the endonuclease VIII will break the phosphodiester backbone at the abasic sites leaving 5′ and 3′-phosphate groups . These 5′ and 3′ overhangs are subsequently fixed in a blunt

end repair step that uses T4 polymerase and the kinase PNK, which means adapter ligation and adapter fill-in steps can be performed thereafter (Briggs *et al.* 2010).

2.5. Illumina® Next Generation Sequencing libraries

Following USER™ treatment, DNA libraries were prepared by following the Meyer and Kircher's protocol for Illumina® sequencing (Meyer & Kircher 2010) with some reagents substitutions and slight modifications. Briefly, this protocol starts with a blunt end repair step, followed by adapter ligation and adapter fill-in. Modifications on this protocol 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. Indexing PCR comprises the last step and each 25 μL PCR reaction 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.

2.6. Illumina® Next Generation Sequencing

DNA libraries were quantified either by using the Agilent 2100 Bioanalyzer High Sensitivity DNA kit or the Agilent Tapestation 2200. For endogenous DNA content screening, samples were pooled in equimolar concentrations and the pool was quantified again using the same methods plus a QuantiT dsDNA HS Assay kit (Invitrogen®). These were then sequenced on an Illumina® MiSeq at TrinSeq, the Trinity Genome Sequencing Laboratory, located in the Institute of Molecular Medicine (IMM). A PhiX genome library

was added as a sequencing control for each run. For deeper sequencing of samples with good endogenous content, libraries were quantified and/or pooled (depending on the sequencing strategy) at Trinity College Dublin and sent for sequencing at Macrogen, Inc. Korea, in Seoul, Republic of Korea, on an Illumina® HiSeq 2000.

2.7. Screening for Endogenous DNA

2.7.1. FastQ Screen

For samples where species determination was not clear from bone morphology, FastQ Screen was run on fastq files for species identification (Andrews 2011). FastQ Screen uses Bowtie/Bowtie2 or BWA (Langmead *et al.* 2009; Li & Durbin 2009) to align fastq files to a collection of user-defined genomes belonging to the species we would like to screen. This feature of FastQ Screen is also useful in quickly detecting high levels of human or animal contamination, if present, in cattle samples. So, it is an extremely useful tool for screening libraries prior to greater depth sequencing. Furthermore, it is also possible to get a rough estimate of endogenous DNA content if the species to which the specimen belongs to is present in the screening genomes. Consequently, and because typically samples are only aligned to the genome of the species being studied, FastQ screening allowed for identification of many more high quality specimens that would be discarded otherwise. An example of the graphical output that is possible from FastQ Screen is shown in Figure 2.1, where (A) shows a *Bos taurus* sample and (B) shows a sample assigned as a *Bos* specimen that screening returned as a horse. FastQ screen calculates the percentage of reads aligning to multiple genomes, or to a single genome. For species that will have high sequence similarity in their genomes, the percentage of a single or multiple reads aligning to multiple genomes will be higher if those species are present in the user-defined genomes for screening. An example of this is shown in Figure 2.1A, where species belonging to the *Bovidae* family (cow, sheep, goat, deer, tibetan antelope) are more similar to each other than the other species present.

Thus in this case the percentage of hits/reads aligning to a single genome are the defining measure for species identification.

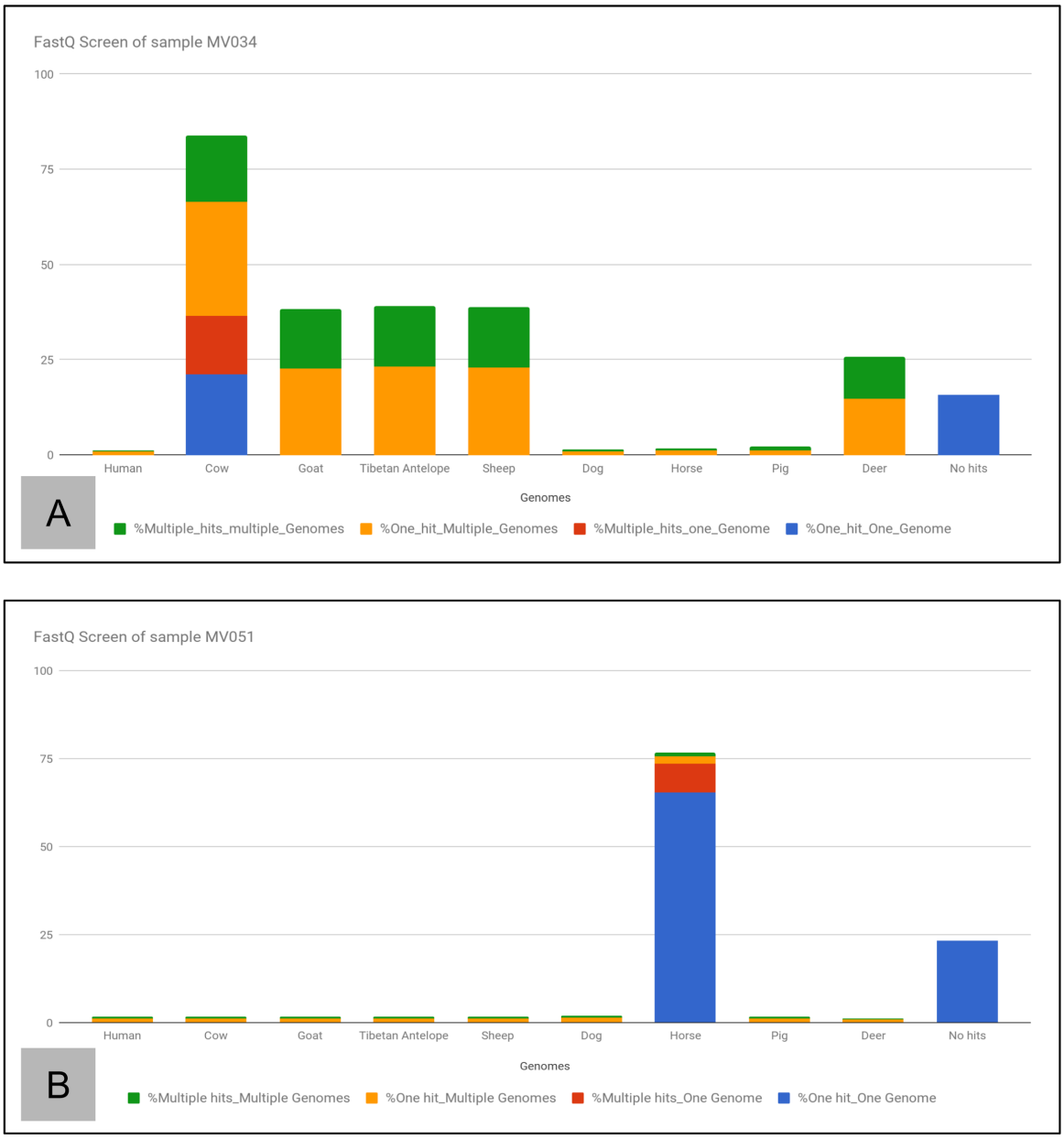


Figure 2.1 - FastQ Screen. (A) *FastQ Screen for sample MV034, and ancient cattle sample.* ***(B)*** *FastQ Screen for sample MV051 an ancient horse sample. Colours defining percentage of: multiple reads aligning to multiple genomes (green), one read aligning to multiple genomes (orange), multiple reads aligning to a single genome (red) or a single read aligning to a single genome.*

2.7.2 Quality control of high throughput sequencing

Quality control was done on raw data in fastq format using FastQC (Andrews 2011). FastQC: a quality control tool for high throughput sequence data. Available online at: http://www.bioinformatics.babraham.ac.uk/projects/fastqc).

2.8. Alignment of NGS reads to cattle reference genome

All raw reads were processed through a standardized pipeline adapted for this project. Adapters were removed using cutadapt (Martin 2011) (-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 (-0 1 option); and reads shorter than 30 base pairs in length were discarded (-m 30 option). The reference genome used for alignment was the BosTau6 reference genome (UCSC UMD3.1) with the addition of the Y chromosome from BosTau7 and mitochondria reference and designated as bos_genome_18_5_16.fa, created in house for the purpose of this project. Alignment was performed using the Burrows-Wheeler Alignment Tool (BWA) (Li & Durbin 2009) 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 BAM files (binary format of SAM files - Sequence Alignment/Map format). Indel Realignment was performed using the Genome Analysis ToolKit (GATK) (McKenna *et al.* 2010). BAM files were sorted using SAMtools (Li *et al.* 2009) and subsequently subjected to post-alignment filtering that included removal of PCR duplicates (*rmdup* -s), removal of unaligned reads (*view* -F4) and a filter for mapping quality of Q25 (*view* -q25). Furthermore, in order to minimize the effect of deamination in analyses, soft clipping was performed for 2 base pairs at the ends of reads, using an in-house python script (Victoria Mullin). The resulting BAM files were the input for most of the population genetic methods described. Quality control of

alignment sequencing data and coverage statistics were calculated using Qualimap (García-Alcalde *et al.* 2012).

2.8.1. Calculating Percentage endogenous DNA

Endogenous DNA content was calculated for each sample following sequencing on the Illumina Miseq and alignment described in Section 2.7. The percentage of endogenous DNA was calculated for all samples using the following formula:

(Reads aligned to *B.taurus genome* (Q25)x100) / (Total reads)

2.9. Sexing

Morphological methods for sex determination are quite successful in determining the sex of adult skeletons, however when it comes to sex-determination of juvenile skeletons or just parts of a skeleton such methods are much less powerful (Skoglund *et al.* 2013). Also, it is impossible to distinguish a female and male based solely on a petrous or temporal bone without any other skeletal element for comparison, which is the case for most excavated animal petrous bones. Previous genetic-based methods typically used PCR to amplify a fragment of the amelogenin gene, for example, by making use of sex-specific oligonucleotides in order to determine the sex of an ancient sample. However, such methods do not take into account the possibility of the presence of contaminating sequences that could lead into an erroneous sex determination (Stone *et al.* 1996; Skoglund *et al.* 2013). Sexing of all animals was done when sufficient reads were available, using a in-house Rscript that can predict the sex by linear regression (Eppie Jones & Russell Mclaughlin, unpublished). This method looks at the number of reads versus the length of the chromosomes. In theory, we would expect longer chromosomes to have higher number of reads and shorter chromosomes to have lower. A best fit line is drawn and

whenever a male animal is present its X chromosome should be an outlier because only one copy is present.

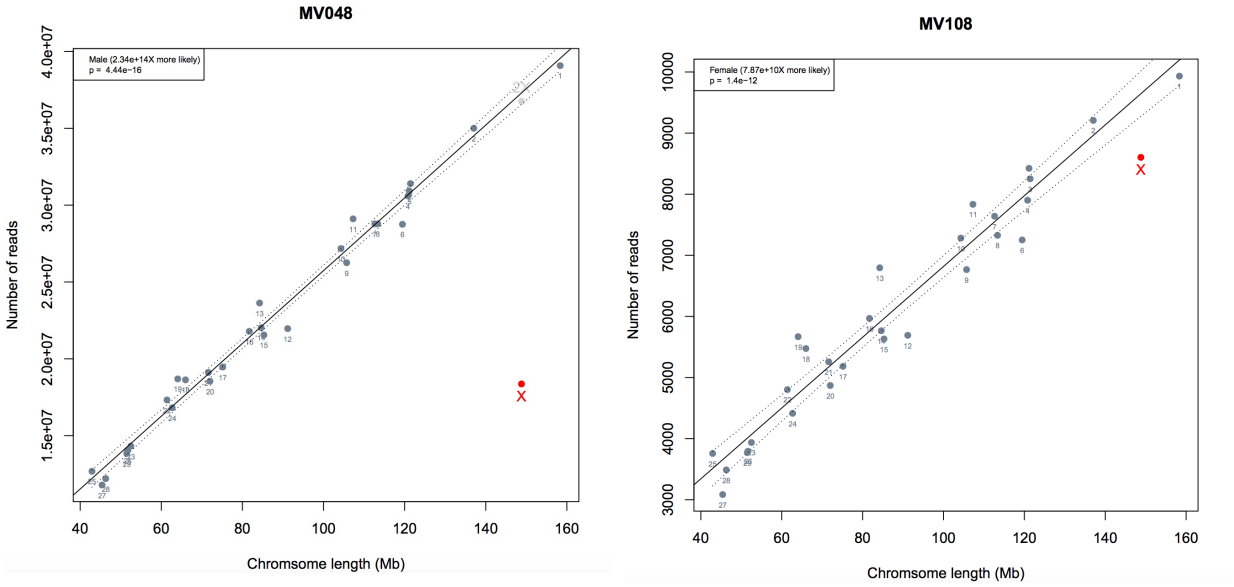


Figure 2.2 - Sexing of ancient animals. *Left plot showing a male individual. Right plot showing a female individual.*

2.10. aDNA damage patterns

As was previously mentioned, ancient DNA is structurally and chemically damaged. Although this presents a difficulty in assessing good quality bases and sequences, it also presents an advantage for ancient DNA authentication. In other words, damage patterns can be used to authenticate real ancient/endogenous DNA sequences. The method described below was applied to all ancient DNA samples.

Firstly, an advantage of high throughput sequencing over PCR is that the complete length of a single ancient DNA molecule may be sequenced. This has been used to identify deamination patterns, which are characteristic to the ends of reads (Briggs *et al.* 2007; Stoneking & Krause 2011). Therefore, when working with ancient samples it is advantageous to look for such patterns of damage in order to confirm the authenticity of

specific sequences as "ancient" and distinguish those from modern contaminating sequences (Jónsson *et al.* 2013). *mapDamage* is a Python software package that does this for next generation sequencing reads and uses a Bayesian statistical approach to provide estimates on average length of overhangs, nick frequency, cytosine deamination rates in double-stranded regions and cytosine deamination in overhangs; all typical of ancient DNA sequences. The pattern of cytosine deamination observed in ancient DNA, and while using the Meyer and Kircher (2010) library protocol, is that of increased cytosine deamination (C→ T substitution) at the 5'-end of sequencing reads and the complementary G→ A substitutions increase at the 3'-end. Figure 2.2 is an example of the plots produced by mapDamage showing the rates of cytosine deamination at both ends of the sequencing reads. In these figures there are shown two examples, one of an authentic ancient sample (A) and one corresponding to a modern cattle sample (B) (Meyer & Kircher 2010; Jónsson *et al.* 2013).

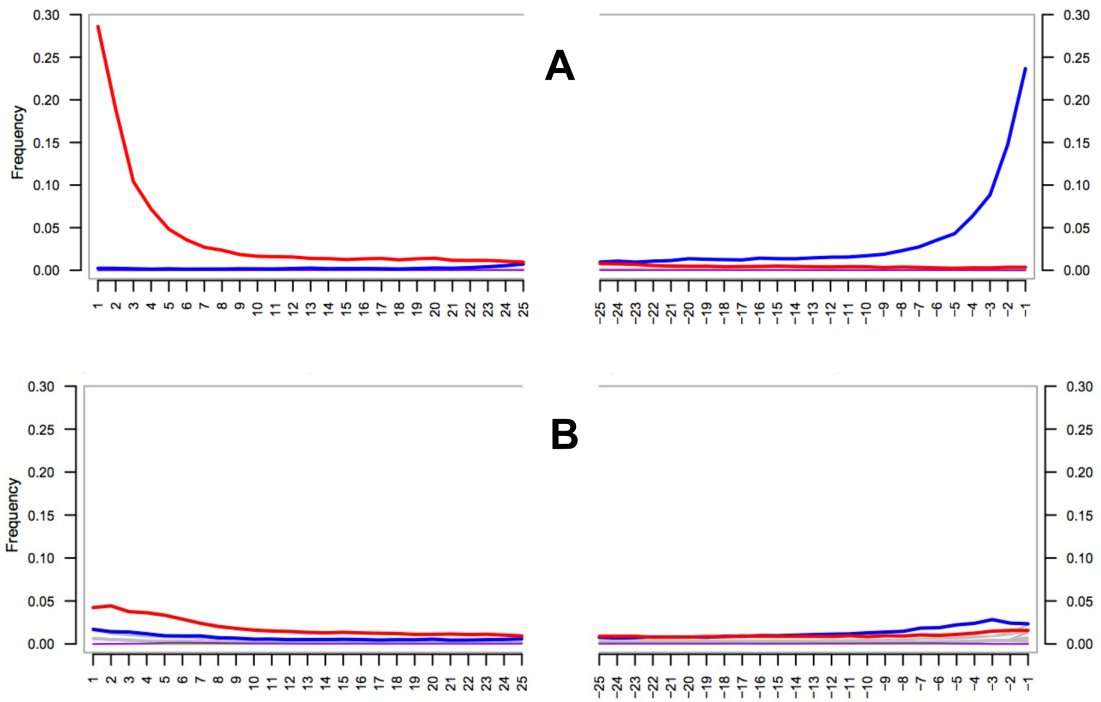


Figure 2.3 - mapDamage fragment misincorporation plots. ***(A)*** *example of a fragment misincorporation plot from an ancient samples, with the expected higher frequency deamination occurring at the ends of reads (C->T, at 5' end; G->A, at 3' end.* ***(B)*** *showing the same for a modern cattle sample, where deamination patterns are non-existent.*

2.11. Modern SNP Dataset curation

The modern SNP dataset used was the Illumina bovine 700K SNP chip data and was curated by Matthew Teasdale. This comprised a mix of in-lab samples (TCD) and the publicly available WIDDE dataset (Sempéré *et al.* 2015). WIDDE SNPs were flipped to forward strand and both TCD and WIDDE dataset merged with PLINK. 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 excluded. 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*) (Appendix Table 9.1.1). It is important to note that the 700K Bovine SNP dataset could imply some ascertainment bias towards European taurine breeds, which comprise the majority of breeds for SNP discovery, although some indicine and two outgroups (Yak, Gaur) were included.

2.11.1. Genotype Calling with 700K SNP dataset

SNPs were called with the Genome Analysis ToolKit (GATK) (McKenna *et al.* 2010) with the Pileup function and the 700K Bovine SNP data. Pileup files were then converted to plink format using an in-house script (available at: https://github.com/teasdalm/pileupTools) that converts into plink format by randomly picking a base in case of a tie, and filters for minimum base quality score of 30, excludes tri-allelic SNPs. Plink format files for ancient samples and the modern dataset (700K) were merged with PLINK (http://pngu.mgh.harvard.edu/purcell/plink/) (Purcell-2007).

2.12. Modern Genomes Dataset

A modern genomes dataset was produced by sequencing 15 *Bos* individuals. These comprised 9 *Bos taurus*, 4 *Bos indicus*, 1 *Bos gaurus* and 1 *Bos javanicus* individuals. A summary of these can be found in Table 9.1.3 in the Appendix. The mean coverage obtained for these was 26x. A set of publicly available genomes was also downloaded from EBI (http://www.ebi.ac.uk/ena). Both modern genomes datasets were curated using the same pipeline for consistency, which is described below. The reference genome used for alignment was the BosTau6 reference genome (UCSC UMD3.1) with the addition of the Y chromosome from BosTau7 and mitochondria reference and designated as bos_genome_18_5_16.fa, created in-house (Victoria Mullin) for the purpose of this project. Alignment was performed using the Burrows-Wheeler Alignment Tool (BWA) (Li & Durbin 2009) with the sub-command *aln* for both fastq.gz files of paired end sequencing data. Read groups were added using the BWA sub-command *sampe* with the -r option and converted into BAM format using the samtools *view* sub-command. Samtools *fixmate* was run to fill in mate coordinates and BAM files were subsequently filtered with samtools by including reads mapping in proper pair (-f2) and excluding reads where mate is unmapped (-F8). Files were sorted with samtools before removal of duplicates with *picard* (MarkDuplicates, with the option REMOVE_DUPLICATES set to True). Indel Realignment was performed using the Genome Analysis ToolKit (GATK) (McKenna *et al.* 2010). Quality control of alignment sequencing data and coverage statistics were calculated using *Qualimap* (García-Alcalde *et al.* 2012).

3. Population Genetic/Genomic Analyses: Concepts and Computational Approaches

3.1. Principal component analysis

As part of a preliminary screening process for interesting and relevant samples, Principal Component Analysis is useful to investigate population structure and can be a good indicator of the number of clusters, useful for cluster-based methods like ADMIXTURE (Patterson *et al.* 2006; Alexander *et al.* 2009a). It is a commonly used population genetics approach that uses genome-wide SNP data. It is able to reduce multidimensional data into fewer dimensions, in which axes are called principal components (PCs) or eigenvectors. The first two PCs represent the largest amount of variation and each subsequent PC explaining less of the variation within a dataset. PCA differs from Multidimensional scaling (MDS) approaches in that it calculates a covariance matrix based on raw genotypes rather than depending on genetic distances (Menozzi *et al.* 1978; Patterson *et al.* 2006; Jobling *et al.* 2014).

3.1.1. Procrustes Projection PCA

The 700K Bovine SNP chip data was used in LASER, which needs whole genome SNP genotypes from a set of reference individuals. Principal component analysis was done on the basis of Procrustes analysis using LASER (Version 2.03) (Wang *et al.* 2010; Wang *et al.* 2015). Due to the varying percentages of surviving endogenous DNA in ancient specimens, high coverage genomes are not always possible to achieve and therefore such methods can be highly valuable to ancient DNA. LASER 2.0 takes a dataset of reference individuals, which in this case were the 700K Bovine SNP chip dataset, for which genotype data is available.

It runs a projection Procrustes analysis, which allows the integration of a higher number of usable loci (from the reference data) for the study samples. Furthermore, it analyses each sample individually and it is projected onto the reference PCA space, whereas typical PCA approaches analyse all samples together. This is thus highly valuable for low endogenous/low coverage samples (Wang *et al.* 2015). The 700K reference dataset was formatted to the LASER input format by Matthew Teasdale. 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 and a minimum base quality of 20. Input files for LASER were then generated using the pileup2seq.py python script (available with the software package).

3.2. ADMIXTURE analysis

ADMIXTURE analysis is an unsupervised model-based clustering method and was performed on the 700K bovine SNP chip data (Alexander *et al.* 2009a). Put simply, this analysis asks to which population does an individual belong, and this is achieved by estimating the maximum likelihood of individual ancestries from a SNP dataset. Genetic similarity will then group individuals into K number of clusters, so that individuals belonging to the same cluster will be more similar to each other than to individuals outside that cluster (Alexander *et al.* 2009a). In cattle studies, K=3 is typically used, which distinguishes between indicine, African taurine and European taurine cattle. Higher numbers of K in cattle might be difficult to interpret because they will most likely represent breed variation, which is not useful when looking at ancient cattle.

For analyses including data of very low coverage only minimal filtering of the data was done in order to maximize the number of variants for analysis.

However, a linkage disequilibrium (LD) pruning step was always applied in order to remove markers in strong LD because the ADMIXTURE model does not take LD into consideration and recently admixed populations will have a higher degree of admixture LD (Alexander *et al.* 2009a). Pruning for LD was done in Plink (Purcell *et al.* 2007) with the command --indep-pairwise 200 25 0.5 to account for linkage disequilibrium between markers. The maximum likelihood estimation of individual ancestries was run for K=1 to K=5, for 200 replicates. Hereford animals were removed (to minimize biases towards the reference), on a pseudo-diploid dataset, to accommodate for the low coverage samples, and with transitions removed to account for damage in samples that were either only partially or not USER treated.

3.3. *D*-statistics

To formally test admixture, *D*-statistics were used on these samples using both the AdmixTools package and the ANGSD *-doabbababa* program (Patterson *et al.* 2012; Korneliussen *et al.* 2014).

Patterson's *D*-statistic is four-genome comparison where a test population's relative genetic closeness is compared to two other reference populations (ref1 and ref2) (Figure 2.3). If no gene flow has happened then we would expect the *D*-statistic to be zero (Null hypothesis); positive if there is gene flow between test and ref2 (ABBA tree); negative if there is gene flow between test and ref1 (BABA tree) (Patterson *et al.* 2012). A block Jackknife is used to obtain standard error on the *D*-statistic, which can then produce a *Z*-score giving statistical significance if $|Z|>3$ (Reich *et al.* 2009; Haak *et al.* 2015).

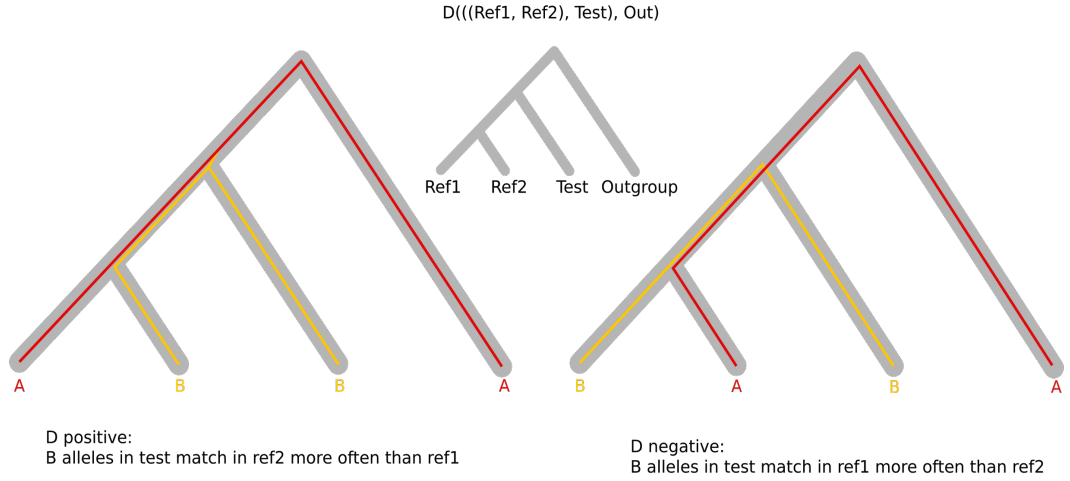


Figure 3.1. - D-statistic. *Showing the two trees expected when there is a significant deviation of the D-statistic from the Null Hypothesis of no gene flow. A for ancestral alleles, B for derived alleles. On the left, if the D-statistic is positive we expect an ABBA tree, where B (derived) alleles of test match the alleles in Ref2 more often than Ref1. On the right, if the D-statistic is negative we expect a BABA tree, where B alleles in test match Ref1 more often than Ref2.*

3.3.1. AdmixTools

The AdmixTools (Patterson *et al.* 2012) package to compute *D*-statistics was used with the 700K Bovine SNP data. *D*-statistics are calculated for any 4 populations (W,X,Y,Z) using the *qpDstat* program where w,x,y,z are population or sample allele frequencies and:

$$D = \text{numerator} \ / \ \text{denominator}$$

with

$numerator = (w - x)(y - z)$

$denominator = (w+x - 2wx)\ (y + z - 2yz)$

Given these four populations (W,Y,X,Z), if the Z-score is positive then, gene flow has occurred either between W and Y or X and Z; and if the Z-score is negative then gene flow has occurred either between W and Z or X and Y.

The AdmixTools package (Patterson *et al.* 2012) was used as per manual instructions with transitions removed and pseudodiploid individuals created by picking a read at random at each site and setting that individual is homozygous at a given allele, as standard approach in ancient DNA (Skoglund *et al.* 2016). The significance of Z-scores were set at |3| for this statistical test as it is common practice (Green *et al.* 2010; Reich *et al.* 2010; Skoglund *et al.* 2016).

3.3.2. ANGSD

D-statistics were also computed using the ANGSD software in order to compare results for ancient DNA samples. ANGSD is able to take BAM files as input and perform the ABBA/BABA calculations directly by sampling a single base at each position in the genome and therefore does not rely on called genotypes. In cases of dealing with very low coverage data, it is supposed to minimize biases due to differences in coverage among samples (Korneliussen *et al.* 2014). The ANGSD program was used to perform the *Abbababa* (*D*-statistics) test on whole genome sequences directly from BAM files as per manual's instructions (available at: http://www.popgen.dk/angsd/index.php/ANGSD) (Korneliussen *et al.* 2014). The computation of D is based on the following equation previously defined by Green *et al.* (2010): D = (nABBA-nBABA)/ (nABBA+nBABA)

ANGSD was run with the -doAbbababa 1 command, with transitions removed from the analysis to account for ancient damage (-rmTrans 1); with a filter of minimum base quality of 20 (-minQ 20) and of minimum mapping quality 25 (-minMapQ 25). The jackknife estimator was run with default settings. The significance of Z-scores were set at |3| for this statistical test as it is common practice (Green *et al.* 2010; Reich *et al.* 2010; Skoglund *et al.* 2016).

3.4. *F*-Statistics

3.4.1. f_4-ratio estimation

The f_4-ratio (Reich *et al.* 2009) is a similar test for admixture as the *D*-statistic in that it is a test for admixture but differs in that it can estimate admixture proportions when the tree topology we are testing is correct. An advantage of this statistical method is proportions can still be calculated even when the true ancestral populations for the admixture event are not available (Durand *et al.* 2011; Patterson *et al.* 2012). To calculate f_4-ratios the AdmixTools package was used with the 700K Bovine SNP modern dataset and run only on transversions and as per manual's instructions (Patterson *et al.* 2012). The significance of Z-scores were set at $|3|$ for this statistical test as it is common practice (Green *et al.* 2010; Reich *et al.* 2010; Skoglund *et al.* 2016).

3.4.2. f_3-statistics

Another formal test of admixture that is commonly used is called the f_3-statistic or the 3-population test (Reich *et al.* 2009; Patterson *et al.* 2012). Reich *et al.* (2009) describes this statistic as "a 3-population generalization of *FST*". The tree below shows an hypothetical tree, where target C' population is formed by two source populations A' and B'. And these three populations are then affected by genetic drift giving rise to modern populations A, B and C. In order to calculate the expected value of F_3, the average/mean over all genotyped sites is given for the product of allele frequency differences between C and A, and C and B (Figure 3.2).

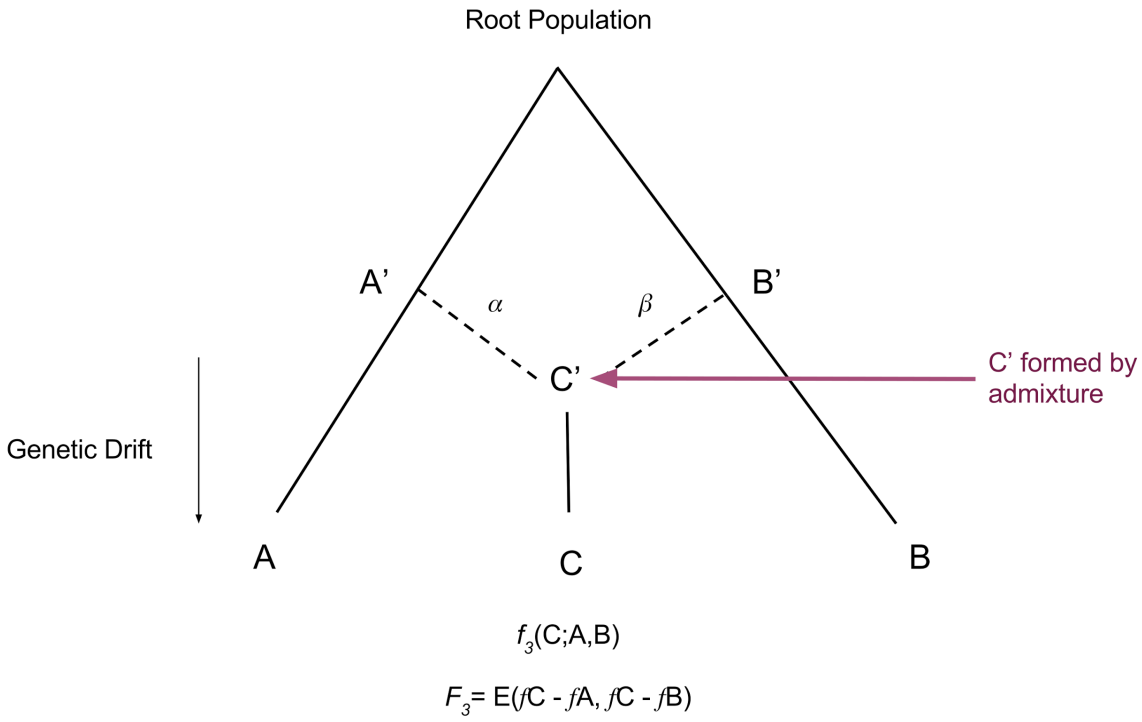


Figure 3.2 - f_3-statistic tree. *Figure redrawn and adapted from Reich et al. 2009.*

As defined by Reich *et al.* (2009) if population C has arisen without any admixture the expected f_3 value should be positive, whereas if population C is the product of an admixture event with subsequent drift the expected F_3 should be negative. Therefore, when a significantly negative F_3 value is observed it will be considered a signal for admixture. Therefore, using the AdmixTools package given the test f_3 (C;A,B), if the statistic yields a non-negative mean we consider C to be unadmixed. On the contrary, if the f_3-statistic results in a negative mean we interpret as C being admixed with populations A' and B' (Figure 3.2). The program was run as per manual instructions and with default settings and significance of Z-scores were set at |3| for this statistical test as it is common practice (Green *et al.* 2010; Reich *et al.* 2010; Skoglund *et al.* 2016).

3.4.3. Outgroup f_3

Outgroup f_3 is a three-population test, that like other f-statistics is based on allele frequency comparisons between populations. This statistic can be used to test two different things: admixture or shared drift. For the first f_3 tests whether a target population C is admixed by two source populations A and B. In the second, f_3 measures the genetic drift shared between populations A and B from an outgroup C (Patterson *et al.* 2012; Raghavan *et al.* 2014). The significance of Z-scores were set at |3| for this statistical test as it is common practice (Green *et al.* 2010; Reich *et al.* 2010; Skoglund *et al.* 2016).

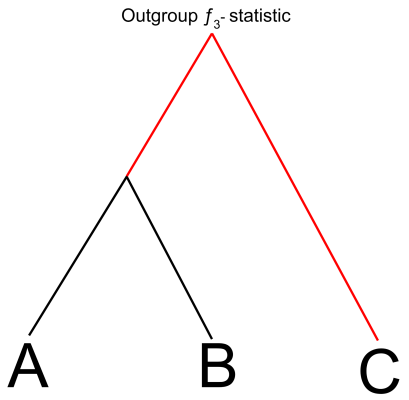


Figure 3.3 - Outgroup f_3-statistics.

3.5. Mitochondrial Genomes

In order to obtain full mitochondrial genomes from samples, fastq files were aligned to the mitochondrial genome simultaneously for each sample with the nuclear genome alignment with BWA (Li & Durbin 2009). Mitochondria-only aligned sequences were then extracted from the full genome alignment and a mitochondria-only BAM file was created for analysis. A consensus mitochondria FASTA file was created using ANGSD *-doFasta* 2, which calls the most common base and in the case of a tie a random base is chosen among the bases with the same maximum counts leaving N's or filtered

bases ignored (Korneliussen *et al.* 2014). The FASTA sequences for each mitochondria were put through Multiple Sequence Alignment using MUSCLE (Edgar 2004) and Neighbour joining tree were calculated with a bootstrap of 100 (or other specified) in Seaview (Gouy *et al.* 2010).

3.6. Y chromosome phylogenies

Y chromosome reads were extracted from BAM files of whole genome alignment, which included the Y chromosome reference sequence from UCSC Genome Browser assembly ID: bosTau7. Variants were subsequently called on a merged BAM file with GATK UnifiedGenotyper, using the option -ploidy 1 (for haploid sequences). A minimum base quality of 20 (-mbq 20) and a minimum mapping quality of 25 (-mmq 25) filter were also applied. SNPs were called within the Male Specific region of the Y chromosome (MSY), which includes X-degenerate single copy genes such as: *TBL1X*, *EIF1AY*, *USP9Y*, *DDX3Y*, *ZFY* (Skaletsky *et al.* 2003; Chang *et al.* 2013). The produced VCF file was then filtered using vcftools for no missingness (--max-missing 1); if the coverages allowed a read depth filter was also applied (--minDP 2).

The final VCF was then put through PGDSpider (Lischer & Excoffier 2012) (Available at: http://www.cmpg.unibe.ch/software/PGDSpider/) to convert the VFC into FASTA format. Seaview (Gouy *et al.* 2010) was used to run a muscle multiple alignment (Edgar 2004), and a NJ tree was drawn with 1000 replicates. Y chromosome coverages for all samples can be found in Appendix Table 9.1.6.

3.7. IBS - Identity by State

To test the genetic relationships on a whole genome level across all these samples, Identity by state (IBS) analysis was done using ANGSD (Korneliussen *et al.* 2014). The method implemented calculates genotype likelihoods (-GL 1, SAMtools method) from sampling a single base at random (-doIBS 1), with major and minor alleles inferred from

the genotype likelihoods (-doMajorMinor 1). Furthermore, a minimum minor allele frequency of 0.05 (-minFreq 0.05) was used in addition to minimum mapping quality of 25 (minMapQ 25); minimum base quality of 20 (-minQ 20); with the exclusion of transitions (-rmTrans 1) and tri-allelic sites (-skipTriallelic 0). Moreover, only sites where all individuals had coverage were kept (-minInd [total number of individuals for analysis]). The output generated a pairwise IBS matrix, where the average distance between pairs of individuals was calculated scaled between 0 and 1. The pairwise IBS matrix was subsequently used as an input matrix to the R package Ape (Paradis *et al.* 2004) to calculate a rooted Neighbour-Joining tree, with the wild yak (*Bos mutus*) as an outgroup.

4. Going global: The Domestication and Spread of *Bos taurus*

"Second hand books are wild books, homeless books; they have come together in vast flocks of variegated feather, and have a charm which the domesticated volumes of the library lack."

Virginia Woolf, Street Haunting

4.1. Introduction

4.1.1. A Near Eastern origin for Bos taurus

It is generally accepted that the two domestic cattle taxa, *Bos taurus* and *Bos indicus*, were domesticated separately, in the Near East and in South Asia respectively. The earliest genetic evidence for a separate domestication event of *Bos taurus* in the Near East came from mitochondrial DNA (mtDNA) sequences. The deep divergence of indicine and taurine mitochondrial sequences, estimated to be in the order of ~300,000 years ago, clearly prior to domestication, suggests that *taurus* and *indicus* were likely domesticated from two separate and diverged aurochs populations (Loftus, MacHugh, Bradley, *et al.* 1994; Troy *et al.* 2001; Achilli *et al.* 2009; Bonfiglio *et al.* 2010). Further support for this deep divergence of taurine and zebu cattle prior to domestication has been building, with comparisons of selected autosomal sequences (MacHugh *et al.* 1997; Bovine HapMap Consortium *et al.* 2009; Murray *et al.* 2010) and with high density SNP typing of hundreds of thousands of autosomal variants (Decker *et al.* 2014; Porto-Neto *et al.* 2013; Park *et al.* 2015). An almost complete absence of European aurochs P mtDNA haplogroups in modern European taurine cattle gives further support to a domestication centre for *Bos taurus* in the Near East. However, the discovery of two divergent haplogroups (Q and R) in modern Italian cattle has challenged this view (Achilli *et al.* 2009).

4.1.2. Contribution of wild aurochs to the domestic gene pool

It has been suggested that introgression between wild cattle and early domestics could have happened in North Africa (Bradley *et al.* 1996; MacHugh *et al.* 1997), in Europe (Gotherstrom *et al.* 2005; Achilli *et al.* 2009; Park *et al.* 2015; Upadhyay *et al.* 2017) and in South Asia (Murray *et al.* 2010). The complete sequencing of a British Mesolithic aurochs (CPC98) in 2015 allowed whole genome comparisons pertaining to the questions surrounding European cattle origins. Park *et al.* (2015) demonstrated a significant genetic contribution from British aurochs into the ancestors of British and Irish domestic cattle. Furthermore, gene flow from a CPC98-like aurochs population has also been detected in modern Iberian cattle (Upadhyay *et al.* 2017). Other possible aurochs admixture events in other continents remain largely unexplored due to lack of ancient DNA data from those regions.

4.1.3. Spread of domestic cattle into Africa or a third domestication centre?

Although generally accepted that the first domestic cattle in the African continent were taurine brought from the Near East after domestication it is still debated whether a separate domestication could have also occurred (Bradley *et al.* 1996; MacHugh *et al.* 1997; Gifford-Gonzalez & Hanotte 2011; Stock & Gifford-Gonzalez 2013; Decker *et al.* 2014). The general consensus is that taurine cattle were introduced into Africa either via the Horn of Africa or by the Isthmus of Suez through the Nile Valley (Stock & Gifford-Gonzalez 2013) around 6500-5500 BC. The archaeological findings that argue against this view come from animal remains that predate these by approximately 3000 years (Gautier 1984; Linseele *et al.* 2014). However, these are not directly dated, are highly fragmented and are scarce (Stock & Gifford-Gonzalez 2013). Nevertheless, it is clear that humpless or taurine animals were the first domestic cattle in Africa, with evidence from animal remains and rock art (Gifford-Gonzalez & Hanotte 2011).

Genetic analyses have played an essential role in trying to disentangle the demographic history of wild and domestic cattle in Africa. Initially the high frequency of the T1 mitochondrial haplogroup in Africa and low frequency elsewhere was thought to represent a separate African domestication event (Bradley *et al.* 1996; Troy *et al.* 2001). However, this view has since been challenged by whole mitochondrial genome analyses (Achilli *et al.* 2008; Achilli *et al.* 2009), which support a single origin for T mitochondria. In addition, early microsatellite marker distributions, Y chromosome studies and genome-wide SNP data have suggested that gene flow from African wild aurochs to domestic cattle is likely to have happened (MacHugh *et al.* 1997; Decker *et al.* 2009; Pérez-Pardal, Royo, Beja-Pereira, Curik, *et al.* 2010).

4.2. Aims and context

The first aim of this chapter is to provide a global picture of early *Bos taurus* genetic variation from the time of domestication in the Near East to its subsequent expansion into Europe by looking at genetic diversity in both autosomes and mitochondrial genomes. Moreover, population genomic analyses like *D*-statistics should detect possible gene flow from extinct European *Bos primigenius* populations and Near Eastern *Bos primigenius* into ancient domestics. Furthermore, the separation of modern European and African *Bos taurus* on both PCA and Admixture analyses has been debated over many decades on whether this is resulting of a separate domestication or input from the wild. These questions are explored by the inclusion of Neolithic to Bronze Age Near Eastern ancients, some of which revealed a high proportion of African taurine ancestry.

In this chapter, 79 ancient cattle genomes from the Near East and Europe across 46 different archaeological sites and spanning ~10,000 years are presented (Figure 4.1; Table 4.1). Samples from the Near East comprise only ancient individuals from the Early Neolithic period up to the Middle Bronze Age, as subsequent periods in this region will

be the scope of Chapter 6. However, samples from Europe comprise a collection from the Mesolithic to Medieval and modern day individuals.

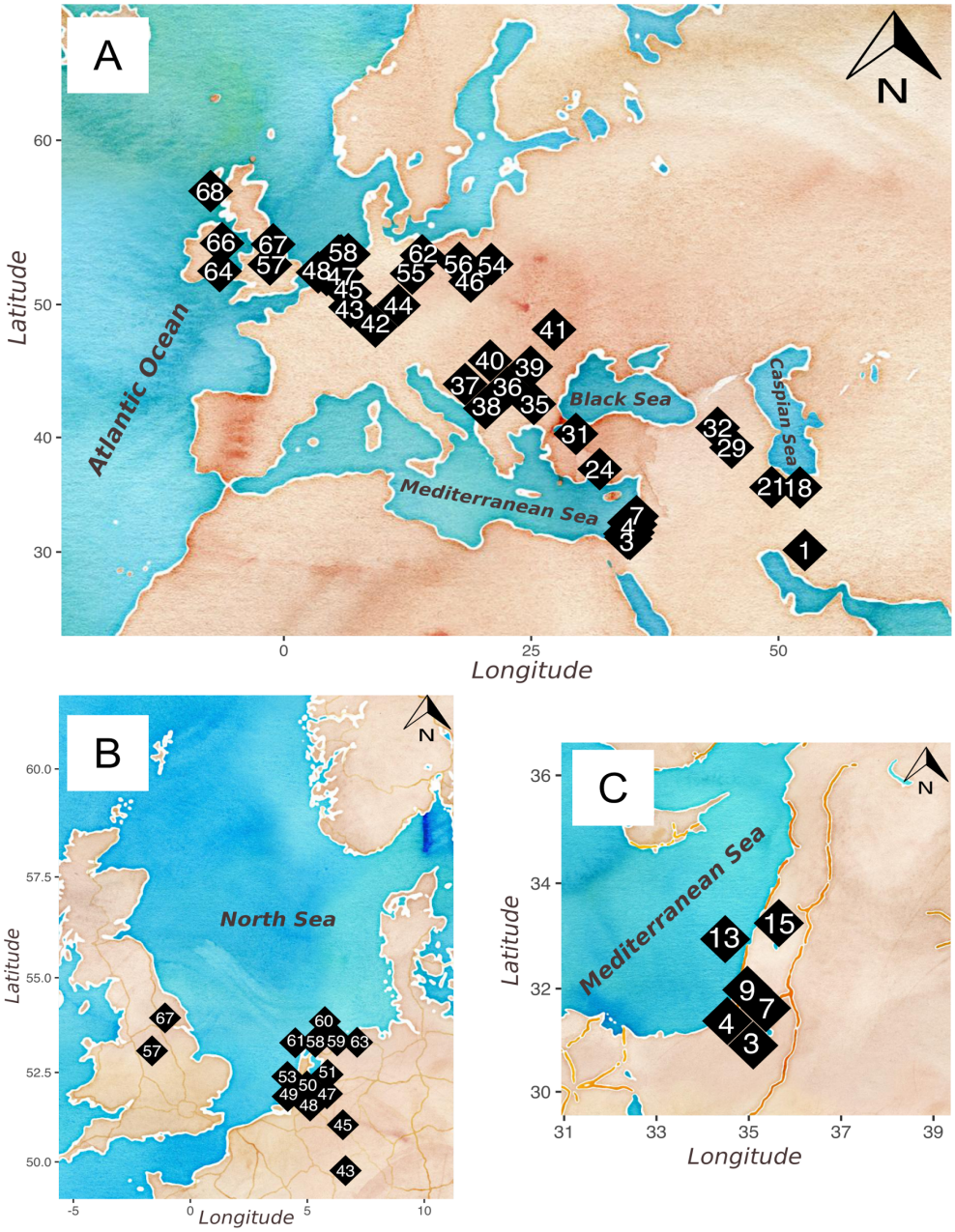


Figure 4.1- Archaeological sites yielding cattle aDNA Data. (A) *Europe and the Near East.* ***(B)*** *The Netherlands and Britain.* ***(C)*** *The Southern Levant. (1) Miyanroud; (3) Nahal Tillah; (4) Ashkelon; (7) Jerusalem; (9) Tel Dalit; (13) Tel-Hreiz; (15) Tel Dan; (18) Maral Tappeh; (21) Tapeh-Sang-e-Caxmaq; (24) Suberde; (25) Çatalhöyük; (29) Kültəpə (Azerbaijan,Iran); (31) Menteşe; (32) Gyumri; (35) Dzulhunitsa; (36) Plöcnik; (37) Bubanj; (38) Blagotin; (39) Belovode; (40) Stubline; (41) Birnova/Byrnova Luka; (42) Herxheim; (43) Trier-Brüderkrankenhaus; (44) Kirschbaumhöhle; (45) Bedburg-Königshoven; (46) Kalisz; (47) Elst; (48) Zijderveld; (49) Schipluiden; (50) Houten; (51) Bunnik-Odijk; (53) Stevenshofjespolder; (54) Ludwinowo; (55) Dyrotz; (56) Kierzkowo; (57) Carsington Pasture Cave; (58) Dronrijp-zuid; (59) Oosterbeintum; (60) Firdgum; (61) Britsum; (62) Falkenwalde; (63) Winsum; (64) Dublin; (66) Newgrange; (67) York; (69) Cladh Hallan;*

Table 4.1- Summary of archaeological samples for DNA analyses. *Archaeological details for each specimen. Samples marked with (*) were processed by Amelie Scheu (University of Mainz) and samples marked with (^) were processed by Victoria Mullin (Trinity College Dublin). CPC98 is the published B.primigenius sample from Park et.al 2015.*

ID	Bone	Country	Site	Archaeological Context	Date
Bed3*	petrous	Germany	Bedburg-Königshoven	early Mesolithic	9608 ± 151 cal. BC
Bed4*	petrous	Germany	Bedburg-Königshoven	early Mesolithic	9758 ± 191 cal. BC
Bel1	petrous	Serbia	Belovode- Veliko	Late Neolithic	5050/4925-4900/4800 cal BC
Bel2	petrous	Serbia	Belovode- Veliko	Late Neolithic	5050/4925-4900/4800 cal BC
Bir1	tooth	Moldova	Birnova/Byrnova Luka	Cucuteni-Trypillian	c.5200 - 3500 BC
Bir2	astragalus	Moldova	Birnova/Byrnova Luka	Cucuteni-Trypillian	c.5200 - 3500 BC
Bir3	astragalus	Moldova	Birnova/Byrnova Luka	Cucuteni-Trypillian	c.5200 - 3500 BC
Bla1	petrous	Serbia	Blagotin	Early Neolithic Starčevo	6200-6000 cal BC
Bla2	petrous	Serbia	Blagotin	Early Neolithic Starčevo	6200-6000 cal BC
Bri1	petrous	Netherlands	Britsum	Roman	257-421 cal AD
Bub1	petrous	Serbia	Bubanj	Neolithic	c.6000-5600 BC
Bun1	petrous	Netherlands	Odjik	Middle Iron	500-250 BC
Bun2	petrous	Netherlands	Odjik	Middle Iron	500-250 BC
Ch22*	Scapula	Turkey	Çatalhöyük	Neolithic	c.7500 BC to 5700 BC
Cla1^	petrous	UK	Cladh Hallan	Late Bronze	1054-826 BC
Cla2^	petrous	UK	Cladh Hallan	Late Bronze	1118-924 BC

CPC98	humerus	UK	Carsington Pasture Cave	Mesolithic	4788 cal. BC
Dan1	petrous	Israel	Tel Dan	Pottery Neolithic/ Early Bronze	3500-3000 BC
Dav1	petrous	Israel	Jerusalem	Middle Bronze	1929-1753 cal BC
Dav2	petrous	Israel	Jerusalem	Middle Bronze	2200-2000 BC
Dav3	petrous	Israel	Jerusalem	Middle Bronze	2200-2000 BC
Dav4	petrous	Israel	Jerusalem	Middle Bronze	2200-2000 BC
Dro1	petrous	Netherlands	Dronrijp-zuid	Middle Roman	AD 100-300
Dub1^	petrous	Ireland	Dublin	Medieval	AD 900-1000
Dyr1*	petrous	Germany	Dyrotz 25	late slavic	9th-13th century
Dzh1*	petrous	Bulgaria	Dzulhunitsa	Early Neolithic	5831 ± 51 - 6049 ± 25 cal. BC
Dzh2*	petrous	Bulgaria	Dzulhunitsa	Early Neolithic	5605 ± 33 cal. BC
Els1	petrous	Netherlands	Elst	Roman	AD 1-70
Fal7*	?	Germany	Falkenwalde	early slavic	AD 1100-1250
Far1	petrous	Iran	Miyanroud	Late Neolithic	6000-5500 BC
Fir1	petrous	Netherlands	Firdgum	Early Medieval	AD 450-1050
Gil1	petrous	Israel	Gilat	Chalcolithic	c.4300–3300 BC
Gyumri2	petrous	Armenia	Gyumri	Neolithic	5310 cal. BC
Hou1	petrous	Netherlands	Houten-Loerik	Medieval	AD 450-1500
Hou2	petrous	Netherlands	Houten-Hoogdijk	Medieval	AD 1100-1199
Hxh1*	petrous	Germany	Herxheim	early Neolithic (LBK)	c.5000 BC

Hxh2*	petrous	Germany	Herxheim	early Neolithic (LBK)	c.5000 BC
Kalisz1	petrous	Poland	Kalisz	No info	No info
Kalisz2	petrous	Poland	Kalisz	No info	No info
Kalisz3	petrous	Poland	Kalisz	No info	No info
Kie1	petrous	Poland	Kierzkowo	Late Neolithic	c.3000 BC
Kie2	petrous	Poland	Kierzkowo	Late Neolithic	c.3000 BC
Kir4*	petrous	Germany	Kirschbaumhöhle	Late Neolithic	2794 ± 78 cal. BC
Lud1	petrous	Poland	Ludwinowo	Early Neolithic	c. 5500 BC
Lud2	petrous	Poland	Ludwinowo	Early Neolithic	c. 5500 BC
Lud3	petrous	Poland	Ludwinowo	Early Neolithic	c. 5500 BC
Lud4	petrous	Poland	Ludwinowo	Early Neolithic	c. 5500 BC
Mar1	scapula	Iran	Maral Tappeh	Neolithic	c.5000 BC
Men1	astragalus	Turkey	Menteşe	Neolithic	c.6000-5500 BC
Men2	petrous	Turkey	Menteşe	Neolithic	6048-5893 cal. BC
Nah1	petrous	Israel	Nahal Tillah	Early Bronze I	3300-3050 BC
New1^	petrous	Ireland	Newgrange	Neolithic	2795-2580 BC
New2^	petrous	Ireland	Newgrange	Late Iron	AD 321-425
New3^	petrous	Ireland	Newgrange	Neolithic	c.2800 BC
New4^	petrous	Ireland	Newgrange	Neolithic	c.2800 BC

New5^	petrous	Ireland	Newgrange	Neolithic	3024-2894 BC
Otb1	petrous	Netherlands	Oosterbierum	Middle Roman	AD 100-300
Plo1	petrous	Serbia	Pločnik	Neolithic	5275/5125-5100/5000 cal BC
Plo2	petrous	Serbia	Pločnik	Neolithic	5025/4950-4850-4650 cal BC
Plo3	petrous	Serbia	Pločnik	Neolithic	5100/5000-5025/4950 cal BC
Plo4	petrous	Serbia	Plocnik	Neolithic	5100/5000-5025/4950 cal BC
Plo5	petrous	Serbia	Plocnik	Neolithic	4850/4650-4600/4500 cal BC
Plo6	petrous	Serbia	Plocnik	Neolithic	5275/5125-5100/5000 cal BC
Plo7	petrous	Serbia	Plocnik	Neolithic	5100/5000-5025/4950 cal BC
Plo8	petrous	Serbia	Plocnik	Neolithic	5100/5000-5025/4950 cal BC
Sac3	?	Iran	Tapeh-Sang-e-Caxmaq	Late Neolithic	5673 cal. BC
Sch1	petrous	Netherlands	Schipluiden	Mid-Neolithic	3500-2850 BC
Ste1	petrous	Netherlands	Stevenshofjespolder	Iron/Roman	800BC- AD 400
Stu1	petrous	Serbia	Stubline	Neolithic	4800-4500 cal BC
Sub1	petrous	Turkey	Suberde	Neolithic	6221-6024 cal. BC
Tda1	petrous	Israel	Tel-Dalit	Early Bronze	3050 BC
Thr1	petrous	Israel	Tel-Hreiz	Pottery Neolithic	5100-4300 BC
Tri1*	metatarsus	Germany	Trier-Brüderkrankenhaus	Mesolithic	8261-7960 cal. BC
Viz1	petrous	Netherlands	Zijderveld	Bronze	1500-1300 BC

Viz2	petrous	Netherlands	Zijderveld	Bronze	1500-1300 BC
Win1	petrous	Netherlands	Winsum	Roman	AD 100-300
Yor1^	petrous	UK	York	Roman	AD 110
Yor2^	petrous	UK	York	Viking	AD 801-901
Yor3^	petrous	UK	York	Norman	AD 1350
Yor4^	petrous	UK	York	Viking	AD 950

4.3. Methods

4.3.1. Radiocarbon Dating

The individuals chosen for radiocarbon dating are described in Table 4.3 and their radiocarbon dates are shown. Samples of key geographical, archaeological context and of good DNA preservation were chosen for radiocarbon dating. Calibration curve plots produced by OxCal (Ramsey 2009) can be found in the Appendix (Section 9.5).

4.3.2. Procrustes Projection PCA

Principal component analysis was performed on the basis of Procrustes analysis using LASER (Version 2.03), as described in 3.1.1.

4.3.3. ADMIXTURE

In order to investigate individual ancestries ADMIXTURE was run using the bovine 700K data. The pipeline followed was as described in 3.2., with LD pruning to account for linkage disequilibrium. After filtering for transversions only ADMIXTURE was run on 123,612 variants and 811 cattle, including ancients and modern breeds.

4.3.4. D-statistics

The formal test of admixture *D*-statistic (Patterson *et al.* 2012) was computed as explained in section 3.3, with transitions removed and individuals pseudo-haploidized. A minimum of 2000 SNPs were accepted for the AdmixTools output for each test. *D*-statistic was calculated only with transversions and the Yak (*Bos grunniens*) used as an outgroup for every test.

4.3.5. Mitochondrial phylogeny

Mitochondrial alignments for all samples in this chapter were achieved as described in section 3.5. Due to the poor preservation of certain samples, individuals where a clear mitochondrial haplogroup assignment due to poor alignment was not possible, were excluded. A NJ phylogeny was drawn in Seaview with a bootstrap of 100.

4.4. Results

4.4.1. Specimen preservation and whole genome sequencing

A subset of samples are presented in each chapter, however, the extensive and varied collection of ancient samples presented in this thesis provide the opportunity for a general overview on ancient animal bone preservation. Figure 4.2. summarizes the percentage endogenous DNA obtained for each ancient individual in this thesis.

Latitude has been described as a major factor in ancient DNA preservation, where typically specimens from higher latitudes or permafrost tend to show a higher degree of DNA preservation than specimens from temperate or tropical climates. However, many other factors can contribute to DNA preservation: type of bone/specimen, exposure to radiation, soil chemistry and proximity to free water, for example (Campos *et al.* 2012). Nevertheless, there is higher chance that a sample from higher latitude and colder climate will be well preserved, which seems to be consistent with the data in Figure 4.2. The percentage endogenous sequence obtained was highly variable but typically samples from warmer climates tended to yield less DNA. It is important to note, however, that latitude does not fully explain the variation in the data (adjusted r^2=0.6658; p-value: 3.209×10^{-8}). Individual percentages and latitudes can be found in Table 9.2.1 in the Appendix.

The average endogenous DNA percentage obtained across this chapter's dataset was 32%, a high value which is due in part to the preference of petrous bones to long bones (Table 4.2). The lowest endogenous percentage was obtained from a Neolithic Moldovan individual (Bir2), 0.05%, extracted from an astragalus bone; whereas the highest percentage (68%) came from a Late Slavic (11^{th} Century) domestic from Germany (Dyr1) extracted from a petrous bone. The average coverage for the nuclear genome obtained across all samples was 3x, and 310x for the mitochondrial genome. Coverages

for the nuclear genome ranged from 0.0002x to 23x. Coverages obtained for the mitochondrial genome ranged from 0.04x to 3521x.

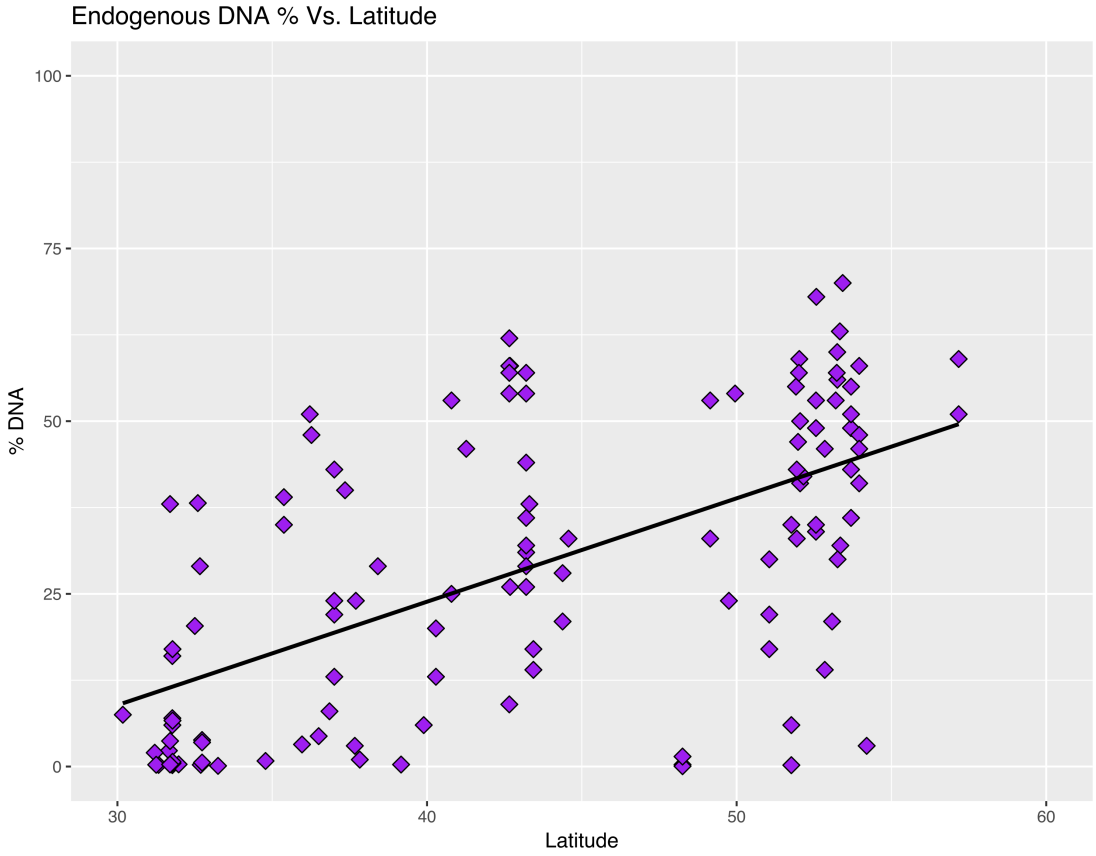


Figure 4.2 - Ancient DNA preservation Vs. Latitude in ancient cattle samples. *Each diamond shape representing a single individual. Percentage of endogenous DNA for each individuals was calculated as described in 2.7.1; For some individuals latitudes may be approximates.* ***Plot and summary statistics drawn and calculated in R.***

Table 4.2- Endogenous DNA and Coverages. *Endogenous DNA % percentage is given for each specimen based on the calculation: (number of reads q25 x100/ number of total reads). Whole genome average coverage and mitochondrial genome coverage were calculated using Qualimap (García-Alcalde et al. 2012). Sexing was done as per section 2.8. Samples marked with (*) were processed by Amelie Scheu (University of Mainz) and samples marked with (^) were processed by Victoria Mullin (Trinity College Dublin). (**) CPC98 is the published B. primigenius sample from Park et.al 2015.*

ID	Species	% DNA	Coverage	Mitochondria	Sex
Bed3*	*Bos primigenius*	30	18	3521	Female
Bed4*	*Bos primigenius*	17	2	657	Female
Bel1	*Bos taurus*	21	0.09	12	Female
Bel2	*Bos taurus*	28	0.1	26	Male
Bir1	*Bos taurus*	0.27	0.002	1	Female
Bir2	*Bos taurus*	0.05	0.001	4	Female

Bir3	*Bos taurus*	1.45	0.003	2	Female
Bla1	*Bos taurus*	14	0.02	4	Male
Bla2	*Bos taurus*	17	0.005	1	Male
Bri1	*Bos primigenius*	56	3	207	Male
Bub1	*Bos taurus*	38	0.4	53	Female
Bun1	*Bos taurus*	41	2	242	Female
Bun2	*Bos taurus*	50	2	253	Female
Ch22*	*Bos primigenius?*	3	0.31	45	Male
Cla1^	*Bos taurus*	59	15	679	Female
Cla2^	*Bos taurus*	51	2	187	Male
CPC98**	*Bos primigenius*	21	4	10	Male
Dan1	*Bos taurus*	0.1	0.0002	0.04	Female
Dav1	*Bos taurus*	16	5	946	Female
Dav2	*Bos taurus*	5	0.004	2	Male
Dav3	*Bos taurus*	7	0.01	4	Female
Dav4	*Bos taurus*	6	0.01	12	Male
Dro1	*Bos taurus*	53	3	318	Male
Dub1^	*Bos taurus*	32	2	153	Female
Dyr1*	*Bos taurus*	68	2	103	Female
Dzh1*	*Bos taurus*	58	10	2043	Male
Dzh2*	*Bos taurus*	26	4	976	Female
Els1	*Bos taurus*	55	3	179	Male
Fal7*	*Bos primigenius*	30	2	189	Male
Far1	*Bos taurus*	7.5	0.03	5	Female
Fir1	*Bos taurus*	60	3	185	Female
Gil1	*Bos taurus*	0.24	0.0007	0.2	Female
Gyumri2	*Bos primigenius*	25	2	477	Male
Hou1	*Bos taurus*	59	3	202	Male
Hou2	*Bos taurus*	57	3	195	Female
Hxh1*	*Bos taurus*	33	8	980	Female
Hxh2*	*Bos primigenius*	53	23	2209	Male
Kalisz1	*Bos primigenius*	0.2	0.0006	1	Male

Kalisz2	*Bos primigenius*	35	3	417	Male
Kalisz3	*Bos primigenius*	6	0.01	11	Male
Kie1	*Bos taurus*	14	0.04	5	Male
Kie2	*Bos taurus*	46	0.2	13	Male
Kir4	*Bos taurus*	54	15	813	Female
Lud1	*Bos taurus*	34	0.1	10	Female
Lud2	*Bos taurus*	49	0.4	29	Female
Lud3	*Bos taurus*	53	0.3	31	Male
Lud4	*Bos taurus*	35	0.2	16	Female
Mar1	*Bos taurus*	3.2	0.04	4	Male
Men1	*Bos taurus*	13	3	334	Male
Men2	*Bos taurus*	20	2	88	Female
Nah1	*Bos taurus*	0.26	0.0004	0.2	Male
New1^	*Bos taurus*	55	17	778	Male
New2^	*Bos taurus*	36	4	194	Male
New3^	*Bos taurus*	49	5	346	Male
New4^	*Bos taurus*	43	4	244	Female
New5^	*Bos taurus*	51	5	322	Male
Otb1	*Bos taurus*	57	3	167	Male
Plo1	*Bos taurus*	44	0.1	10	Female
Plo2	*Bos taurus*	36	0.3	36	Female
Plo3	*Bos taurus*	57	3	153	Male
Plo4	*Bos taurus*	54	3	154	Male
Plo5	*Bos taurus*	31	0.08	13	Male
Plo6	*Bos taurus*	26	0.1	8	Male
Plo7	*Bos taurus*	32	0.1	19	Female
Plo8	*Bos taurus*	29	0.2	24	Female
Sac3	*Bos taurus*	4.4	0.02	3	Female
Sch1	*Bos taurus*	47	2	159	Female
Ste1	*Bos taurus*	42	1	257	Female
Stu1	*Bos taurus*	33	0.2	20	Male
Sub1	*Bos taurus*	40	13	1344	Male
Tda1	*Bos taurus*	0.32	0.001	0.3	Male

Thr1	*Bos taurus*	0.25	0.001	0.2	Male
Tri1	*Bos primigenius*	24	2	822	Female
Viz1	*Bos taurus*	33	0.7	574	Male
Viz2	*Bos taurus*	43	2	251	Male
Win1	*Bos taurus*	63	19	856	Female
Yor1^	*Bos taurus*	58	8	603	Female
Yor2^	*Bos taurus*	41	4	213	Male
Yor3^	*Bos taurus*	48	2	201	Male
Yor4^	*Bos taurus*	46	3	242	Female

4.4.2. Radiocarbon Dating

The Armenian aurochs, Gyumri2, dated to 5036-5076 cal. BC and thus was contemporary to Near Eastern Neolithic early domestics (Table 4.3). Both Men2 and Sub1, from Anatolia, were securely dated to the Neolithic period in Anatolia (Arbuckle *et al.* 2014), dating to 6048-5893 cal. BC and 6221-6024 cal. BC, respectively. The Southern Levantine individual, Dav1 was confirmed to be from the Middle Bronze Age (Liora Horwitz, personal communication) dating to 1929-1753 cal. BC. The Dutch individual from Winsum (Win1) also confirmed its archaeological context as Roman (Canan Çakırlar, personal communication), dating to 417-561 cal. AD.

***Table 4.3. - Radiocarbon Dates**. Measured radiocarbon dates in C14 BP with error; Calibrated dates in BC and BP based on 2-sigma calibration (95% probability).*

Sample ID	Conventional C14 age (BP)	Calibrated Date BC/AD (cal. BC/AD) 95% probability	Calibrated Date BP (cal. BP) 95% probability
Dav1	3520+/-30	1929-1753	3879-3703
Gyumri2	6330+/-30	5036-5076	6986-7026
Men2	7092+/-40	6048-5893	7998-7843
Sub1	7247+/-51	6221-6024	8171-7974
Win1	1566+/-31	417-561 cal. AD	1533-1389

4.4.3. Projection PCA

The 700K Bovine PCA is shown in Figure 4.3 and it demonstrates the genetic variability within this dataset, which will be used throughout this thesis as the modern background to most population genetic analyses. The PCA shows a familiar triangular pattern, which has been previously observed in nuclear microsatellite, 50K and 700K SNP data (MacHugh *et al.* 1997; Loftus *et al.* 1999; Decker *et al.* 2014; Park *et al.* 2015; Upadhyay *et al.* 2017). 17.6% of the variance is explained by PC1, which separates *Bos taurus* from *Bos indicus*. Modern breeds that are known to be admixed, e.g. Turkish and Iranian breeds, fall in the middle of PC1. Furthermore, two outgroups are shown *Bos grunniens* (Domestic Yak) and *Bos gaurus* (Gaur; Indian Bison). In addition, 3.6% of the variation in this dataset is explained by PC2, in which there is a clear separation of European *Bos taurus* versus African *Bos taurus* and their hybrids.

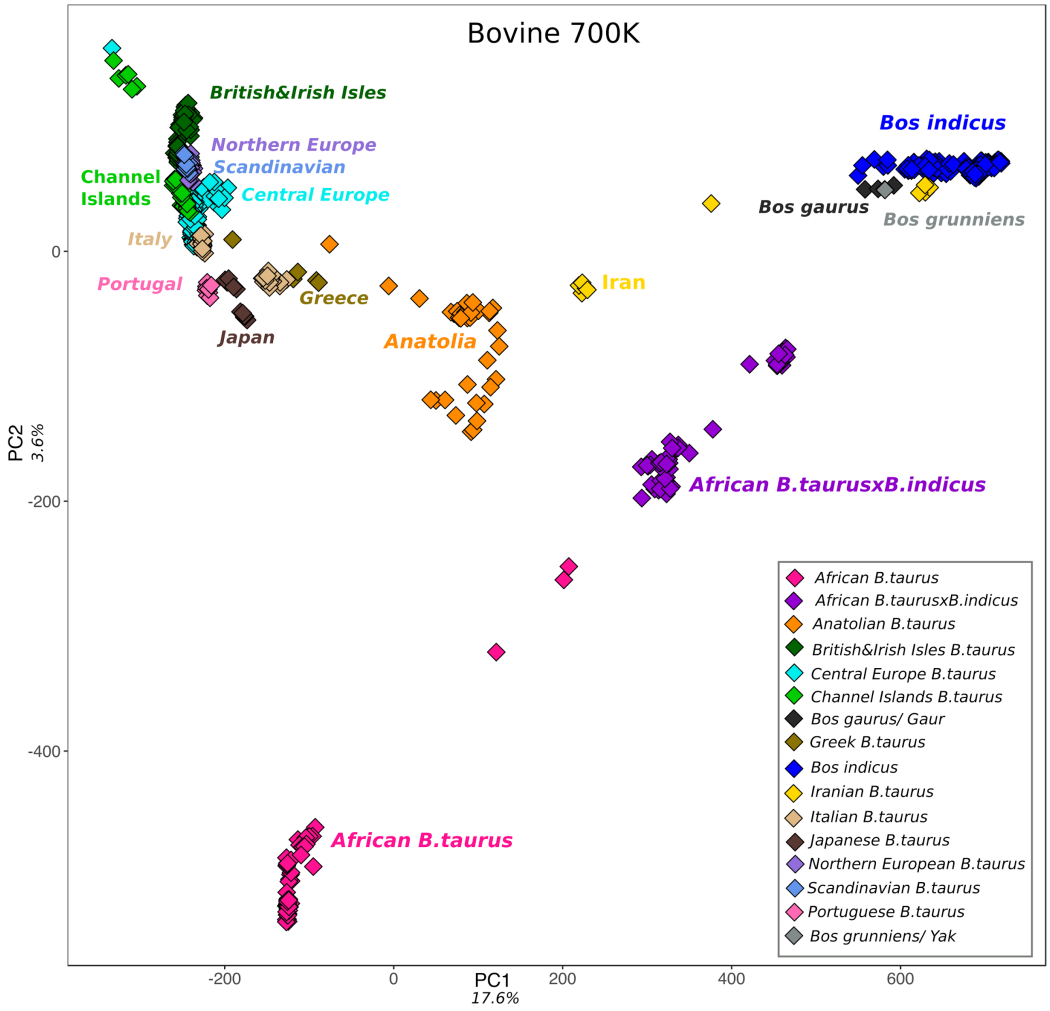


Figure 4.3 - 700K Bovine PCA. *Principal components analysis for the 700K bovine dataset. PC1 separating Bos taurus from Bos indicus individuals and PC2 separating African Bos taurus and European Bos taurus. Also including outgroups Bos gaurus (Gaur) and Bos grunniens (Yak).*

The projection PCA for ancient cattle samples is shown in Figure 4.4. From this analysis, clues about population ancestries across the Near East and Europe start to emerge. The Southern Levant, which is here represented by samples from Israel, shows a clustering away from all ancient and modern domestic and aurochs variation. This persists from the Neolithic/Chalcolithic until the Middle Bronze Age (Figure 4.4A), an intermediate locale between modern European taurine and modern African taurine. This may point toward separate aurochs strain contribution to Neolithic Levantine populations, perhaps from local *B. primigenius* or from early gene flow from Northern

Africa. It is important to note that, especially for Neolithic specimens, very low coverage was typically obtained within the Levant sampling and thus ancestry is estimated on a low number of SNPs (Appendix Table 9.2.2), especially the Bronze Age Levantine Dan1 sample (122 SNPs), whose position on the PCA might be dubious.

Neolithic Anatolia and Iran are close to each other but in two separate clusters. Neolithic Anatolia includes the *Bos* individual Ch22, which is likely a *primigenius* sample. The ~5000 cal. BC aurochs, Gyumri2, from Armenia, seems to cluster quite closely to these groups.

Within ancient European diversity, a geographical structure is evident and a stepping stone model is suggested, with Balkans (Serbian and Bulgarian) individuals clustering near to modern day central European Breeds. Also, ancient European continental domestics seem to group and fall within modern continental European diversity. Within these, some ancient domestics seem to fall outside their contemporary ancient population ancestry: Bir3 and Bir1 Neolithic (c. 5200 - 3500 BC) from Moldova; Kir4, a domestic from a Late Neolithic (~2794 cal. BC) German cave; Kie1 and Kie2 from Late Neolithic Poland (c.3000 BC); and Dzh2 an Early Neolithic from Bulgaria (~5605 cal. BC). These could reflect gene flow from the wild or domestic migrations.

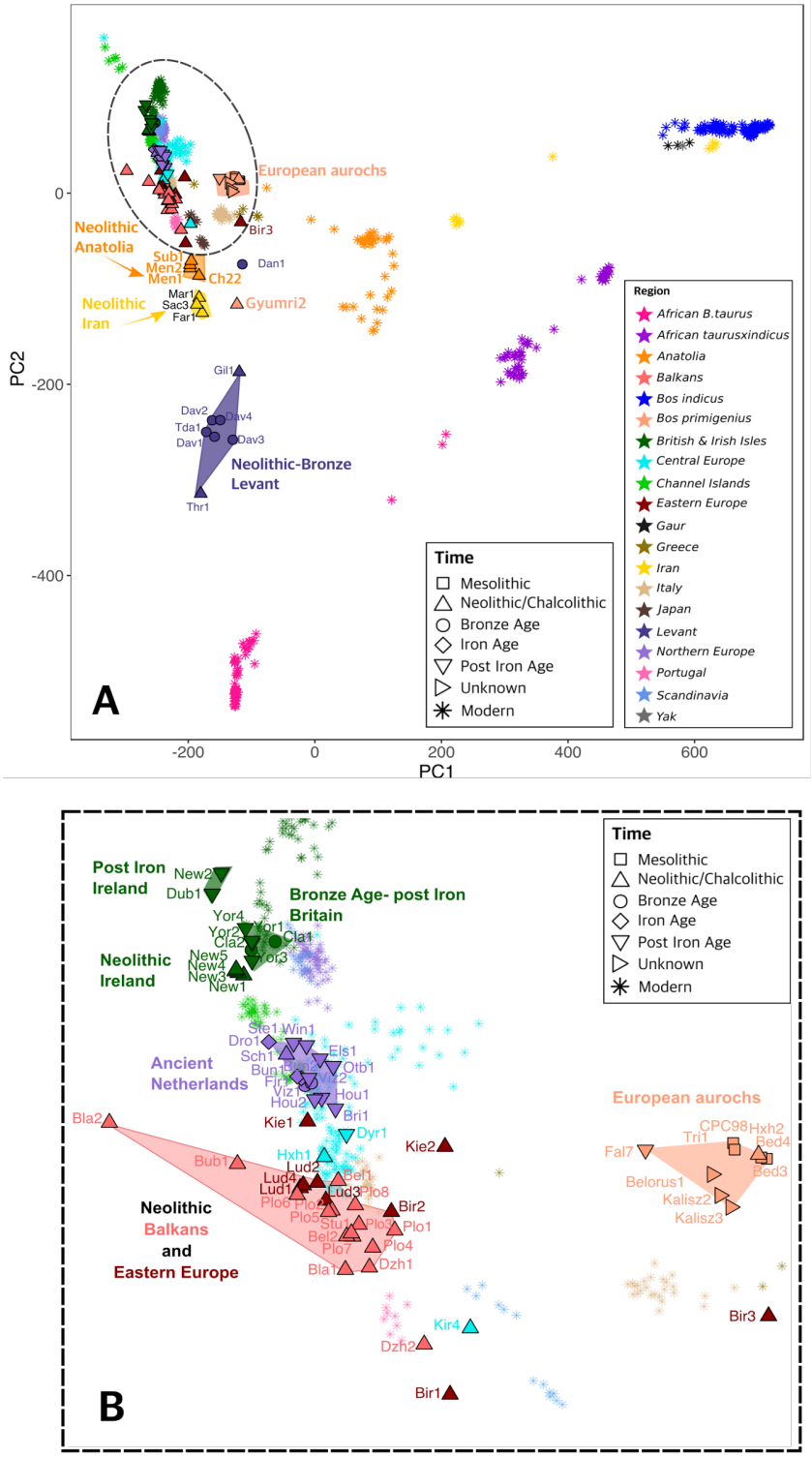


Figure 4.4 - Projection PCA. (A) *PCA of all Ancients; showing ancient clusters of ancient Near Easterners and European Bos primigenius.* ***(B)*** *Zoom of ancient Europeans (circled area in plot A); showing ancient clusters of Balkans, Eastern Europe, ancient Netherlands, Germany, Britain and Ireland. Ancient individuals origins and/or breed origins/taxa are shown as different colours. Time is given by shapes.*

Ancient specimens from the Netherlands cluster within modern French and Swiss breeds, Charolais and Simmental, and this is observed from the Neolithic through to Medieval times. Furthermore, ancient individuals from Neolithic Newgrange (Ireland), show higher genetic affinity to modern British and Irish Breeds like Kerry and Highland and cluster together; whereas later Irish ancients post-Iron-Age cluster together and separately from these (Figure 4.4B). These results suggest some genetic continuity from early domestics into Medieval times in Central and Northern Europe.

Bos primigenius individuals from Europe (Germany, Britain, Poland), cluster together away from European *Bos taurus* variation. This result agrees with what has been previously observed with the British Mesolithic aurochs (also included in Figure 4.4), using the 50K bovine SNP dataset (Park *et al.* 2015). As suggested by Park *et. al*, this reinforces previous studies of European *B.primigenius* being an outgroup to both modern and ancient domestic taurine cattle (Edwards *et al.* 2010; Park *et al.* 2015). Furthermore, the genetic isolation of the Armenian Gyumri2 from Northern and Eastern European aurochs, suggests that differentiated Eurasian aurochs subpopulations existed at the time of domestication. Also, the individual Bri1, from a Roman period site in the Netherlands, assigned as a *Bos primigenius* (Canan Çakırlar, personal communication) (Table 4.2) does not cluster with European aurochs but with contemporary Northern European *Bos taurus*.

4.4.4. ADMIXTURE

The combined ADMIXTURE analysis is split into three plots for ancient and modern samples according to their archaeological context (Appendix Tables 9.2.3 and 9.2.4). Kalisz2 and Kalisz3 from Poland, for whom dating or archaeological context was not available were included in both ancient maps (Figure 4.5A and B) and are marked with a question mark.

The three-population model (K=3) has been shown previously to distinguish between indicine (yellow), African taurine (blue) and European taurine cattle (pink) and this is maintained within this analysis (Figures 4.5 and 4.6) (Bovine HapMap Consortium *et al.* 2009; Park *et al.* 2015). Neolithic Southern Levantine ancients show a dominance of the African taurine component, in contrast to Anatolian or Iranian ancients, which are dominated by the European taurine component. This structure is also seen in the Early Bronze Age Southern Levant (Figure 4.5 B), however with an increase in the European taurine coefficient. A clear outlier to this trend is the sample Nah1, from Early Bronze Age Nahal Tillah, which is predominantly of African taurine ancestry (75%) and shows a surprisingly high percentage of indicine coefficient (25%). This could perhaps represent a local aurochs population. Furthermore, the only Near Eastern aurochs present in this dataset (Gyumri2), dating to ~5000 cal. BC, and thus contemporary to these domestics, shows a tripartite structure which has also been observed in a Mesolithic aurochs from Britain (Park *et al.* 2015). However this sample, shows a higher fraction of the African taurine component in comparison to the European aurochs (Figure 4.5A). For all European aurochs a similar tripartite structure is observed and comparable to that of CPC98 (Park *et al.* 2015). A notable example is that of Bir3, a Neolithic *Bos* Moldovan individual which was previously shown in PCA to cluster away from other Eastern European samples. Here, it shows a tripartite structure similar to that of European aurochs, which contrasts with contemporary individuals from the same site (Figure 4.5A). A slight reduction in the balance of ancestral components is observed as domestic cattle expand from the Near East into continental Europe in a south to north direction (Figure 4.5A). Furthermore, this is more pronounced with time in Europe, where ancient individuals from Central and Northern Europe from the Bronze Age onwards become almost completely composed of the European taurine fraction (Figure 4.5B), which is extended to modern day breeds (Figure 4.6). These included the Roman individual Bri1, morphologically assigned as a *primigenius*.

Present day cattle populations (Figure 4.7) reflect some of the ancient structure observed here. However, it is important to note the influence of known secondary admixture processes, for example following the introgression of indicine to the Near East and Africa (MacHugh *et al.* 1997; Loftus *et al.* 1999; Edwards, Baird, *et al.* 2007; Kim *et al.* 2017).

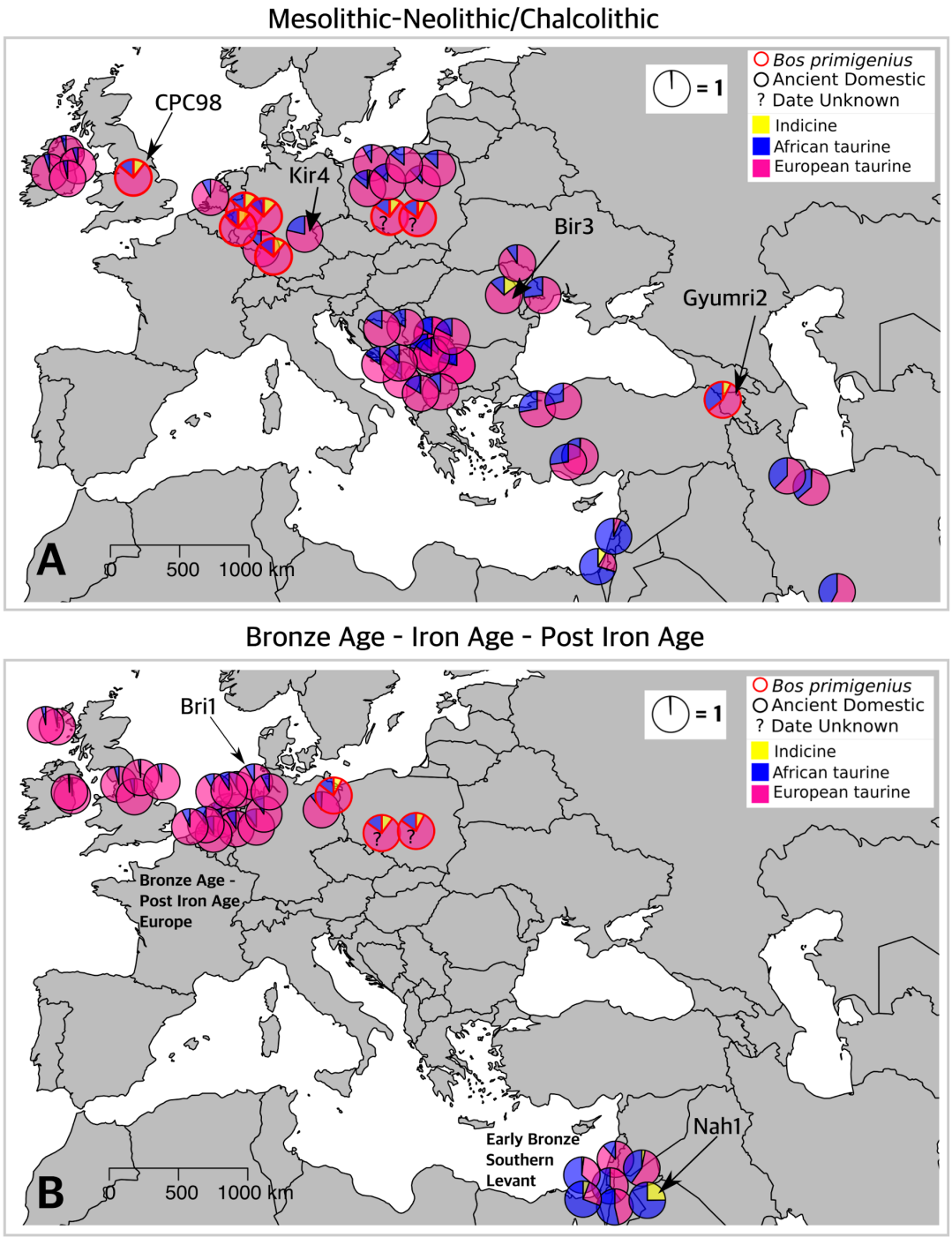


Figure 4.5 - Ancient ADMIXTURE (K=3). (A) *Mesolithic-Neolithic/Chalcolithic period.* ***(B)*** *Bronze, Iron and Post Iron Age. Individuals for which no dating was present are marked with a question mark. Admixture components are represented by colours. Individuals are plotted by approximate geographical location to archaeological site to allow for better display of data. Key samples mentioned in the text are labelled.*

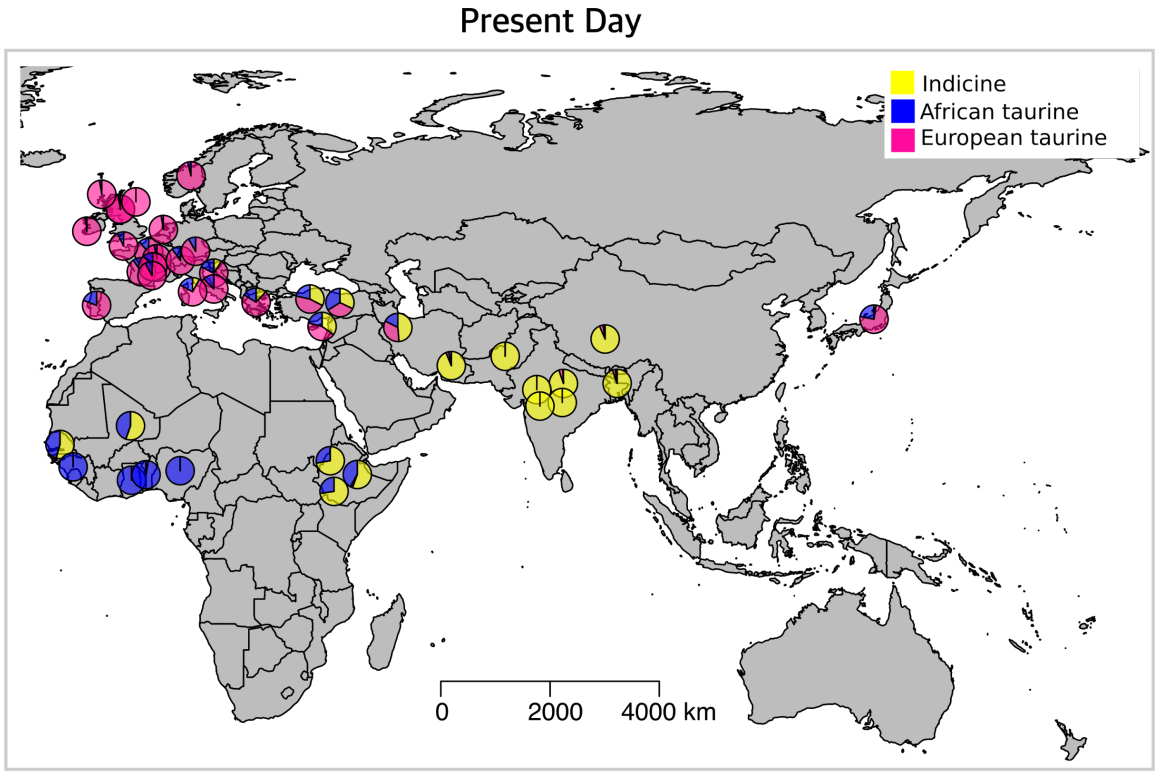


Figure 4.6 - Modern ADMIXTURE (K=3) map. *Modern cattle breeds from the 700K dataset are shown, where each pie chart corresponds to the median value for each component, across a group of individuals belonging to the same breed. Admixture components are represented by colours: European taurine (pink), African taurine (blue), Indicine (yellow). Individuals are plotted by approximate geographical location to allow for better display of data. Computed values from ADMIXTURE for each breed (median) and for each individual can be found the in Appendix in tables 9.2.4. And 9.2.5.*

4.4.5. Formally testing European aurochs introgression

To formally test admixture from European *Bos primigenius* individuals into European *Bos taurus* *D*-statistics were calculated for the test: *D*(((Test,Sub1),Bed3),Yak) (Figure 4.7; Appendix Table 9.2.6). Bed3, a Mesolithic *primigenius* from Germany (~9608 cal. BC), was used as a representative of the European aurochs population. Sub1, a Neolithic specimen from Southern Anatolia (~6221 cal. BC) was used as an example of an early ancient Near Eastern domestic that is non-admixed with European *primigenius* - previously tested.

Firstly, as it would be expected, all other European aurochs gave a positive *D*-statistic, sharing higher number of derived alleles with Bed3 than with Sub1. This also included Kalisz2 from Poland of unknown date (*D*=0.152, Z=15.3), suggesting it belongs to the same European aurochs population. Contrastingly, the Armenian aurochs Gyumri2 shows no significant gene flow signal from Bed3, with a *D* value of -0.0081 (Z=-0.791).

Secondly, early domestics from Anatolia, Iran, Balkans, Central and Eastern Europe do not give significant signatures of admixture with Bed3, with the exception of the sample Bub1 from Bubanj, Serbia. However, this sample is only one of 79 samples that has not been USER™ treated and this result may be affected by spurious signal due to ancient DNA deamination - causing false genetic variability due to damage. Furthermore, as this is an outlier compared to contemporary individuals from the same region it could be possible that this is an intrusive, much younger sample than context suggests.

Significant *D* values are observed from ~5000 years BP (~3000 BC) in North and East Europe (Sch1, Kie2). The results of aurochs introgression from this *European Bos primigenius* population is detectable from then onwards in Central and Northern Europe (including Britain and Ireland), stretching to Roman times (Dro1), although some individual exceptions are observed (Otb1, Hou1). Kir4, a late Neolithic Germanic individual (~4000 years BP), shows no evidence for introgression with Bed3 (*D=0.0056, Z=0.536*) from information on 103,979 SNPs.

Furthermore, in contrast to what is observed in Europe at ~3500 years BP, the Middle Bronze Age Southern Levant individual, Dav1, shows no evidence for an introgression with this European-type aurochs population, *D*=-0.0186, Z=-1.868, on 102,265 SNPs (Figure 4.7). Other Levantine individuals of this time period were of too low coverage and thus yielded a low number of sites (< 1000 SNPs) for this analyses. However, we also expect such introgression to be unlikely.

For a complete overview of the contribution that European wild aurochs might have made to ancient cattle populations after domestication, *D*-statistics were also

computed on the modern breeds from the 700K SNP dataset (Figure 4.8; Appendix Table 9.2.7). This has previously been done using 50K/700K SNP data for the British Mesolithic aurochs CPC98 (Park *et al.* 2015; Upadhyay *et al.* 2017).

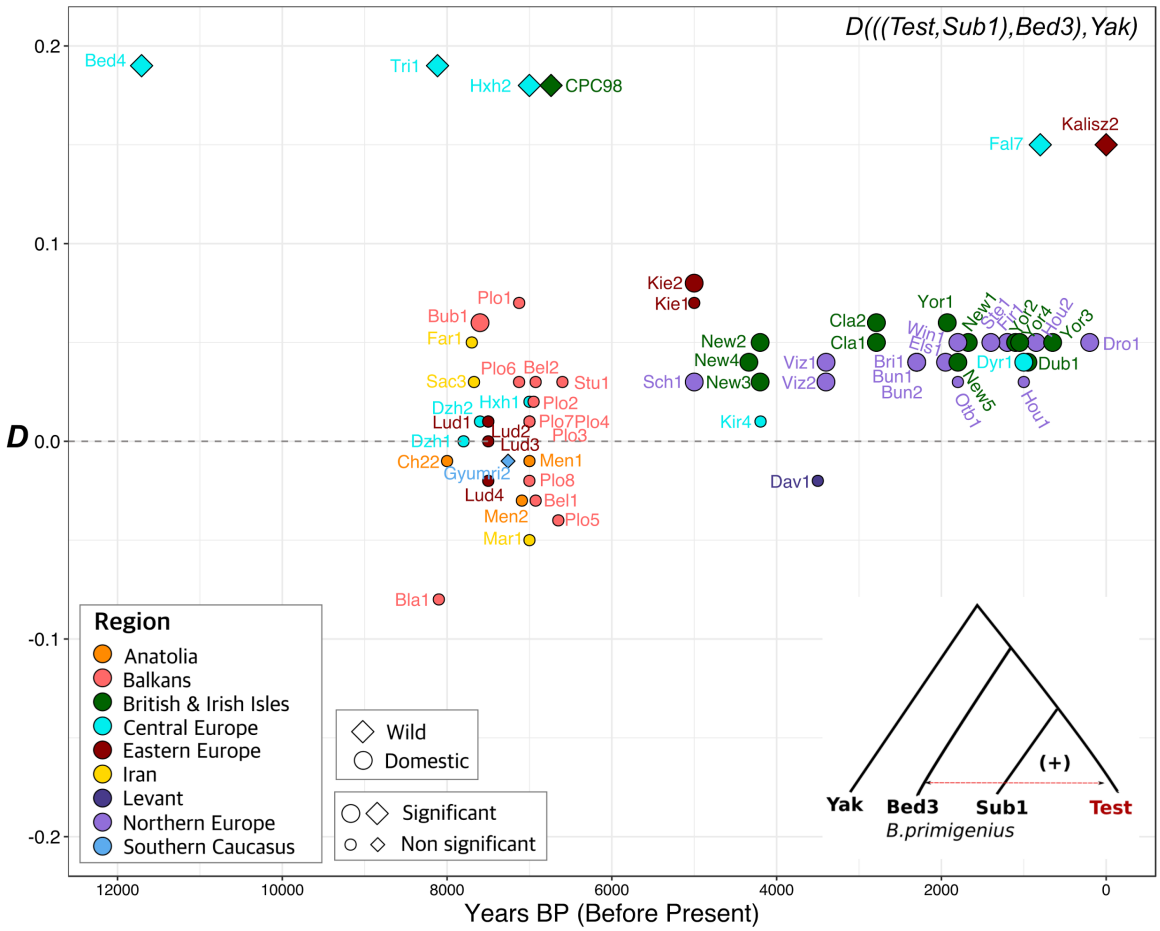


Figure 4.7 - D(((Test,Sub1),Bed3),Yak) vs Years BP. *Bed3 is a representative of European Bos primigenius and Test are ancient individuals. Positive D values indicate gene flow from Bed3 to Test. Ancient populations are shown in different colours. Significance given by point size. Confirmed primigenius are shown as diamonds and ancient domestics as circles.*

Significant *D* values based on ~104,000 SNPs for genomic admixture between Central European aurochs are seen in modern cattle breeds such as: Galloway (*D*=0.0394, *Z*=4.8), Highland (*D*=0.0352, *Z*=4), Kerry (*D*=0.033, *Z*= 4.3), Jersey (*D*=0.0289; Z=3.6), Guernsey (*D*=0.0281; Z=3.6) and Norwegian Red Cattle (*D*=0.0262; Z=3.3) (Figure 4.8). The top three estimates of aurochs-derived alleles were British and Irish breeds and all significant Northwestern European cattle breeds gave positive *D* values. In contrast,

Asian and African modern cattle breeds all revealed negative *D* values, suggesting no gene flow from Central European aurochs (Figure 4.8). Finally, it is important to notice that Southern European breeds from Italy (Maremmana, Romagnola) and from Greece (Sikias), strongly contrast with Northwestern European breeds, showing significantly negative *D* values, therefore suggesting no gene flow between Bed3 and the ancestors of these modern cattle breeds. These results support what has been previously observed for the CPC98 British Mesolithic aurochs, in which Balkan-Italian breeds showed less shared derived alleles with this aurochs than Northwestern and Iberian breeds do (Upadhyay *et al.* 2017).

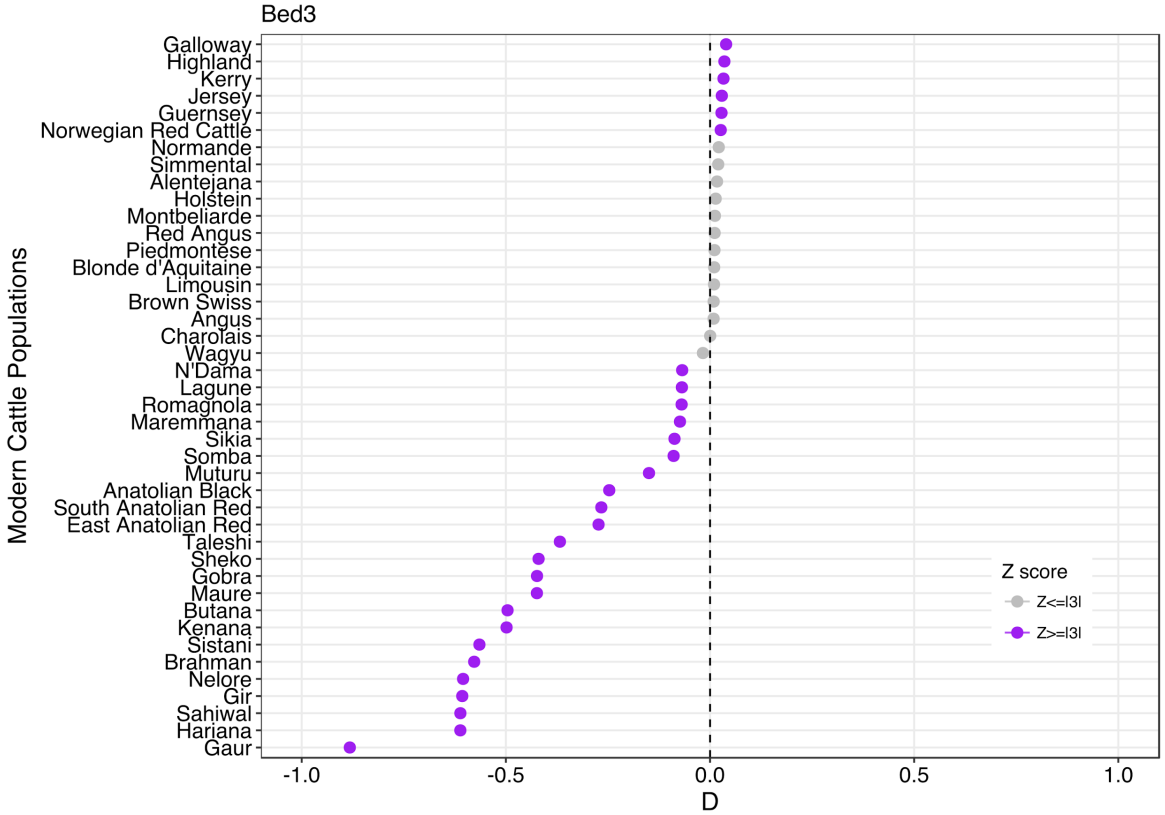


Figure 4.8 - D(((Moderns,Sub1),Bed3),Yak). *Bed3 is a representative of European Bos primigenius and Test are modern cattle breed populations from the 700K dataset. Positive D values indicate gene flow from Bed3 to Test. Statistical significance is coloured: significant (purple), non significant (grey).*

4.4.6. Formally testing African Bos taurus introgression

In order to formally test admixture of African taurine into early domestics from the Levant the following *D*-statistic test was performed: *D*(((Sub1, Test), Somba), Yak).

Here with Somba representing an African taurine population that, in the case of admixture, would break the clade of ancient cattle from the Levant and Sub1- an Neolithic Anatolian domesticate. Southern Levantine samples yielded too few sites to compute *D*-statistics apart from the Middle Bronze Age Dav1. This gave a significant positive *D* value (*D*=0.10, Z=11), which is evidence for gene flow between African taurine and Dav1, in contrast to all other ancients tested.

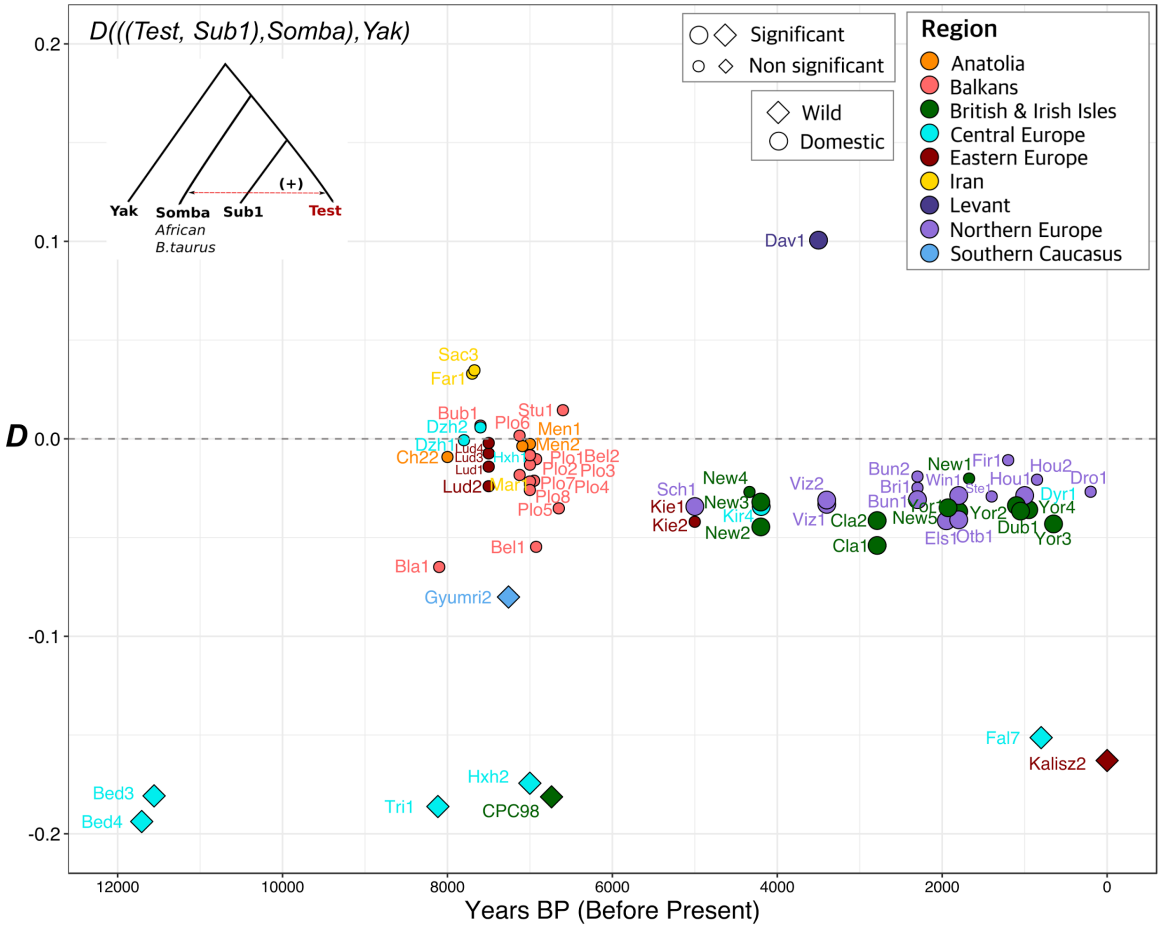


Figure 4.9 - D(((Test,Sub1),Somba),Yak) vs Years BP. *Somba is the representative of African Bos taurus and Test are ancient individuals. Positive D values indicate gene flow from Somba to Test. Ancient populations are shown in different colours. Significance given by point size. Confirmed primigenius are shown as diamonds and ancient domestics as circles.*

A similar *D*-statistic was computed to test introgression into Sub1: *D*(((Test, New1), Somba), Yak); New1 is an individual from Neolithic Newgrange Ireland. Dav1 produced a highly significant *D* value (*D*= 0.11, Z=12.9); Sub1 yielded a *D* value of 0.02 with a non-significant Z-score of -2.2 (Figure 4.9).

4.4.7. Introgression with Near Eastern aurochs

Gyumri2, an Armenian aurochs contemporary to early domestic *Bos taurus* represent a source of secondary wild genetic influx to early domestics in the Near East. From PCA (Figure 4.4), Gyumri2 seems to cluster closer to early Near Eastern *Bos taurus* individuals than to European *Bos primigenius*. To assess this the *D*(((Test, Sub1), Gyumri2),Yak) was calculated (Figure 4.11). Early ancient domestics should form a clade with Anatolian domestic Sub1 unless there is admixture with Gyumri2. No individual showed a significant positive *D* value that supported a higher number of shared derived alleles with Gyumri2. For European aurochs, a significant negative *D* value is observed. However, the Iranian Neolithic (6000-5500 BC) individual Far1, from Miyanroud (Fars province), seems to be an outlier with a positive *D* value of 0.09 but with a nonsignificant *Z*-score of 1.6. It is important to mention, notwithstanding, that this *D*-statistic was computed solely on ~3000 SNPs and that perhaps more data will in fact reveal significant introgression from the Armenian aurochs.

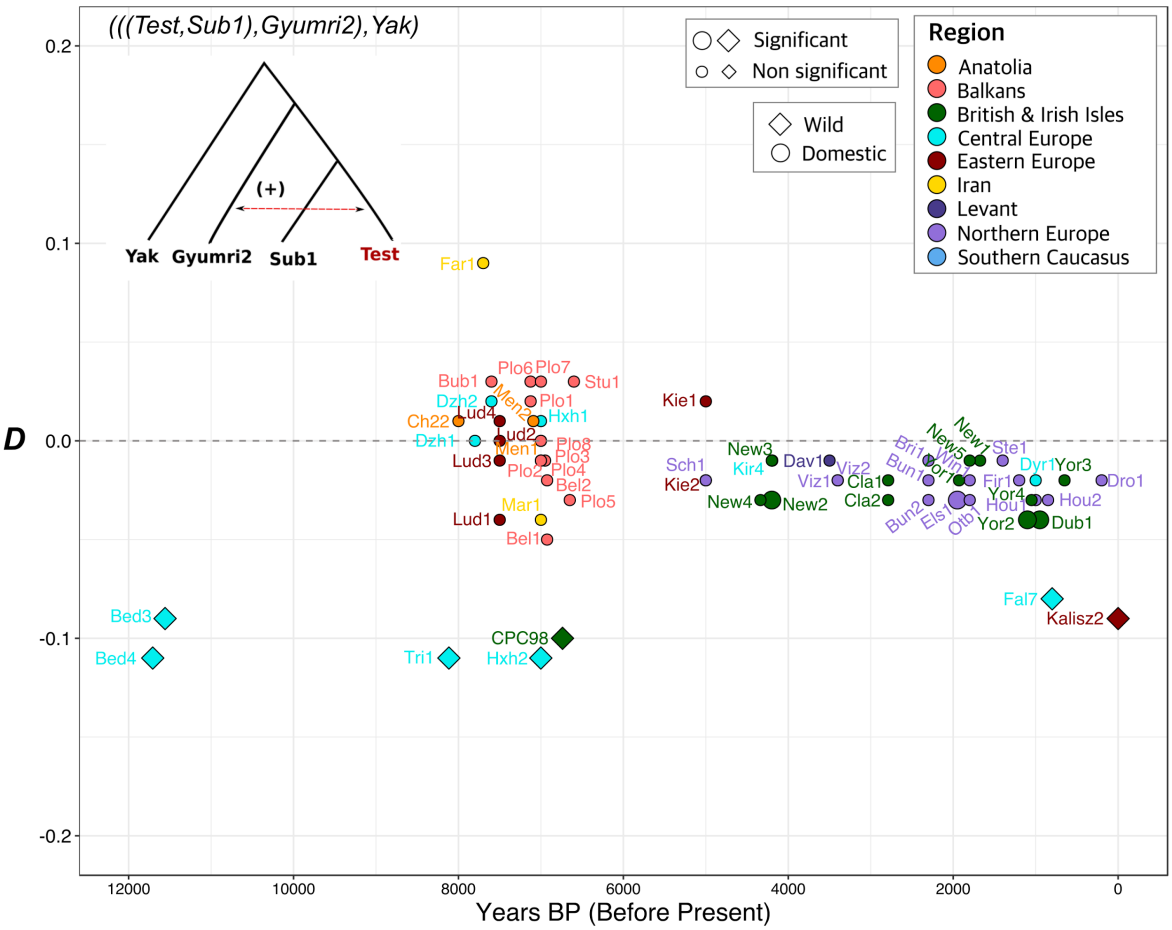


Figure 4.10 - D(((Test,Sub1),Gyumri2),Yak) vs Years BP. *Gyumri2 is the Near Eastern aurochs and Test are ancient individuals. Positive D values indicate gene flow from Gyumri2 to Test. Ancient populations are shown in different colours. Significance given by point size. Confirmed primigenius are shown as diamonds and ancient domestics as circles.*

D-statistics were also computed on the modern breeds from the same 700K SNP dataset (Figure 4.11) and no significant gene flow was detected from the Near Eastern aurochs, Gyumri2, into any of the modern breeds. Therefore, there is no evidence for significant contribution from this Armenian aurochs population into the ancestors of modern day cattle.

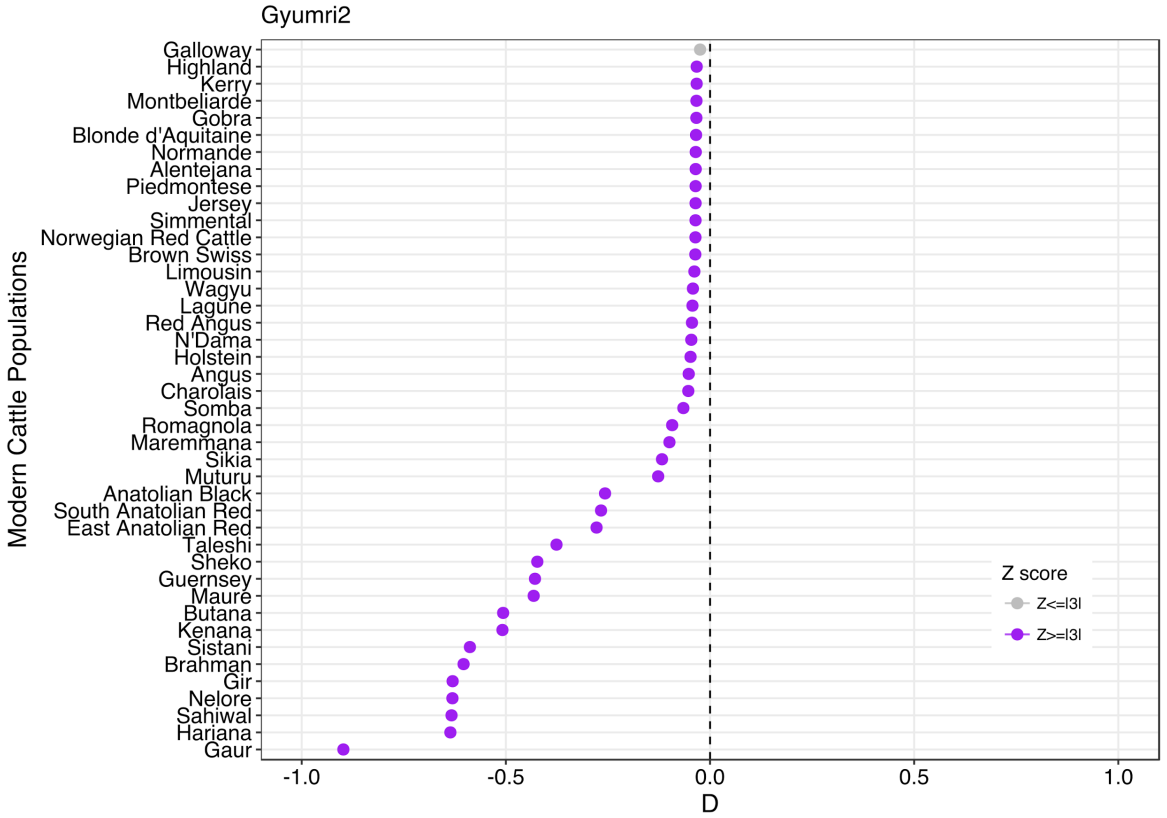


Figure 4.11 - D(((Modern,Sub1),Gyumri2),Yak). *Gyumri2 is the Near Eastern aurochs from Armenia and Test being all modern cattle breed populations from the 700K dataset. Positive D values indicate gene flow from Gyumri2. Statistical significance is coloured: significant (purple), non significant (grey).*

4.4.8. Ancient mitochondrial diversity of aurochs and ancient domestics

The mitochondrial phylogeny for both ancient and modern cattle individuals (Figure 4.12; Appendix Table 9.1.2 and 9.1.5) shows the early split of *Bos indicus* and *Bos taurus*. One late Neolithic sample, Kir4, from the Kirschbaumhöhle (Cherry Tree Cave) in the Franconian Alps, places as an outgroup to the rare mitochondrial haplogroup R. Firstly observed in Italian modern cattle, this haplogroup forms a sister clade with the PQT branch and is estimated to have diverged around 137,000 years ago (Achilli *et al.* 2009). Most European *Bos primigenius* individuals, with the exception of Kalisz3 from Poland (unknown age) which belongs to haplogroup Q, belonged to the Northern and Central European *B.primigenius* haplogroup P. Interestingly, the Moldovan Neolithic

sample Bir3, which in ADMIXTURE has shown a tripartite structure characteristic of aurochs, also possessed a typical European aurochs P haplogroup.

The Near Eastern Armenian aurochs, Gyumri2, places as an outgroup to the Q haplogroup. Furthermore, Gyumri2 shares a single mutation out of 17 before the QT split (16264A) and 1 mutation out of 9 (10717A) before the Q branch split into Q1 and Q2 (Bonfiglio *et al.* 2010). Neolithic ancient domestics like Mar1 and Sac3 from Iran; Bel1, Bel2, Plo1, Plo2 from Serbia; and Men2 from Anatolia belonged to the Q haplogroup, a minority domestic clade. This is unsurprising as it has been previously observed in early ancient individuals from Southeastern Europe and modern Near Eastern cattle (Achilli *et al.* 2009; Scheu *et al.* 2015).

Other Neolithic individuals from Anatolia (Sub1), Serbia (Plo4, Plo8) and Moldova (Bir2) belonged to the taurine mitochondrial haplogroup T2, which is not uncommon for Near Eastern individuals (Troy *et al.* 2001; Edwards *et al.* 2004; Meiri *et al.* 2017). Most mitochondrial sequences from ancient individuals from Europe and Anatolia (Ch22, Men1), revealed a T3 haplogroup, which is very common in taurine animals, and present at very high frequency in Europe (Troy *et al.* 2001; Bollongino *et al.* 2006; Achilli *et al.* 2009). These included the supposedly aurochs individual from the Netherlands, Bri1.

Finally, concordant with what has been observed so far from whole genome data, ancient Levantine individuals seem to belong almost exclusively to the T1 haplogroup (Dan1, Dav2, Dav3, Dav4, Nah1, Thr1); as well as an individual from Southwest Iran (Far1) and an individual from Moldova (Bir1). T1 is almost fixed in modern African populations (Troy *et al.* 2001). Dav1, a Middle Bronze Age (3879-3703 cal. BP) individual from the Levant is an exception, belonging to the T3 haplogroup. Finally, the haplogroup assignment of the Israeli sample Tda1 is insecure due to extremely low coverage, and thus its position as an outgroup to T5 haplogroup cannot be confirmed.



Figure 4.12 - Bovine Mitochondrial phylogeny. *Phylogenetic tree for taurine and indicine mitogenomes, including mtDNA reference data (bold). Each haplogroup/sub-haplogroup is coloured differently and the tree was rooted with a domestic yak (Bos grunniens). Node support for 100 bootstrap replicates are shown. The Tda1 sample is shown in black as it's position on the tree is insecure due to the low coverage of the mitochondrial genome for this individual. Ancients are coloured with assigned haplogroup and primigenius specimens are starred.*

4.5. Discussion

The Near East as the centre of domestication for *Bos taurus* has been generally accepted and is supported both through archaeology and genetics. The genetic analyses of ancient specimens, however, have been mostly confined to mitochondrial DNA analyses due to poor preservation of samples from hot climates and to the technological limitations of PCR-based methods for ancient DNA. The introduction of specialized techniques for extraction and sequencing of ancient DNA, as well as the development of software and computer pipelines to deal with the challenges of ancient DNA molecules have all significantly pushed the field forward. In this chapter, a completely new dataset of ancient specimens from the locus and time surrounding domestication has allowed for a deeper exploration of the questions surrounding *Bos taurus* domestication and its subsequent expansion from the Near East into the European continent.

4.5.1. Whole mitochondrial data supports a Near Eastern origin of Bos taurus

The mitochondrial DNA phylogeny showed a complete dominance of ancient cattle belonging to the QT clade, with clear higher frequency of the macro-haplogroup T; and within this an overall higher frequency of T3 mitochondria, particularly for European ancient domestics. However, T1 dominated the southern Levantine individuals.

Thus, when looking at early domestics from Anatolia, Iran, Southern Levant, and Europe there are a few patterns that emerged from the mitochondrial phylogeny. The first, is that in Anatolia and Iran the predominating haplogroups for early Neolithic domestics were Q (Mar1, Sac3, Men2), T2 (Sub1) and T3 (Men1, Ch22), which have been previously observed in ancient Near Eastern cattle (Scheu *et al.* 2015). The second being that typical mitogenomes from the Neolithic to Bronze Age southern Levant belong to the mitochondrial T1 haplogroup. Thirdly, in Neolithic ancients from the Balkan Peninsula (Serbia, Bulgaria) both Q and T (T2,T3) haplogroups were present at high frequency.

Fourthly, as animals move into Europe T3 seems to be the dominant haplogroup for Central and Northern Europe from the Neolithic to the Early Medieval Period.

In conclusion, mitochondrial DNA diversity of early ancient individuals from the Near East and Europe support a domestication of haplogroup T and Q in the Near East and their subsequent expansion into Europe through human migration. This is also supported with extant cattle, where T3 is present at very high frequency in Northern and Central Europe (Troy *et al.* 2001); and Q more common to Southern European breeds (e.g. Chianina, Romagnola, Italian Red Pied and Cabannina) (Achilli *et al.* 2009). More recently, the Q haplogroup has also been found, albeit at very low frequency in modern cattle breeds from Egypt (Nile Delta region), which is uncommon for the African continent where T1 is almost fixed (Olivieri *et al.* 2015). The Q haplotype identified in the two cattle in that study did not share any private mutations with those previously identified by Achilli *et al.* 2009 and Bonfliglio *et al.* 2010 in Europeans suggesting that they were not a result of gene flow from European animals but rather a legacy of movement of animals from the Near East into the African continent (Olivieri *et al.* 2015). Finally, the complete absence of the I haplogroup in this collection and the deep bifurcation between the two main haplogroups in these two main taxa further reiterates the centre of domestication of *Bos indicus* to be distinct from that of *Bos taurus*.

4.5.2. Ancient whole genome data supports a Near Eastern origin of Bos taurus

Genomewide data analyses, based on the 700K SNP dataset, further support the origin of *Bos taurus* in the Near East. Principal component analysis revealed a clustering of early Neolithic ancient domestics from Anatolia which included a possible *Bos primigenius* (Ch22). A clear stepping-stone clustering of ancient individuals forming a south to north cline in ancient Europeans, which overlays and reflects the modern day breed variation of European cattle. Moreover, ADMIXTURE on Anatolian and European Neolithic samples have revealed a bipartite structure that is characteristic of modern *Bos taurus* individuals.

There is a clear cline (South to North) starting in Anatolia, moving into the Balkan Peninsula and into Central and Northern Europe with increasing fraction of the modern European taurine component.

One exception to this is the individual Bir3 from Cucuteni–Trypillia Neolithic culture in Moldova, which revealed a P mtDNA haplogroup, together with an ADMIXTURE tripartite genetic structure characteristic of European aurochs (Troy *et al.* 2001; Edwards, Bollongino, *et al.* 2007; Scheu *et al.* 2008; Mona *et al.* 2010; Zeyland *et al.* 2013; Park *et al.* 2015). It also revealed to be an outlier in in PCA analysis to other ancient Eastern European cattle, clustering with modern Italian breeds. This individual therefore could present a *Bos primigenius* individual or a possible wild-domestic crossbred. Another possibility is that this individual is dated to a much later period and indicine admixture could have happened (Loftus *et al.* 1999; Edwards, Baird, *et al.* 2007).

Furthermore, all *Bos primigenius* individuals, regardless of geographical origin showed a 3-component structure made up of modern indicine, African taurine and European taurine population ancestry. This composition was previously observed in CPC98, a British Mesolithic aurochs, by Park *et al.* (2015). This tripartite genetic structure seems also to be uniform across European aurochs from different time periods. Interestingly, the Near Eastern aurochs from Gyumri (Armenia), showed a relatively higher fraction of the modern African taurine component than the European aurochs. This genetic ancestry was also clear in PCA, where this individual clearly shows a higher genetic affinity to early ancient Near Eastern domestics relative to European *Bos primigenius*. This tripartite genetic structure likely reflects the ancestral structure of wild cattle before domestication, which partitioned through population separation and drift into modern African and European components; which now drive the ADMIXTURE algorithm.

Importantly, it is easily argued from geography and historical records that the tripartite structure seen in some modern day breeds (Figure 4.7) is a result of more recent admixture events, rather than a legacy of initial domestication from Western Asia (Edwards, Baird, *et al.* 2007; Magee *et al.* 2014; Park *et al.* 2015).

4.5.3. Ancient genome wide data supports gene flow between ancient European domestics and wild European aurochs

The idea of possible introgression of wild and domestic cattle in Europe after their arrival with migrating farmers has been extensively debated (Troy *et al.* 2001; Gotherstrom *et al.* 2005; Bollongino *et al.* 2006; Edwards, Bollongino, *et al.* 2007; Achilli *et al.* 2008; Edwards *et al.* 2010; Bonfiglio *et al.* 2010; Park *et al.* 2015; Sinding & Gilbert 2016; Upadhyay *et al.* 2017). Recently, genome-wide evidence has emerged supporting the genetic contribution of British aurochs to the ancestors of modern British and Irish cattle (Park *et al.* 2015). Furthermore, gene flow between a population of a CPC98-like aurochs and the ancestors of Iberian cattle has also been detected (Upadhyay *et al.* 2017).

Principal component analysis on this larger dataset of European *Bos primigenius* individuals has confirmed a clustering of *primigenius* individuals parallel to modern and ancient European domestics along PC1 that remains constant through ~11,000 years. *D*-statistics are useful in detecting admixture, even when the ancestral/admixing populations are not available (Patterson *et al.* 2012; Park *et al.* 2015; Upadhyay *et al.* 2017) and was implemented here using the modern 700K dataset. The ancient dataset presented here allows for a direct admixture test in early ancient individuals. Using a continental European Mesolithic aurochs (Bed3) as a representative of the aurochs population, several patterns have emerged from the computed *D*-statistics. All European aurochs shared higher numbers of derived alleles with Bed3 than with the early domestic from Anatolia (Sub1), which supports European *Bos primigenius* as an outgroup for early domestic taurine variation. Moreover, the Near Eastern aurochs, Gyumri2, shared a higher number

of derived alleles with Sub1 than with the European aurochs Bed3, which is consistent with there being a subpopulation of Near Eastern aurochs from which taurine cattle were domesticated and that were genetically distinct from the European aurochs populations.

Secondly, there was no evidence here of significant gene flow from European *primigenius* into early domestics from the Near East (Neolithic Anatolia, Iran, Southern Levant), the Balkan peninsula (Neolithic Serbia and Bulgaria), or Central and Eastern Europe. However, *Bos primigenius* admixture in Europe with ancient domestics from ~3000 BC is evident from the significant *D*-statistics in eastern (Poland) and northern Europe (Netherlands, Ireland). Considering that *Bos primigenius* populations were not present in Ireland, it is assumed that the gene flow detected in those animals was a imported phenomenon from Britain (Felius *et al.* 2014; Magee *et al.* 2014). Continuation of gene flow from the wild seems to have been consistent from the Neolithic to Roman times in northern (Britain, Ireland, Netherlands) and central Europe (Germany). However, Kir4, a Neolithic individual radiocarbon dated to 2894-2670 cal. BC from a cave in Germany is an exception. Its cave location and association with the Corded Ware culture (Seregély 2014), could mean that this individual perhaps has a distinct ancestry atypical of the region, which is also apparent from its mitochondrial DNA. Recently, human DNA studies from Late Neolithic Corded Ware culture have revealed that 75% of ancient German genomes can trace back their ancestry to the Yamnaya (Haak *et al.* 2015; Allentoft *et al.* 2015), which supported a massive migration from the Russian steppe to the west of Europe around ~3100 BC. The Yamnaya moved on horse-back and used wheeled wagons drawn by oxen to not only to provide shelter but to transport women, children and the elderly, in a mobile lifestyle (Cunliffe 2015). Thus, it is possible that this *Bos* individual is a legacy of such migrations and thus does not possess admixture with local northern European aurochs.

Also, it is not possible to exclude, with this ancient dataset, European aurochs introgression in southern parts of the European continent, which has been previously suggested by mitochondrial DNA analyses and genome-wide SNP data (Anderung *et al.* 2005; Upadhyay *et al.* 2017).

Analysis on genomewide SNP data from modern cattle produced similar results to those presented by Park *et al.* (2015) and Upadhyay *et al.* (2016). Evidence for gene flow from European aurochs into the ancestors of modern British and Irish cattle was shown and, even though our cattle dataset varies slightly in modern breeds included, results of significant *D*-statistic values are observed in both for British and Irish breeds: Highland and Kerry. Furthermore, results also showed a higher shared number of aurochs-derived alleles in Iberian cattle (Alentejana) than Italian cattle (Romagnola, Maremmana), consistent with what was previously reported (Upadhyay *et al.* 2017).

4.5.4. Whole mitochondria phylogeny reveals two novel haplogroups

The single Near Eastern aurochs mtDNA is an outgroup to Q and may present a novel haplogroup that has never been sampled before in extinct or extant cattle. The origin of the mitochondrial haplogroup R is contentious. First described in modern Italian breeds (Achilli *et al.* 2009; Bonfiglio *et al.* 2010), it has been hypothesized that there was a separate domestication for the R haplogroup in Italy, since it had not been found elsewhere. Here, a novel haplogroup has been identified that forms a clade that is an outgroup to R and to taurine and European *Bos primigenius* variation, and therefore prior to the REPQT node split (Achilli *et al.* 2009; Bonfiglio *et al.* 2010). It is not possible to clearly define and place this novel haplogroup, especially since it belongs to a possible migratory Late Neolithic German sample and no other ancient individuals in this dataset share the same mitochondrial haplogroup. Based on previous estimates it is likely that this haplogroup split from the taurine lineages before 43,000 years ago (estimated time of the R node divergence) (Achilli *et al.* 2009; Bonfiglio *et al.* 2010). This pre-dates the

archaeological context from which Kir4 belongs, and therefore this could be indicative of an admixture event from a previously unknown aurochs matriline.

4.5.5. Ancient whole mitochondria and the nuclear genome reveal new clues on Q haplogroup geographical distribution

A European aurochs from Poland (Kalisz3) with a mitogenome of 11x coverage, revealed a Q1 mtDNA. This not only contrasts with what is expected of European *Bos primigenius* individuals, which belong almost exclusively to the P haplogroup (Edwards, Bollongino, *et al.* 2007; Troy *et al.* 2001; Scheu *et al.* 2015), but shows this haplogroup is not restricted to ancient Near Eastern and Southeastern European individuals or extant Italian cattle (Achilli *et al.* 2009; Bonfiglio *et al.* 2010; Scheu *et al.* 2015). It could be argued that because there is no temporal information on this individual, it could represent an early domestic rather than an aurochs. However, principal component analysis from genome wide SNP data does not support this, as this individual clearly clusters away from domestic individuals from Neolithic Poland and shares higher genetic similarity to European *Bos primigenius*. Moreover, ADMIXTURE analysis reveals a similar population structure to European aurochs. Therefore, this could reflect an introgression event involving a female taurine individual and a male *Bos primigenius* individual; or that the matrilines of *B.primigenius* from Northern Europe were more genetically diverse than previously thought.

4.5.6. Genome wide data reveals an African taurine ancestry in Levantine domestics

The mitochondrial haplogroup T1 is the dominant haplogroup in Africa and it is not present at high frequencies elsewhere; although it has been observed in Near Eastern cattle and Southern European modern taurine cattle (Cymbron *et al.* 1999; Troy *et al.* 2001). In this collection of ancient individuals from the Southern Levant, the T1 haplogroup

dominates (75%). The procrustes PCA revealed a clear clustering of Levantine individuals and suggested ancestry shared with African taurines, as they fall intermediate to modern European taurine and African taurine variation. Moreover, they seem to form a clear and distinct cluster from all other ancient Near Eastern individuals from Anatolia, Iran and Southern Caucasus. This PCA result was echoed by ADMIXTURE analyses, in which Levantine samples showed a significantly higher fraction of the component shared with modern African taurine than their contemporary Near Eastern ancient domestics from Anatolia and Iran. The only Levantine individual, for which enough data was available for *D*-statistics was Dav1, a Middle Bronze Age individual from Jerusalem. This sample showed a significantly higher number of shared derived alleles with the African taurine Somba versus Sub1, which confirms the ancestral African taurine structure seen in both PCA and ADMIXTURE analyses. These results could suggest capture from an unknown wild aurochs population native to the southern Levant or gene flow from such. Archaeological evidence points to some regions of the southern Levant showing a culture of aurochs overhunting due to occupation of fertile regions by agriculturists - overlapping the regions with water resources necessary for thriving *B. primigenius* populations - which could have preceded wild cattle management and domestication (Marom & Bar-Oz 2013). On the other hand, this could also reflect an early backflow of early taurine domestics from North Africa into the Levantine region, which cannot be excluded since cattle had reached the Central Sahara by the end of the 6th millennium BC (di Lernia *et al*. 2013).

4.5.7. Genome wide data reveals no significant genetic contribution of a Near Eastern aurochs into ancient and modern domestic cattle

In this dataset, a 2x genome of a Near Eastern aurochs, contemporary to early domestics, was also used in a test of admixture to assess its genetic input into the gene pool of early taurine animals. Although the projection PCA clustering could be indicative of some genetic similarity to early ancient domestics from Neolithic Iran, *D*-statistics have

not indicated any significant gene flow between this individual and any ancient individuals. Furthermore, to exclude the possibility of gene flow between Gyumri2 and Sub1, a different *D*-statistic test was computed. This revealed that Sub1 does not show any significant excess sharing of derived alleles with Gyumri2. It is important to note, however, that some of the ancient DNA data is of extremely low coverage and therefore the number of sites available to perform the *D*-statistics are significantly reduced, especially for ancient Near Eastern samples from Iran. For example, the sample Far1 0.03x coverage only yielded ~3000 sites for the ABBA/BABA test but is a clear outlier. Therefore its positive *D* value, although not significant, should be investigated further, given that Gyumri2 clusters quite closely in PCA. Finally, the *D*-statistics performed on the modern bovine dataset have also indicated no significant admixture between Gyumri2 and the ancestors of modern day cattle, in agreement with the ancient DNA data from the Near East and Europe.

4.5.8. The strange case of a giant Roman bull

A Roman individual (Bri1), from Britsum (Netherlands) was previously characterised as *Bos primigenius*, based on skeleton size (Canan Çakırlar, personal communication). This individual's mitochondrial genome has revealed a typical domestic taurine mitochondria (T3). It was also revealed in PCA and ADMIXTURE analyses to have similar genetic ancestry to domestic individuals from the same region and same time depth. Furthermore, this individual has shown to have had a typical amount of ancestral gene flow from European aurochs but none from Near Eastern-type aurochs populations extra to that shared with Sub1.

Morphologically, archaeological remains revealed that the size of this bull does not compare to domestic bulls from similar Roman times in this region. This specimen seems to have some possible weight-associated pathologies, which have been associated with draught cattle (Canan Çakırlar, personal communication) (Bartosiewicz *et al.* 1997).

However, the pathologies presented by this bull are atypical in that there is no broadening of the distal metapodials but swelling of its shafts, which can be associated with heavy weight and advanced age. The pathologies of Bri1 are similar to those found in Swedish ancient cattle from Eketorp (Telldahl *et al.* 2011) however the Britsum bull is much bigger in size (Canan Çakırlar, personal communication).

In conclusion, the mitochondrial and nuclear genomes of this individual genetically resemble ancient domestic individuals from the same time period and it is likely that this represents a very large domestic bull.

4.5.9. Conclusion

Whole mitochondrial and whole genome data support previous studies of the Near East as the centre of domestication for *Bos taurus*. The geographically correlated genetic cline in ancestry from PCA and ADMIXTURE supports the origin of *Bos taurus* in the Near East and subsequent migration with early farmers and loss of diversity into Europe with time. The whole mitochondrial genome survey has revealed that the cattle mitochondrial tree has not yet come of age and that there are still novel haplogroups to discover from ancient specimens. Two novel haplogroups have been described, one in a Near Eastern Neolithic *Bos primigenius* individual and another in a Late Neolithic *Bos taurus* individual from Germany. Additionally, analysis of ancient domestics from the Southern Levant showed a higher percentage of African taurine-like ancestry than those of Anatolia. This could be the result of an ancient admixture event by an unknown aurochs from the Levant or an early backflow of domestics from Africa. Relatively higher African taurine-like ancestry is also observed in early domestics from Iran, although their genetic ancestry still resembles early domestics from Anatolia and are likely an import that could have also had some early admixture with wild local aurochs. Moreover, the first complete genome of a Near Eastern aurochs from Armenia has shown that ancestral components which exclusively make up the three main cattle populations (African

taurine, European taurine and indicine) were present in both aurochs from Europe (Park *et al.* 2015). PCA and *D*-statistics revealed a different ancestry of this Near Eastern aurochs to European *Bos primigenius* and showed it to be more closely related to an early domestic from Anatolia (Sub1) than to any of the European *Bos primigenius*.

5. African and Eurasian *Bos primigenius* through time and space

"Their strength and speed are extraordinary; they spare neither man nor wild beast which they have espied… But not even when taken very young can they be rendered familiar to men and tamed."

Julius Caesar

5.1. Introduction

The aurochs, or *Bos primigenius*, is the wild ancestor for modern cattle with the last living specimen dying in 1627 (Poland). The Asian *Bos acutiforms* (Lydekker 1898) is thought to be their ancestor and evolved in the Upper Pliocene around 5-1.8 MYA (Zeuner 1963; Van Vuure 2005). *Bos primigenius* subspecies, and ancestors of *B.taurus* and *B.indicus,* are estimated to have diverged sometime between 330,000 and 850,000 years ago (Loftus, MacHugh, Bradley, *et al.* 1994; MacHugh *et al.* 1997; Achilli *et al.* 2009; Murray *et al.* 2010). These then are thought to have reached Southern Europe (~700,000 years ago) (Estévez & Saña 1999) before they colonised Central Europe (~275,000 years ago) (Lehmann 1949).

There has been some speculation with regards to body size of aurochs, which were described by Julius Caesar as "little below the elephant in size". It has been suggested that this may be an exaggeration and that many such descriptions were not based on actual sight of an aurochs (Wright 2013; Melletti & Burton 2014). However it is apparent from osteology that aurochs were much bigger than domestic cattle, as well as showing greater sexual dimorphism between aurochs bulls and cows (Degerbøl & Fredskild 1970). Furthermore, geographical differences in body sizes have also been described, as well as differences in horns. Three different races have been described: *Bos primigenius primigenius* (Bojanus, 1827) in Eurasia; *Bos primigenius namadicus* (Falconer 1859) in South Asia; and *Bos primigenius opisthonomus/mauretanicus* (Thomas 1881) in North Africa (Grigson 1978;

Grigson 1980; Van Vuure 2005; Melletti & Burton 2014). This taxonomy is still debated, especially for the North African *mauretanicus* versus *primigenius* in Europe which are distinguished more by geographical distribution than clear morphological differences, in comparison to *namadicus* which has been shown to differ from *B. p. primigenius* in cranial morphology (Grigson 1980; Melletti & Burton 2014; Wright 2013).

Ancient DNA sequence from several *Bos primigenius* specimens have been published over the last 20 years. Investigations have mostly focused on mitochondria, (Bailey *et al.* 1996; Troy *et al.* 2001; Anderung *et al.* 2005; Beja-Pereira *et al.* 2006; Edwards, Bollongino, *et al.* 2007; Zeyland *et al.* 2013; Zhang *et al.* 2013). In ancient DNA, a particular focus has been on the control region of the mitochondrial DNA, although improvement in ancient DNA extraction and sequencing techniques have led to whole mitochondrial genomes being published (Edwards *et al.* 2010; Zeyland *et al.* 2013; Zhang *et al.* 2013). However, only a single *Bos primigenius* whole genome sequence, from prehistoric Britain, has become publicly available (Edwards *et al.* 2010; Park *et al.* 2015). Finally, *Bos primigenius* genetic variation from North Africa and the Asian continent remain largely unexplored.

5.2. Aims and Context

This chapter uses whole genome data to infer phylogenetic relationships between aurochs from different temporal and geographical contexts. To this date, the only available whole genome sequences belong to a single European *primigenius* individual and therefore this the first attempt at understanding genetic diversity in other continents inhabited by this species. Mitochondrial and Y chromosome phylogenies will investigate diversity at these single loci and whether unknown haplotypes are present in different continents. PCA, Admixture, IBS and *D* statistics will be used to understand genetic diversity on a whole genome level. Furthermore, it is also the scope of this chapter to determine the extent of the genetic contribution of aurochs to domestic cattle using a large dataset of ancient domestics from Europe, West and Central Asia, spanning a temporal range of almost 14,000 years. Moreover, the question of African taurine genetic variation is also further explored by the addition of a North African *Bos primigenius*, which represents the only specimen sequenced to date that could represent the population of aurochs admixing with the ancestors of modern day African taurine cattle. Using *D*-statistics we aim to pinpoint possible ancient admixture events between this and other aurochs specimens and ancient cattle. This would help in understanding, for example, whether African taurine ancestry is a product of wild genetic input or back-flow of early domestic cattle from North Africa.

A collection of 18 *Bos primigenius* individuals is presented and analysed, from 11 different archaeological sites across Eurasia and Northern Africa (Figure 5.1 and 5.2). In this dataset, 17 are unpublished novel *Bos primigenius* specimens, with Europeans having already been introduced in Chapter 4; and one is the previously published mitochondrial P-type auroch CPC98, from Carsington Pasture Cave (Edwards *et al.* 2010; Park *et al.* 2015). Archaeological details for each specimen are summarized in Table 5.1. In this dataset, two samples were of unknown geographical origin and these were designated as Tango1 and Tango2 for "T auroch of no geographical origin" 1 and 2, respectively, due to

their T mitochondrial haplotypes. Of the complete collection of *Bos primigenius* genomes presented in this chapter, 11 have been drilled and processed at Trinity College and 7 have been drilled and processed by Amelie Scheu, collaborator at the University of Mainz, Germany - starred in Table 5.2.

Table 5.1- Archaeological details. Archaeological details for each specimen. CPC98 is the published B.primigenius sample from Edwards et. al 2010 and Park et.al 2015. Samples marked with an * were processed by Amelie Scheu.

Sample ID	Bone Type	Country	Locality	Site	Archaeological Context	Date
Baikal1	petrous	Russia	Lake Baikal	Barguzin River	Neolithic	10431-10029 cal. BC
Bed3*	petrous	Germany		Bedburg	Early Mesolithic	9608 ± 151 cal. BC
Bed4*	petrous	Germany		Bedburg	Early Mesolithic	9758 ± 191 cal. BC
Belorus1	petrous	Belorus	Brest district	No Info	Unknown	N/A
Ch22*	scapula	Turkey	Konya Plain	Çatalhöyük	Neolithic	c.7500 BC to 5700 BC
CPC98	humerus	U.K.		Carsington Pasture Cave	Mesolithic	4788 cal. BC
Fal7*	?	Germany	Lkr. Uckermarck	Falkenwalde	Early Slavic	1100-1250 AD
Gyumri1	petrous	Armenia	Gyumri district	Gyumri	Mesolithic	11842-11622 cal. BC
Gyumri2	petrous	Armenia	Gyumri district	Gyumri	Neolithic	5036-5076 cal. BC
Hxh2*	petrous	Germany	Rhineland-Palatinate	Herxheim	Early Neolithic (LBK)	around 5000
Kalisz1	petrous	Poland	Prosna River	Kalisz	Unknown	N/A
Kalisz2	petrous	Poland	Prosna River	Kalisz	Unknown	N/A
Kalisz3	petrous	Poland	Prosna River	Kalisz	Unknown	N/A
Kor1	?	Turkey		Kortik Tepe	PPNA	~7950 BC
Tango1	petrous	No Info		No Info	Unknown	N/A
Tango2	petrous	No Info		No Info	Unknown	2470-2297 cal. BC
Th7*	Phalanx 2	Morocco		Taghit Haddouch	Epipalaeolithic	6933 cal. BC
Tri1*	metatarsus	Germany	Nordallee	Trier-Brüderkrankenhaus	Mesolithic	8116 cal. BC

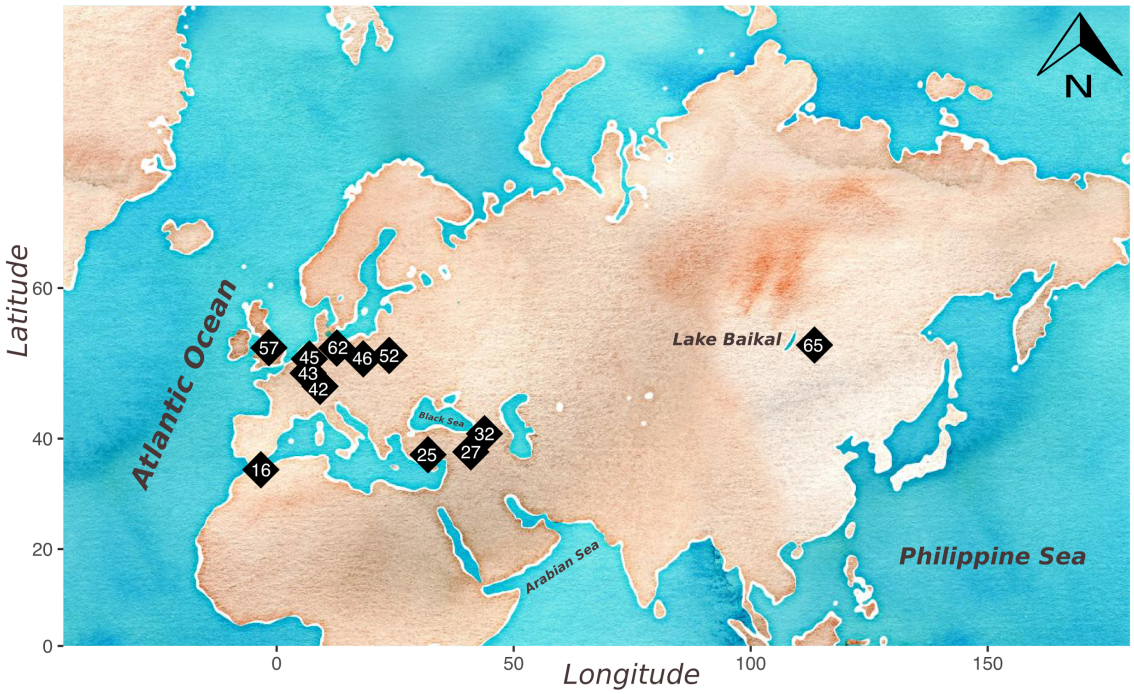


Figure 5.1- Geographical location of archaeological sites of Bos primigenius individuals. *(16) Taghit Haddouch (Morocco); (25) Çatalhöyük; (27) Körtik Tepe; (32) Gyumri (Armenia); (42) Herxheim (Germany); (43) Trier-Brüderkrankenhaus (Germany); (45) Bedburg-Königshoven (Germany); (46) Kalisz (Prosna River); (52) Brest district (Belorussia); (57) Carsington Pasture Cave (Park et al. 2015); (62) Falkenwalde (Germany); (65) Lake Baikal (Russia).*

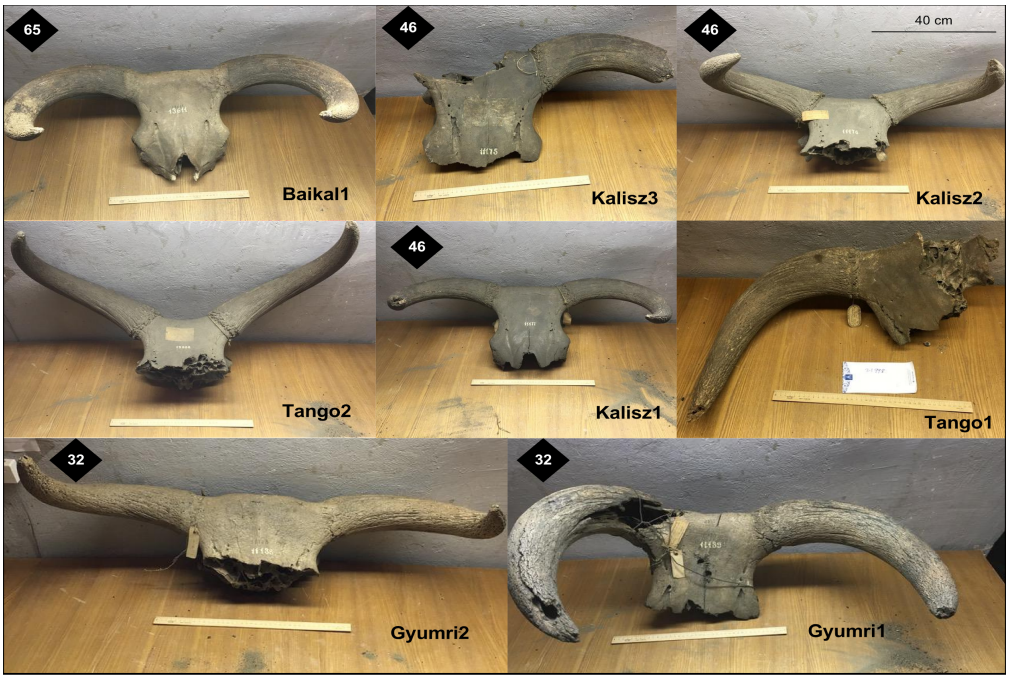


Figure 5.2 - Bos primigenius skulls. *For specimens where a photograph was available are shown above. Each specimen, where geographical origin was known, is labelled with the corresponding site number from Figure 5.1. Photographs by Daniel Bradley.*

5.3. Methods

5.3.1. Radiocarbon Dating

Samples that were thought to be of key interest, due to geographical origin (Near East; Russia) were chosen for radiocarbon dating and are described in Table 5.3 with C14 dates, calibrated to BC and BP. Furthermore, one of the *B.primigenius* specimens of unknown geographical location was also dated (Tango2). Calibration curve plots produced by OxCal (Ramsey 2009) can be found in the Appendix (Section 9.5).

5.3.2. Mitochondrial phylogeny

A neighbour joining (NJ) mitochondrial DNA (mtDNA) tree was drawn following the pipeline described in Section 3.5. For the CPC98 individual, the full mitochondrial genome was downloaded separately (accession: GU985279) (Edwards *et al.* 2010); shown on the phylogeny (Figure 5.3) as the P aurochs clustering with the Belorus1 sample. All published/publicly available mitochondrial genomes (modern and ancient) are summarized on Table 9.1.2 in the Appendix.

5.3.3. Procrustes PCA

Principal component analysis was performed on the basis of Procrustes analysis using LASER (Version 2.03), as described in 3.1.1.

5.3.4. ADMIXTURE

In order to investigate individual ancestries ADMIXTURE (Alexander *et al.* 2009a) was run using calls conforming to the bovine 700K SNP data. The pipeline followed was as described in 3.2. After filtering for transversions only, ADMIXTURE was run on 119,289 variants with 809 cattle, including ancients and modern breeds.

5.3.5. IBS (Identity by state) analysis of ancient genomes

To test the genetic relationships on a whole genome level across all these samples, Identity by state (IBS) analysis used ANGSD as described in section 3.7 (Korneliussen *et al.* 2014). The pairwise IBS matrix generated was used as an input matrix to calculate a rooted Neighbour-Joining tree. Individuals that were of very low coverage such as Kor1, Kalisz1 and Kalisz3 were excluded from this analysis.

5.3.6. D-statistics

D-statistics were used to explore relationships between aurochs clades suggested by IBS and to test for introgression. For this the full ancient dataset for this thesis was included, which is introduced in the beginning of this thesis. The *D*-statistic was computed using two different bioinformatic pipelines and software: AdmixTools (Patterson *et al.* 2012) and ANGSD (Korneliussen *et al.* 2014). For tests involving more than one individual of very low coverage, the ANGSD approach (Section 3.3.2) was preferred in order to maximize the number of sites for analyses. When the use of populations was desirable the 700K dataset was preferred and the AdmixTools approach was used (Section 3.3.1). A minimum threshold was set at a total number of 2,000 ABBA/BABA sites for the ANGSD computation. A minimum of 2000 SNPs for each test was accepted for the AdmixTools output. *D*-statistic was calculated only with transversions.

5.3.7. Outgroup f_3 statistics

In order to investigate the genetic drift shared between each of the different *B. primigenius* individuals and a representative of an early Neolithic domestic from Anatolia (Sub1) outgroup f_3 statistics were calculated using the Admixtools package as described in section 3.4.3 (Patterson *et al.* 2012). For this analysis the 700K Bovine SNP dataset was used, with transitions removed and with the diploid outgroup set as the *Bos indicus* breed

Sahiwal. The sample Kor1 from Körtik Tepe was removed from this analysis due to extremely low coverage.

5.3.8. Y chromosome phylogeny

Y chromosome reads were processed as described in Chapter 3 (Section 3.6). For the VCF generated a filter for missingness was applied and 25,105 out of a possible 1,350,000 sites were kept, using 33 ancient and modern individuals, including a *Bos grunniens* (domestic yak) individual. Seaview (Gouy *et al.* 2010) was used to run a muscle multiple alignment (Edgar 2004), and a NJ tree was drawn with 160 SNPs and 1000 replicates. Y chromosome coverages for all samples can be found in Appendix Table 9.1.6.

5.4. Results

5.4.1. Specimen preservation and whole genome sequencing

Samples were screened for endogenous DNA content and NGS data curated as described in the Chapter 2. Table 5.2 summarizes the endogenous DNA percentages and coverages obtained for each individual as well as sex determinations. Endogenous DNA percentages ranged from 0.2% to 70%; nuclear DNA coverages ranged from 0.0006x to 18x; and mitochondrial DNA coverages ranged from 1x to 3521x.

Table 5.2- Endogenous DNA and Coverages. *Endogenous DNA percentage is given for each specimen based on the calculation: (number of reads q25 x100/ number of total reads). Whole genome average coverage and mitochondrial genome coverage were calculated using Qualimap (García-Alcalde et al. 2012). Samples marked with (*) were processed by Amelie Scheu (University of Mainz). (**) CPC98 is the published B.primigenius sample from Park et.al 2015.*

Sample ID	Species	% DNA	Coverage	Mitochondria	Sex
Baikal1	*Bos primigenius*	70	4	493	Male
Bed3*	*Bos primigenius*	30	18	3521	Female
Bed4*	*Bos primigenius*	17	2	657	Female
Belorus1	*Bos primigenius*	22	2	325	Male
Ch22*	*Bos primigenius*	3	0.3	45	Male
CPC98**	*Bos primigenius*	21	4	10	Male
Fal7*	*Bos primigenius*	30	2	189	Male
Gyumri1	*Bos primigenius*	53	2	226	Male
Gyumri2	*Bos primigenius*	25	2	477	Male
Hxh2*	*Bos primigenius*	53	23	2209	Female
Kalisz1	*Bos primigenius*	0.2	0.0006	1	Male
Kalisz2	*Bos primigenius*	35	3	417	Male
Kalisz3	*Bos primigenius*	6	0.01	11	Male
Kor1	*Bos primigenius*	1	0.0018	12	Female
Tango1	*Bos primigenius*	45	2	339	Male
Tango2	*Bos primigenius*	49	2	295	Male
Th7*	*Bos primigenius*	0.8	0.07	8	Female
Tri1*	*Bos primigenius*	24	2	822	Male

5.4.2. Radiocarbon Dating

The *Bos primigenius* individual from Armenia, Gyumri1, dated to 11,842-11,622 cal. years BC. The auroch individual from the Baikal region in Russia, dated to 10,431-10,029 cal. years BC, predating the other ancient *Bos* specimen of the region published to date (Zhang *et al.* 2013). Tango2, was dated as a contemporary to ancient domestics. The other Armenian auroch (Gyumri2) was revealed as contemporary to Near Eastern Neolithic domestics (Table 5.3).

***Table 5.3 - Radiocarbon Dates**. Measured radiocarbon dates in C14 BP with error; Calibrated dates in BC and BP based on 2-sigma calibration (95% probability).*

Sample ID	Conventional C14 age (BP)	Calibrated Date BC (cal.BC) 95% probability	Calibrated Date BP (cal.BP) 95% probability
Baikal1	10320+/-30	10431-10029	12381-11979
Gyumri1	11990+/-40	11842-11622	13792-13572
Gyumri2	6330+/-30	5036-5076	6986-7026
Tango2	3980+/-30	2470-2297	4420-4247

5.4.3. Mitochondrial phylogeny

In order, to get a first insight into *B. primigenius* genetic variation across this panel of individuals, a NJ mitochondrial tree for the complete mitochondrial genomes was drawn (Figure 5.3). At the top of the tree are modern *Bos indicus* individuals. This matriline is thought to have diverged around ~300,000 years ago from taurine matrilines (Loftus, MacHugh, Bradley, *et al.* 1994; Achilli *et al.* 2009).

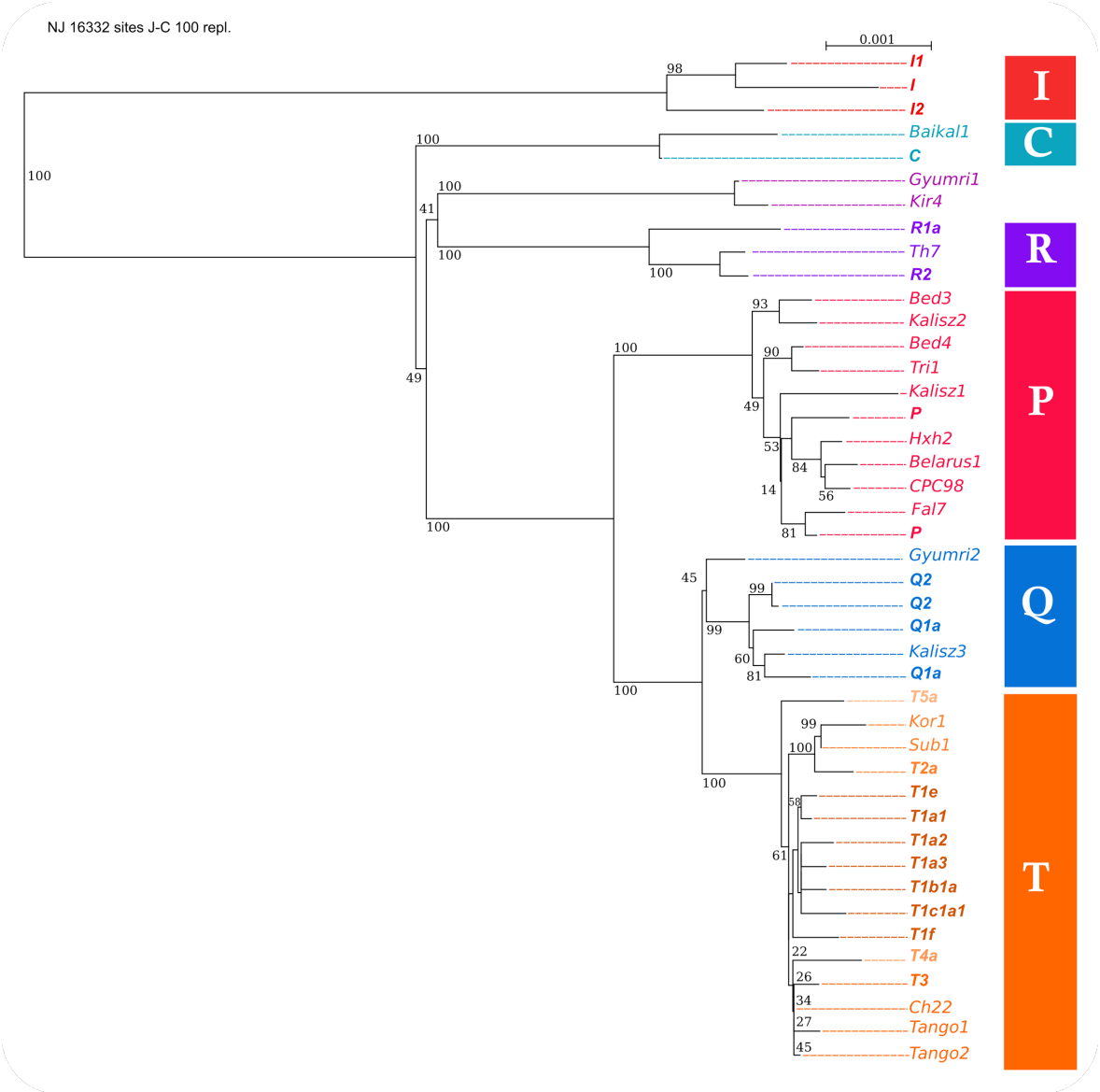


Figure 5.3- Neighbour Joining mitochondrial tree. *Haplogroups are grouped by colours and reference genomes are presented in bold. Bos primigenius samples are coloured according to mitochondrial haplogroup. Neighbour Joining tree drawn in Seaview and bootstrap values are shown for 1000 replicates.*

The *B. primigenius* individual from Russia Baikal1, found in the Barguzin River (Southern Russian Siberia) belonged to the C haplogroup, only previously observed in one ancient Chinese *B.primigenius* specimen. Baikal1 predated the Chinese C individual (8,550 cal. BC) which is ~1,500 Km distant. The P haplogroup is the most frequent (7/8) haplogroup for the European aurochs, comprising individuals from Germany, Poland and Belorussia, spanning from the Mesolithic period to the Early Middle Ages.

The Armenian aurochs Gyumri1 appears to be an outgroup to the R haplogroup, which includes two Italian modern individuals and the ancient Moroccan aurochs Th7 (6933 cal. BC). Gyumri1, securely predates the time of taurine cattle domestication in the Near East (~9,000 BC) and thus represents the first whole mitochondrial and nuclear genome of a wild bovine from this region. It clusters with Kir4 (Chapter 4) from a cave in Neolithic Germany, forming a novel sister clade to the R haplogroup. In addition, Th7, the North African Epipaleolithic *Bos primigenius* was assigned to the R haplogroup, clearly forming a clade with previously described R modern cattle from Italy (Achilli *et al.* 2009). Moreover, the younger aurochs from Armenia (Gyumri2) clusters as an outgroup to the haplogroup Q. Kalisz2 from Poland possesses a Q matriline, which further expands the extent of this haplogroup geographically. Two early Anatolian *Bos*, Kor1 and Ch22 both fall within T haplogroup variation. Kor1, originating from PPNA Körtik Tepe most likely belongs to a wild population (Arbuckle & Özkaya 2006). Its mitochondrial haplogroup T2 has been observed in early domestics from Anatolia such as Sub1 (Figure 5.3), Southeastern Europe and Neolithic Iran (Scheu *et al.* 2015) and in modern Near Eastern cattle (Troy *et al.* 2001). Tango1 and Tango2 present an interesting result given that they clustered with T3 - the most common haplogroup within modern European cattle breeds (Troy *et al.* 2001), although it has been arguably observed in wild cattle from Italy based on PCR-aDNA (Beja-Pereira *et al.* 2006).

5.4.4. Projection Procrustes PCA

Projection procrustes PCA (Figure 5.4) revealed different clusters of *Bos primigenius* when projected onto the modern 700K Bovine dataset. Firstly, the Epipaleolithic Moroccan aurochs Th7 did not cluster with any modern or ancient individuals, and showed a higher genetic affinity to African *Bos taurus* modern breeds than any other aurochs in this study. This positioning on the PCA is close to what was observed in Chapter 4 for Neolithic to Bronze Age samples from Southern Levant (Figure

4.4). Consequently, it is a putative indicator of African taurine gene flow into the Southern Levantine early domestics.

In addition, we see a clustering of two pre-agricultural Asian primigenius: Baikal1 from Southern Siberia and Gyumri1 from Armenia. These are positioned on the PCA nearly equidistant to all unhybridized modern variation and similarly to modern Near Eastern *Bos taurus* admixed (Loftus *et al.* 1999). Given that the dating of these aurochs predates that of the domestication of zebu (~6,500 BC) (Meadow 1993; Loftus, MacHugh, Bradley, *et al.* 1994) this apparent mixed ancestry illustrates a more diverse ancestral population that is present in extant cattle. In addition, Kor1 (~9,290+/-25 cal. BC) (Arbuckle & Özkaya 2006) from a site in the Fertile Crescent (Southeastern Anatolia), placed close to the modern Iranian cattle breed Taleshi (Northern Iran), which is composed of taurine (~50%) and indicine (~50%) ancestry (Chapter 4, Figure 4.6).

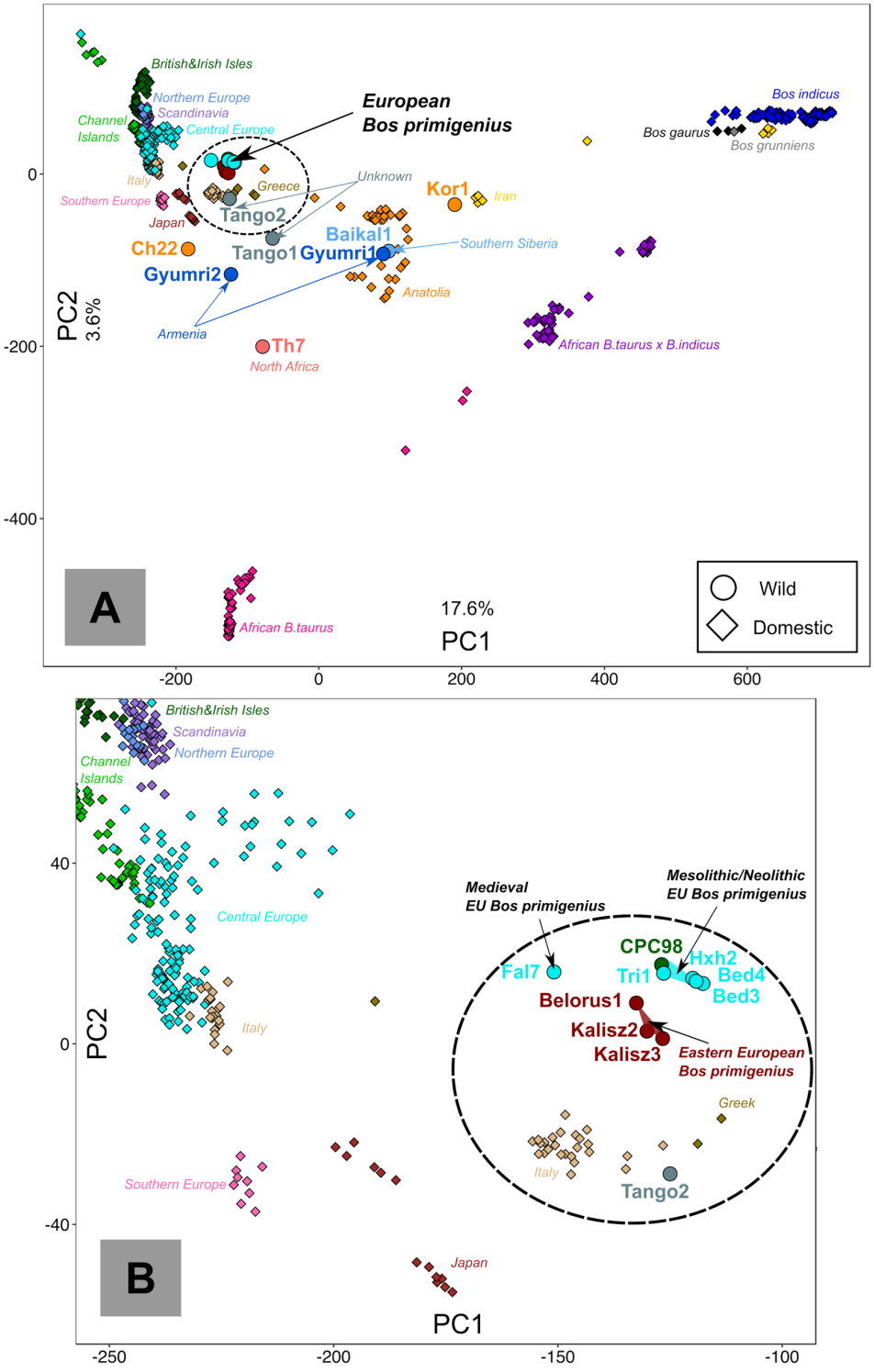


Figure 5.4 - Principal component analysis. ***(A)*** *Projection PCA showing Bos primigenius individuals (circles) projected onto the 700K Bovine SNP dataset (diamonds).* ***(B)*** *Zoom for European aurochs group from the same projection PCA shown in (A). 17.6% of variance is explained by PC1 which separates Bos taurus from Bos indicus and 3.6% of variance is explained by PC2 which separates European taurine from African taurine. Colours indicate geographical origin for both ancients and moderns.*

All European *Bos primigenius* individuals form a cluster to the right of modern European cattle breeds (Figure 5.4 B). Two main clusters of aurochs are observable: a German and British Mesolithic/Neolithic cluster (Bed3, Bed4, Hxh2, Tri1, CPC98) and an Eastern European (Polish, Belorussian) cluster consisting of Kalisz2, Kalisz3 and Belorus1. The Medieval German individual, Fal7, likely represents an admixed *Bos primigenius* with *Bos taurus* as it is closer to modern Europeans than any other aurochs is to extant European cattle breeds.

From Central Anatolia Çatalhöyük (c. 7400–6200 cal BC) (Cessford 2001), Ch22 was previously shown to fall within the variation of Neolithic/Chalcolithic domestic ancients from Anatolia and Iran and does not cluster here with any aurochs group (Figure 5.4A). The classification of Ch22 as a *Bos primigenius* specimen is probable but not certain. It falls closest to the Neolithic Armenian auroch Gyumri2 (5036-5076 cal. BC), which is unsurprising given geographical proximity. The latter, was also shown to fall close to Neolithic Iran (Figure 4.4).

Finally, the two T aurochs of unknown geographical and archaeological context also show interesting placements on the PCA. Tango2 clusters closely to modern Italian and modern Greek *Bos taurus* (Figure 5.4B). Interestingly, a Moldovan *Bos* individual Bir3, introduced in Chapter 4, also falls in a similar space of the PCA. Moreover, Tango2 is closer to the European aurochs cluster than Non-European aurochs (Gyumri1, Gyumri2, Baikal1, Kor1,Th7,Ch22) or Tango1. This clustering plus the T3 mitochondrial haplogroup, could be indicative of the origin of this individual as Southern European origin and of past admixture with populations of domestic cattle. Tango1 shows no close clustering with any aurochs or ancient or domestic cattle groups despite presenting a T3 mitochondrion (Figure 5.3).

5.4.5. ADMIXTURE

ADMIXTURE was run together for *Bos primigenius* individuals and modern cattle populations. The three-population model (K=3) has been shown previously (Bovine HapMap Consortium *et al.* 2009; Park *et al.* 2015) to distinguish between indicine (yellow), African taurine (blue) and European taurine cattle (pink), and is the model used here (Figure 5.5). Modern cattle breed structure for these components can be observed in Figure 4.7 in Chapter 4. The most obvious pattern observed in Figure 5.5 is that all *B. primigenius* individuals showed a composition of the three main components observable in modern day breeds: African taurine, European taurine and indicine, which has been previously observed in the Mesolithic *Bos primigenius* specimen from Britain CPC98 (Park *et al.* 2015; Upadhyay *et al.* 2017). There were some clear differences in the fraction of each component, varying with geographical and/or temporal context (Figure 5.5A and B). It is important to emphasize that these components might not be fully representative of past population structure, as they are based on pre-defined number of populations or clusters to which individuals are assigned (Alexander *et al.* 2009b; Falush *et al.* 2016). Also these are run using the 700K Bovine SNPs, which are ascertained towards domestic cattle.

The oldest aurochs in this collection Gyumri1 (11,842-11,622 cal. BC), Baikal1 (10,431-10,029 cal. BC) and Kor1 (~9,290+/-25 cal. BC) (Arbuckle & Özkaya 2006), report the highest percentages of the indicine component in this analysis: ~39%, ~40%, ~49%, respectively (Table 5.4) (Figure 5.4B).

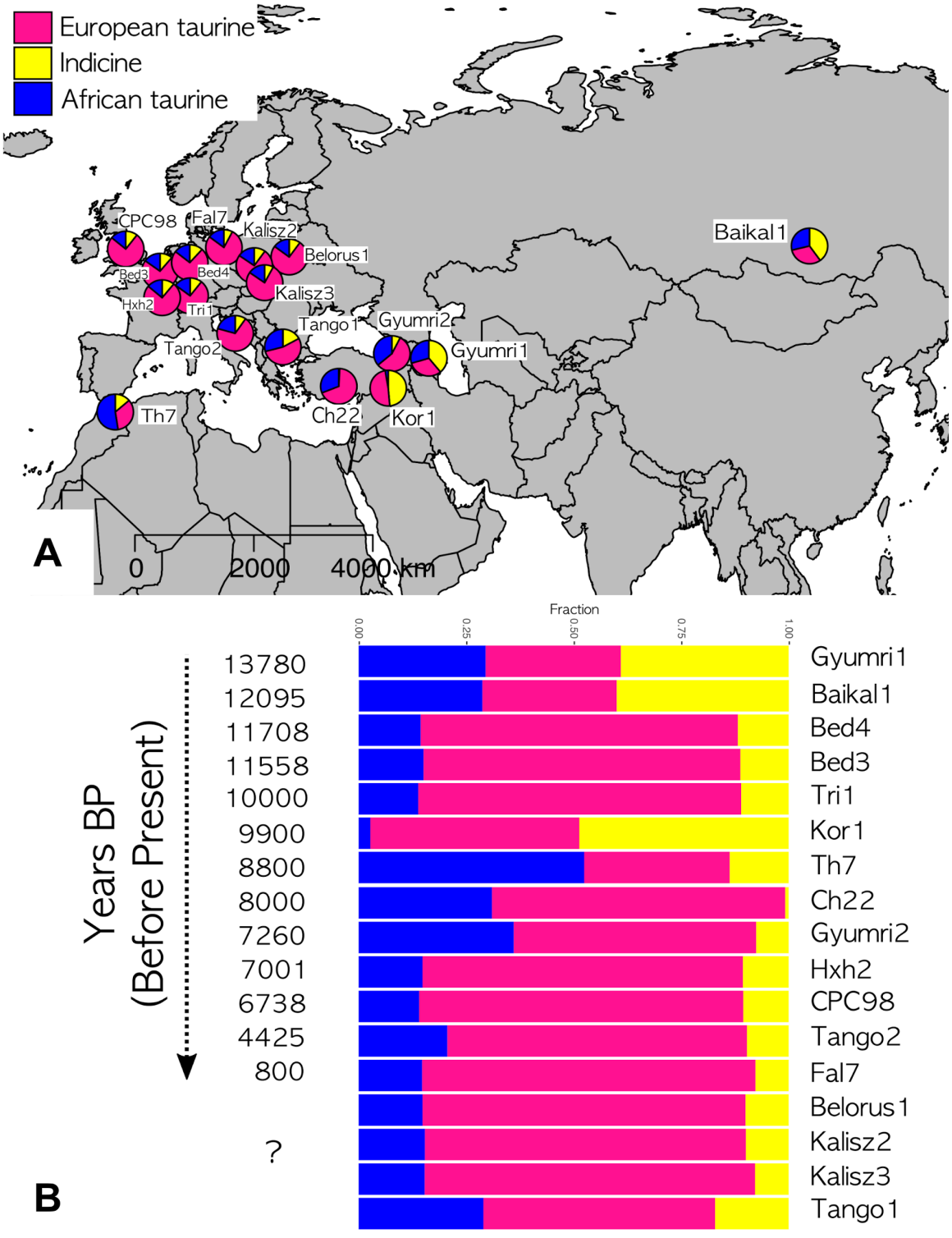


Figure 5.5 - ADMIXTURE for Bos primigenius specimens (K=3). ***(A)*** *Map of ADMIXTURE analyses showing geographical context of each aurochs. Tango1 and Tango2 were assigned a location at random. Pie charts represent single individuals.* ***(B)*** *ADMIXTURE barplots for temporal context of aurochs (approximate years BP are given for non dated samples).*

Both Gyumri1 and Baikal1 show similar percentages of African taurine and European taurine components (Figure 5.5A). Kor1 shows 9-fold smaller fraction of the African taurine component present in Kor1. This higher indicine fraction in Mesolithic Asian aurochs contrasts with contemporaneous pre-Neolithic aurochs specimens from Europe (Bed3, Bed4, Tri1, CPC98) and North Africa (Th7). In the first, the European taurine component is dominant (74-75%); whereas in Th7 the African taurine component is present at the highest fraction (52%), followed by European taurine (34%) and indicine (14%) (Table 5.4).

The dominance of the European taurine component is also visible in the Neolithic and Slavic German aurochs, Hxh2, Fal7, respectively; and for the Polish and Belorussian individuals Kalisz2, Kalisz3 and Belorus1. The highest fraction of European taurine is seen in the German Medieval aurochs Fal7 (78%) (Figure 5.5B, Table 5.4), which supports the inference that this individual is likely admixed with domestic European *Bos taurus*. In European aurochs the percentage of African taurine is consistent among all specimens (14-15%) and the *Bos indicus* component is present at range of 8-12%.

The two Armenian aurochs show contrasting fractions of each coefficient. Gyumri2's genetic structure is dominated by the European taurine component (~56%), followed by ~36% African taurine ancestry (and ~8% indicine) in which it is only second to Th7.

Tango2 shows a similar genetic structure to European aurochs pointing toward a likely geographical origin. Tango1 does not seem to resemble any particular aurochs groups. Its European taurine component is dominant (~54%), whereas the African taurine component (~29%) is higher than the range observed for European aurochs (~14-15%). Tango1 could possibly represent an older specimen within Europe.

Table 5.4 - ADMIXTURE analysis percentages for K=3. *Percentages calculated directly from ADMIXTURE output used to plot Figure 5.5. Percentages given in this table have been rounded to no decimal places.*

Individual	Indicine	European taurine	African taurine
Baikal1	40%	31%	29%
Bed3	11%	74%	15%
Bed4	12%	74%	14%
Belorus1	10%	75%	15%
Ch22	1%	68%	31%
CPC98	11%	75%	14%
Fal7	8%	78%	15%
Gyumri1	39%	31%	30%
Gyumri2	8%	56%	36%
Hxh2	11%	75%	15%
Kalisz2	10%	75%	15%
Kalisz3	8%	77%	15%
Kor1	49%	49%	3%
Tango1	17%	54%	29%
Tango2	10%	70%	21%
Th7	14%	34%	52%
Tri1	11%	75%	14%

5.4.6. Identity by State (IBS)

Identity by state (IBS) analysis was performed on whole genomes, both modern (Appendix 9.1.3) and ancient. Figure 5.6 shows the resulting neighbour-joining tree drawn from the pairwise distance matrix.

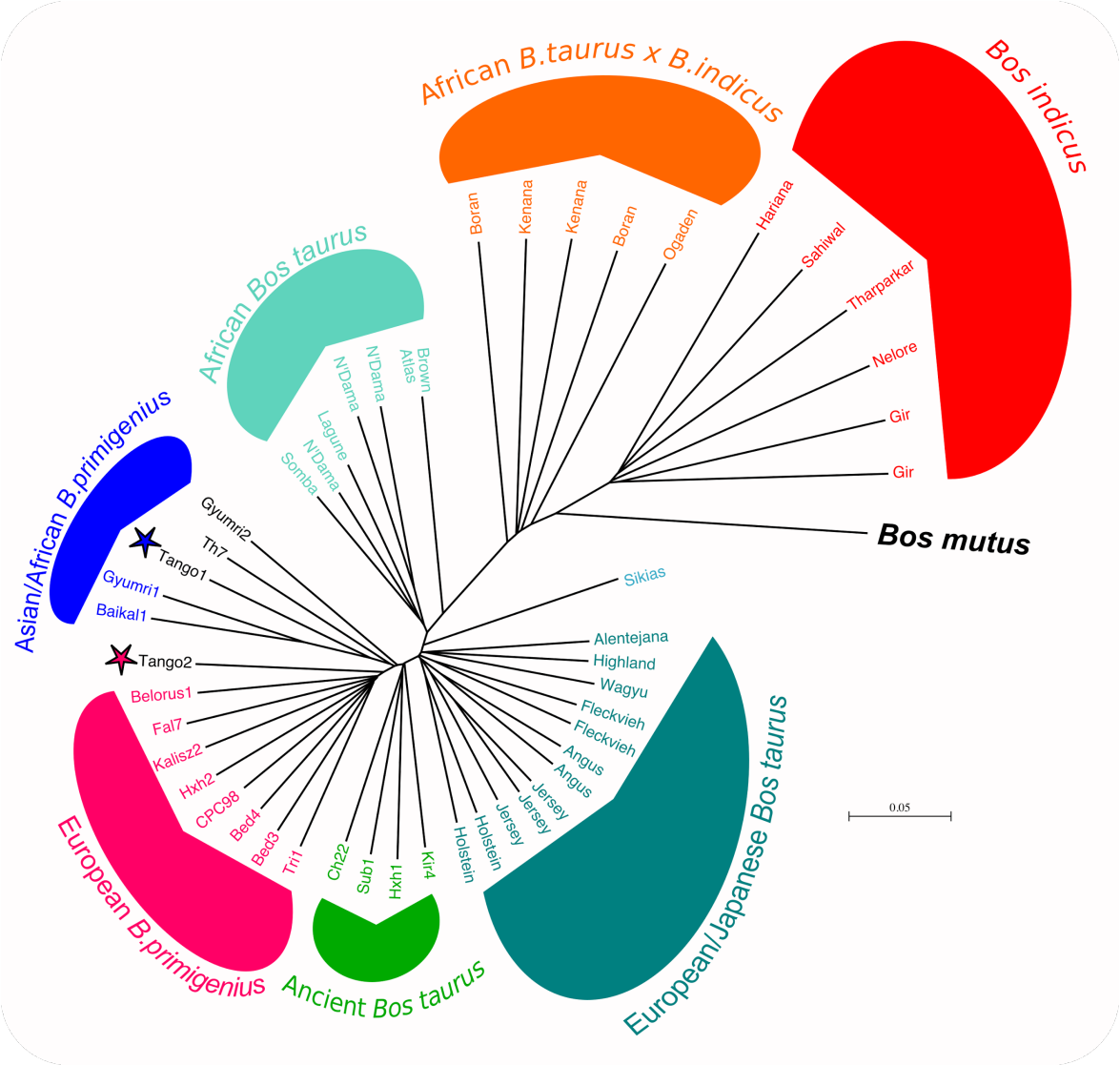


Figure 5.6 - unrooted NJ tree of IBS pairwise distances for ancient and modern domestic and extinct wild cattle*. Individuals of unknown geographical origin are starred for Tango1 and Tango2.*

The tree was rooted with wild yak (*Bos mutus*). Furthermore, *Bos indicus* is shown as outgroup to all *Bos taurus* and *Bos primigenius* individuals, forming a clade. An ancient *Bos taurus* grouping of Neolithic domestics is observed, comprising two Neolithic

individuals from Anatolia (Ch22 and Sub1) and two early and late Neolithic domestic individuals from Germany, Hxh1 and Kir4, respectively. In addition, European aurochs form a clade, including samples ranging from the Mesolithic (Bed3 and Bed4) to the Early Slavic period (Fal7). Tango2 sits basal to this European clade.

Another grouping of *Bos primigenius* individuals emerged, which comprised the Southern Siberian aurochs Baikal1, forming a clade with the Armenian aurochs Gyumri1, Tango1 and the North African aurochs (Th7). Moreover, Gyumri2, the Near Eastern aurochs from Armenia (5036-5076 cal. BC) placed close to this group.

5.4.7. Testing phylogenetic relationships using D-statistics

D-statistics were used to test groupings of aurochs that were suggested by IBS, ADMIXTURE and PCA analyses. Yak (*Bos grunniens*) was used as the outgroup in all the tests and X always means each aurochs in turn. Tests were set up as (H1,H2),H3),Out), where a negative value means that H1 is closer to H3 than H2 is; and a positive value means that H2 is closer to H3 than H1 is (Korneliussen *et al.* 2014). All *D*-statistics results quoted in the text can be found in supplementary tables in the Appendix section 9.3.

5.4.7.1 Asian, African Bos primigenius & Tango1

The grouping of the Russian and Armenian aurochs, Baikal1 and Gyumri1, seems to be consistent in PCA analysis, ADMIXTURE and IBS. Also, mitochondrial phylogeny revealed both as outgroups to European aurochs and ancient and modern *Bos taurus*. The *D*-statistic *D*(Baikal1, Gyumri1),X),Yak) tested this clade and reported no significant *D* value when X was the Eastern European aurochs (Kalisz2, Belorus1), Tango1 and the German Neolithic and Medieval aurochs - Hxh2 and Fal7. Hence, Baikal1 and Gyumri1 seem to form a clade in relation to each of these individuals. By contrast, significant positive *D* values are observed for the other aurochs in this analysis (Figure 5.7). Gyumri1 shares the higher number of derived alleles with the Near Eastern auroch

Gyumri2, the Anatolian Neolithic domestic Sub1, Tango2 and the German Mesolithic aurochs Bed3, Bed4 and Tri1. The significant positive *D*-statistic of Sub1 (6221-6024 cal. BC) (*D*=0.02; Z=3.41) contrasts with the non significance observed for Ch22 from Çatalhöyük (~7500 BC) in Anatolia (*D*=0.01; Z=1.61), which could be due to differences in genome coverage.

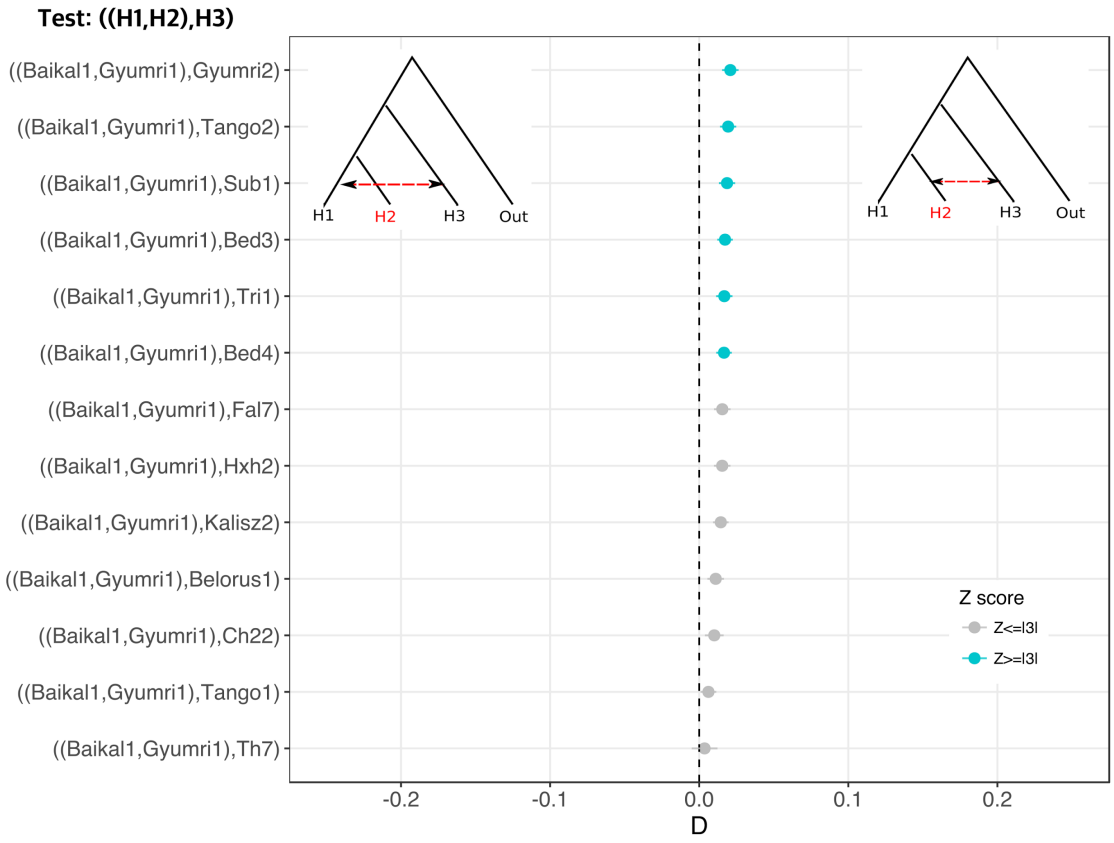


Figure 5.7 - D(((Baikal1,Gyumri1),X),Yak). *Y axis showing each test and X axis showing the corresponding computed D value. Statistical significance is given by colour. The Baikal1-Gyumri1 clade is intact with the exception of when H3 is either Gyumri2, Tango2, Sub1, Bed3, Tri1 or Bed4.*

Another question raised by the phylogeny was whether Tango1 and Th7 were part of this pre-Neolithic Asian aurochs clade. The *D*(((Baikal1/Gyumri1,Tango1),X),Yak) and *D*(((Baikal1/Gyumri1,Th7), X),Yak) tested for the inclusion of Tango1 and Th7 in this clade. Significantly positive *D* values suggested both Tango1 and Th7 are not securely part of this clade (Appendix Table 9.3.3). Subsequently, *D*(((Tango1,Th7),X),Yak) was

computed to test whether Tango1 and Th7 formed a clade in relation to other aurochs. Significant negative *D* values for all European aurochs, Gyumri1, Baikal1 and Tango2 suggest that Tango1 is closer to these than Th7 is (Appendix Table 9.3.4), and that they do not form a clade in such cases. To further test Th7's relationship to other aurochs groups, *D*(((Aurochs,Aurochs),Th7),Yak) revealed Th7 to be closer to Gyumri2 than to any European aurochs, Tango1, Tango2, Gyumri1 or Baikal1 (Appendix Table 9.3.5) agreeing with the placement on the phylogeny. Moreover, *D*(Gyumri2, Sub1/Ch22),Th7),Yak) gave non-significant *D* values supporting it as an outgroup to this Near Eastern Neolithic *Bos* clade. Also, Th7 is an outgroup to European aurochs as demonstrated by non-significant *D* values in *D*(EU_aurochs, EU_aurochs),Th7),Yak) (Figure 5.8).

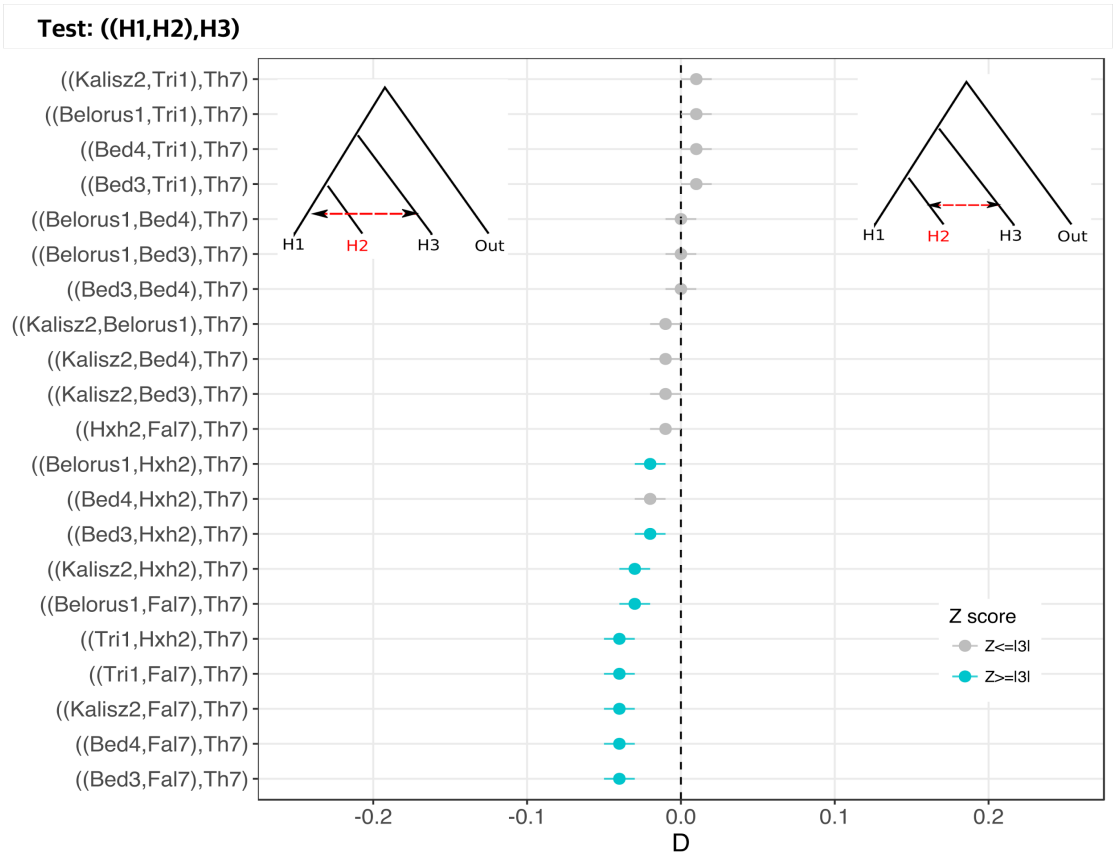


Figure 5.8 - D(((Aurochs,Aurochs),Th7),Yak). *Y axis showing each test and X axis showing the corresponding computed D value. Statistical significance is given by colour. Non significant values for most aurochs combinations for H1 and H2 support Th7 as an outgroup to European aurochs clade. Exceptions involve Fal7 and Hxh2 (German Medieval and Late Neolithic), where other European aurochs are closer to Th7 than these are, which could indicate Fal7 and Hxh2 as admixed.*

5.4.7.2. European Bos primigenius

In order to test the clade of continental European aurochs, the *D*-statistic *D*(((EU_aurochs,EU_aurochs), Pre-Neolithic Asian aurochs),Yak) was calculated, in which EU_aurochs are European aurochs for which archaeological context is available (Figure 5.9). No significant deviation from *D*=0 for European aurochs combinations confirm these as forming a clade to which Asian aurochs (Gyumri1/Baikal1) are outgroups. The sole exception to this is only observed with Fal7, which is likely admixed with domestics.

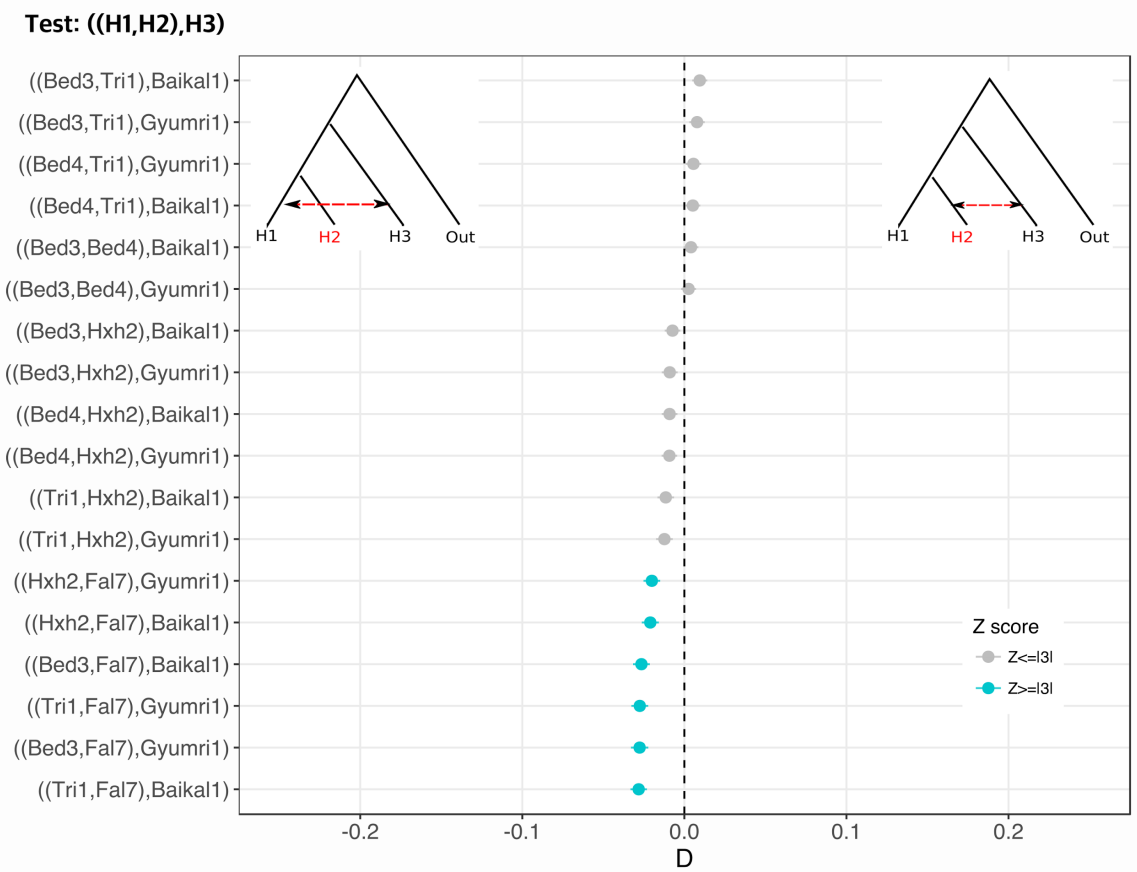


Figure 5.9 - D(((EU_aurochs,EU_aurochs), Gyumri1/Baikal1),Yak). *Y axis showing each test and X axis showing the corresponding computed D value. Statistical significance is given by colour based on Z scores. Majority of non significant D values support European aurochs as a secure clade. Fal7 is likely an admixed individual with domestics, resulting in significant higher shared derived alleles between non-admixed aurochs.*

5.4.7.3. Ancient Anatolian Bos taurus

A subsample of genomes from the Neolithic Near East (Sub1, Ch22) clustered together forming a clade. *D*-statistics were performed on this clade to test its validity in

relation to Eurasian and African *Bos primigenius*. The *D*-statistic for the test *D*(((Ch22,Sub1),X),Yak) gave non significant results, supporting this clade as robust (Appendix Table 9.3.7).

5.4.7.4. Near Eastern Bos primigenius

The IBS NJ tree suggested Gyumri2 as basal to both European and non-European subclades of *Bos primigenius* (Figure 5.6). To further understand Gyumri2's relation to other *primigenius* it was tested as an outgroup to all combinations of aurochs and Figure 5.10 summarizes the results for *D*(((aurochs,aurochs),Gyumri2),Yak).

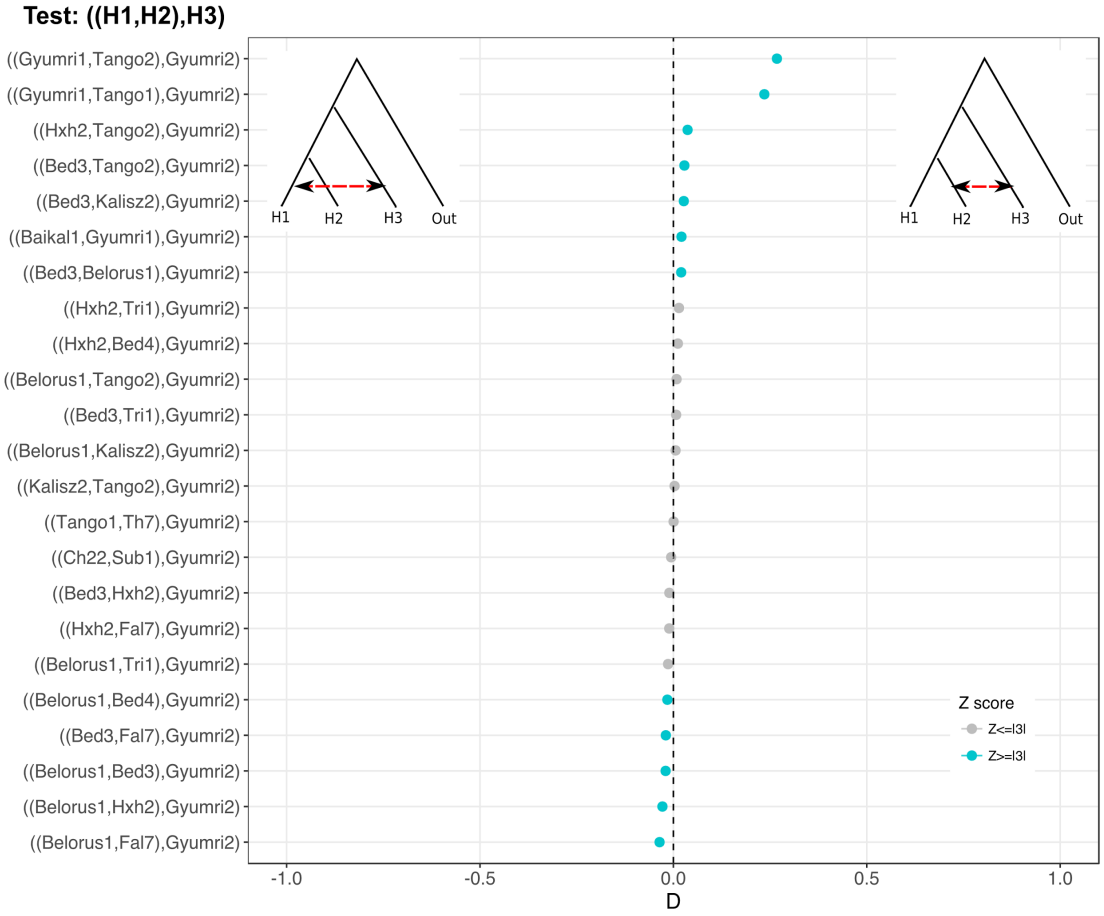


Figure 5.10 - D(((X, Y),Gyumri2),Yak). *X and Y represent each auroch in turn forming a hypothetical clade in respect to Gyumri2. Y axis showing each test and X axis showing the corresponding computed D value. Statistical significance is given by colour. Gyumri2 is an outgroup to most European aurochs. Gyumri2 is an outgroup to ancients from Anatolia (Sub1, Ch22) and shares more derived alleles with Gyumri1 than with the Russian aurochs Baikal1.*

Some patterns emerge that support the IBS tree (Figure 5.6). Firstly, Gyumri2 appears to be an outgroup to ancients from Anatolia (Sub1, Ch22). However, when looking at the oldest aurochs in this dataset (Baikal1 and Gyumri1), Gyumri2 shares more derived alleles with its Armenian counterpart than with the Russian aurochs Baikal1. Secondly, significant *D* values indicate that both Tango1 and Tango2 are closer to Gyumri2 than Gyumri1 is to both these aurochs. Tango2 also shares more derived alleles with Gyumri2 than do the German aurochs Bed3 and Hxh2, which concurs with Tango2 and Gyumri2's basal positioning in relation to European aurochs in IBS tree (Figure 5.6). Thirdly, Gyumri2 seems to be an outgroup to all of Central European *Bos primigenius,* except Fal7. Finally, it seems to share more derived alleles with Eastern European aurochs (Kalisz2 and Belorus1) than with Central European aurochs (Figure 5.10).

5.4.7.5. Tango2

The NJ tree placed Tango2 as a possible outgroup to European aurochs (Figure 5.6). *D*-statistics supported Tango2 to share a higher number of shared derived alleles with Gyumri1 than with Baikal1 (Figure 5.7). Additionally, *D*(((Tango2, European aurochs), Eurasian aurochs,Yak) tested whether Tango2 is an ingroup or an outgroup to European aurochs, and reported only significant negative *D* values. Thus, suggesting Tango2 is closer to Asian aurochs than any European aurochs (Appendix Table 9.3.9).

5.4.8. Outgroup f_3-statistic

f_3-statistics were computed for each auroch and a representative of early Neolithic Near Eastern domesticates (Sub1, 6221-6024 cal. BC). The relatedness of Sub1 to each *Bos primigenius* individual is summarised as a measure of shared genetic drift (f_3), using Sahiwal (*Bos indicus*) as the outgroup (Figure 5.11). Values for standard f_3 errors, Z scores and number of SNPs for each test are shown in Table 5.5.

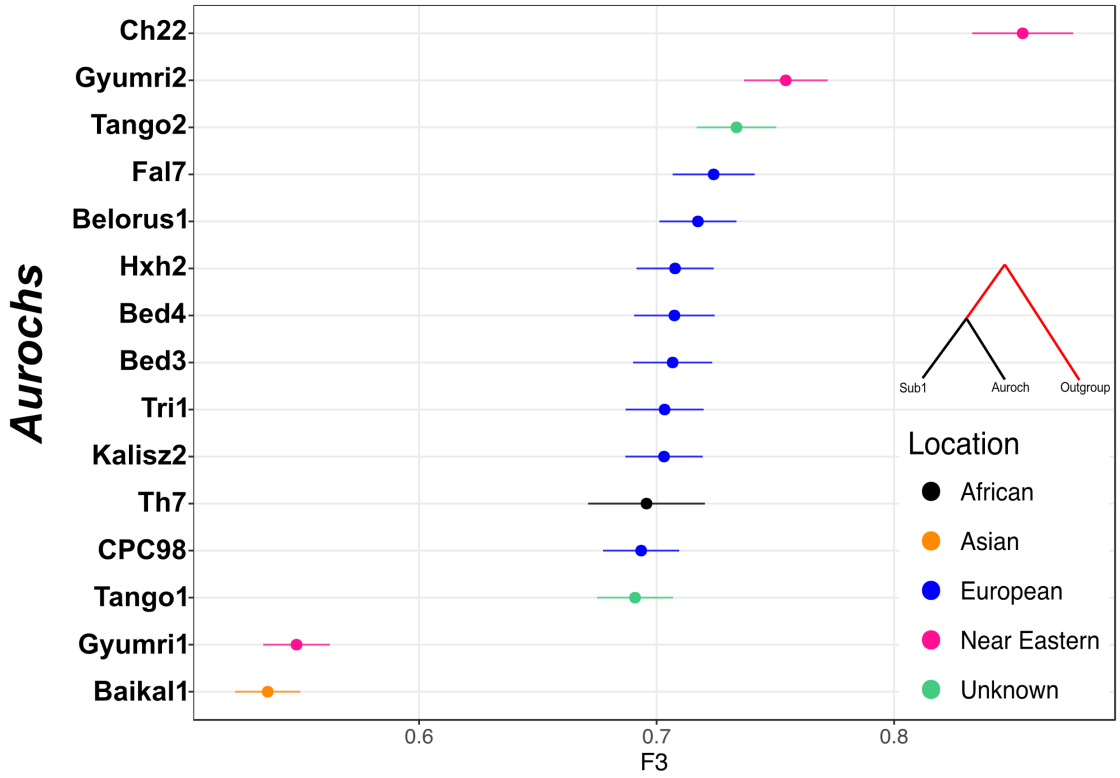


Figure 5.11 - Outgroup f_3 statistics. *Measure of shared drift between Sub1 (proxy for early domesticate) and the different African and Eurasian aurochs. Colours correspond to geographical origin for each individual. The outgroup used for all tests was the Bos indicus breed Sahiwal. Standard error bars are shown. Highest genetic F3 values belong to two Near Eastern individuals Ch22 and Gyumri2, from similar archaeological contexts as Sub1. Lowest F3 values belong to two Asian aurochs that predate domestication of cattle.*

Gyumri1 and Baikal1 - the two aurochs that pre-date the appearance of domesticated cattle - are the individuals with which Sub1 shared the lowest amount of genetic drift. European Mesolithic/Early Neolithic *B.primigenius individuals* (blue), show very similar f_3 values, which are slightly exceeded by Tango1. Fal7, the Medieval aurochs from Germany, shows relatively high shared drift; a reflection of admixture with domesticates. The highest genetic affinity to Sub1 is observed in Near Eastern individuals, the Çatalhöyük sample, Ch22 from Anatolia, and Gyumri2, an Armenian aurochs (~5000 cal. BC). These could represent the populations of aurochs that were locally domesticated.

Table 5.5 - Outgroup f_3 statistic. *Results for outgroup F3 statistic for the test shown in Figure 5.7. Sahiwal (Bos indicus) was used as the outgroup. Highest genetic F3 values belong to two Near Eastern individuals Ch22 and Gyumri2, from similar archaeological contexts as Sub1. Lowest F3 values belong to two Asian aurochs that predate domestication of cattle.*

Auroch	F3	SE	Z	SNPs	Location
Ch22	0.854132	0.021263	40.17	21685	Near Eastern
Gyumri2	0.75438	0.017634	42.78	58503	Near Eastern
Tango2	0.733635	0.016755	43.785	63297	Unknown
Fal7	0.724023	0.017262	41.944	64455	European
Belorus1	0.717406	0.016231	44.2	60451	European
Hxh2	0.707783	0.016245	43.568	72383	European
Bed4	0.707505	0.016961	41.713	62498	European
Bed3	0.706754	0.016669	42.4	72376	European
Tri1	0.703381	0.016427	42.819	65164	European
Kalisz2	0.703141	0.016306	43.122	67212	European
Th7	0.695754	0.024595	28.289	5984	African
Cpc98	0.693502	0.016037	43.243	69173	European
Tango1	0.690922	0.016001	43.181	59382	Unknown
Gyumri1	0.548407	0.01401	39.144	63568	Near Eastern
Baikal1	0.536266	0.013695	39.158	68152	Asian

5.4.9. Testing aurochs introgression into ancient wild and domestic cattle

In order to test for introgression of each *Bos primigenius* individual into ancient wild and domestic cattle, a broad geographical and temporal range of samples were included spanning approximately 14,000 years of cattle prehistory. Individuals where no dating or archaeological context was available (Tango1, Kalisz2, Kalisz3, Belorus1) were placed at 0 Years BP. In this section the *D*-statistics were calculated for the test (((Sub1, Test), Aurochs), Yak), where Sub1 is a Neolithic Anatolian domestic, taken as a non-admixed proxy, and Test is each ancient individual in turn. *D*-statistics were computed using ANGSD and supplementary tables with values quoted in the text can be found in the Appendix Section 9.3.

5.4.9.1 European Bos primigenius

Introgression between Northern European *Bos primigenius* and ancient cattle was first explored in the context of the Neolithic Near East and ancient Europe in Chapter 4. Here, an additional *Bos primigenius* from Europe is examined, Kalisz2, chosen due to its higher coverage amongst Eastern Europeans.

Bed3 (9608 ± 151 cal. BC)

For comparison, Bed3, the Mesolithic aurochs from Germany is also tested here (Figure 5.12). All European aurochs show a positive and significant *D*-statistic, sharing a higher number of derived alleles with Bed3 than with Sub1. In the Balkan Peninsula (Bla1, Dzh1, Dzh2), no significant gene flow is observed in Early Neolithic (~8000 BP). The only exception is the Serbian sample Bub1, however, this individual has not been USER treated and we cannot disregard ancient DNA damage as factor in this result. Furthermore, significant gene flow from Bed3 is observed as early as ~7500 BP in Poland (Ludwinowo) and in Serbia (Pločnik and Belovode).

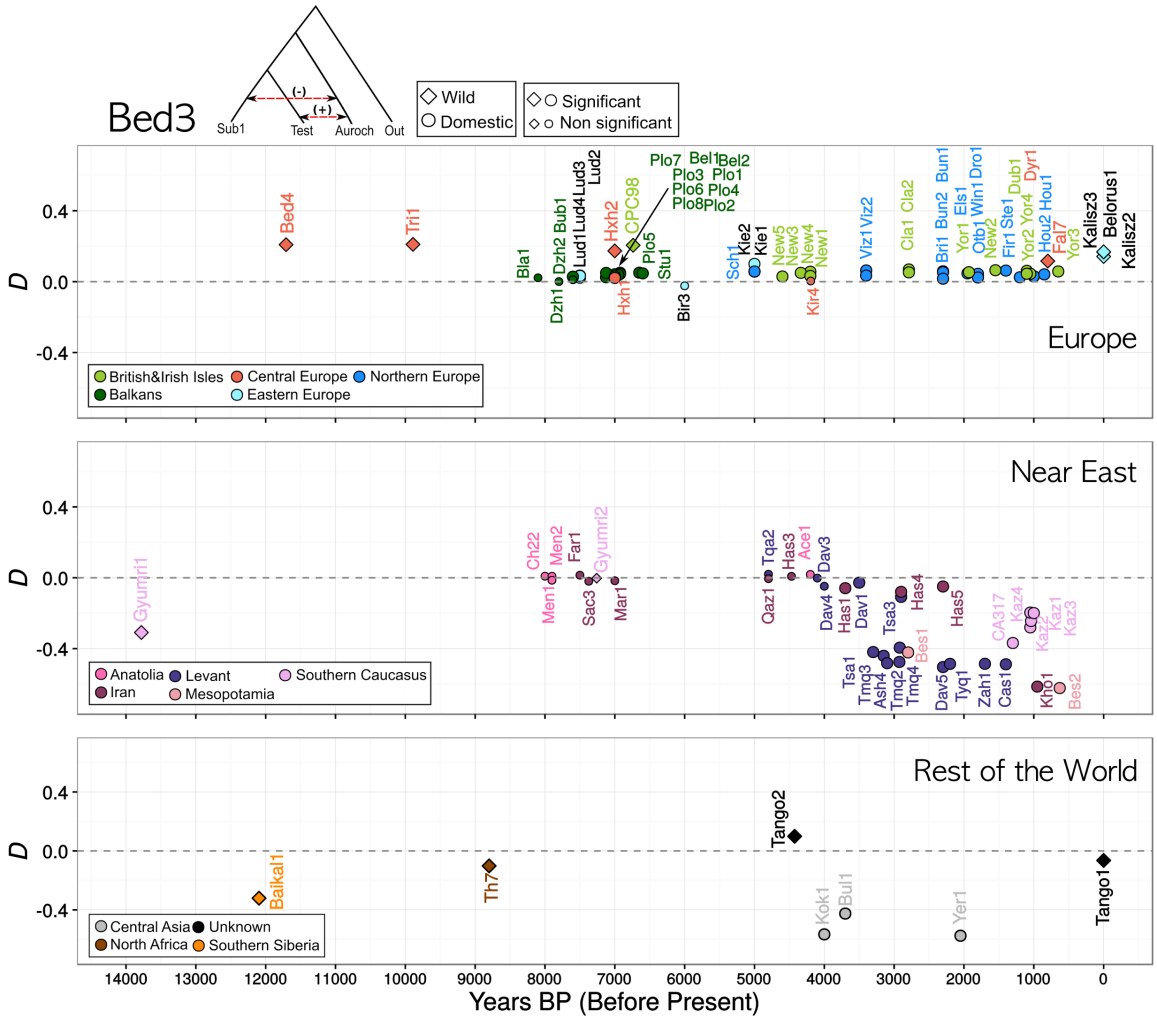


Figure 5.12 - D(((Sub1,Test),Bed3),Yak). *Plot of D-statistic for Europe (top), Near East (middle) and the rest of the World (Central and East Asia, Africa and unknown location). Positive D values indicate gene flow between Test and the aurochs. Wild individuals are shown as diamonds and domestics as circles. Significance is given by size of points: small points indicate non significant Z score (Z<=|3|) and big points indicate significant Z score (Z>=|3|). Each region within each continent is coloured differently. Individuals where no dating or archaeological context was available (Tango1, Kalisz2, Kalisz3, Belorus1) were placed at 0 Years BP.*

Positive gene flow from the European aurochs continues to be observed in the following ~6000 years in Central, Eastern and Northern Europe (including the British and Irish Isles). Two exceptions in Europe are Bir3 and Kir4. Neither show a significant deviation from *D*=0. No significant gene flow was observed from Bed3 to any Near Eastern sample across a temporal context spanning ~10,000 years. However, some individuals gave positive *D* values, e.g. the Late Neolithic Southern Iranian Far1 (6000-

5500 cal. BC) and the Southern Levantine individual Tqa2 (3150-2200 cal. BC). This weakly positive signal, together with early Neolithic and Early Bronze age Levantine samples showing excess African taurine ancestry, could be indicative of gene flow from the wild from a different population of aurochs. Most Bronze Age and post Bronze Age individuals from the Near East revealed significantly negative *D* values, which suggests that Sub1 shares more derived alleles with Bed3 than these individuals do. This is not surprising giving a known influx of zebu (*Bos indicus*), possibly during the Bronze Age in the Near East (Loftus *et al.* 1999; Freeman *et al.* 2005; Edwards, Baird, *et al.* 2007). Finally, the two unknown aurochs, Tango1 and Tango2, differed; Tango1, showed no gene flow from Bed3, whereas Tango2 revealed a significant gene flow (D=0.10; Z=17.8).

Kalisz2

A representative of an Eastern European aurochs, Kalisz2, shows similar patterns for introgression to Bed3. One exception is Kir4, the Neolithic sample (2794 ± 78 cal. BC) from the Kirschbaumhöhle (Cherry Tree Cave) in the Franconian Alps, which revealed significant gene flow from Kalisz2. In addition, the Iranian Has3 Bronze Age domestic (2470 cal. BC) from Northern Iran (Tepe Hasanlu) showed significant gene flow from Kalisz2 (Figure 5.13) but not from Bed3 or the other European aurochs: Hxh2 and CPC98 (Appendix Tables 9.3.18, 9.3.19).

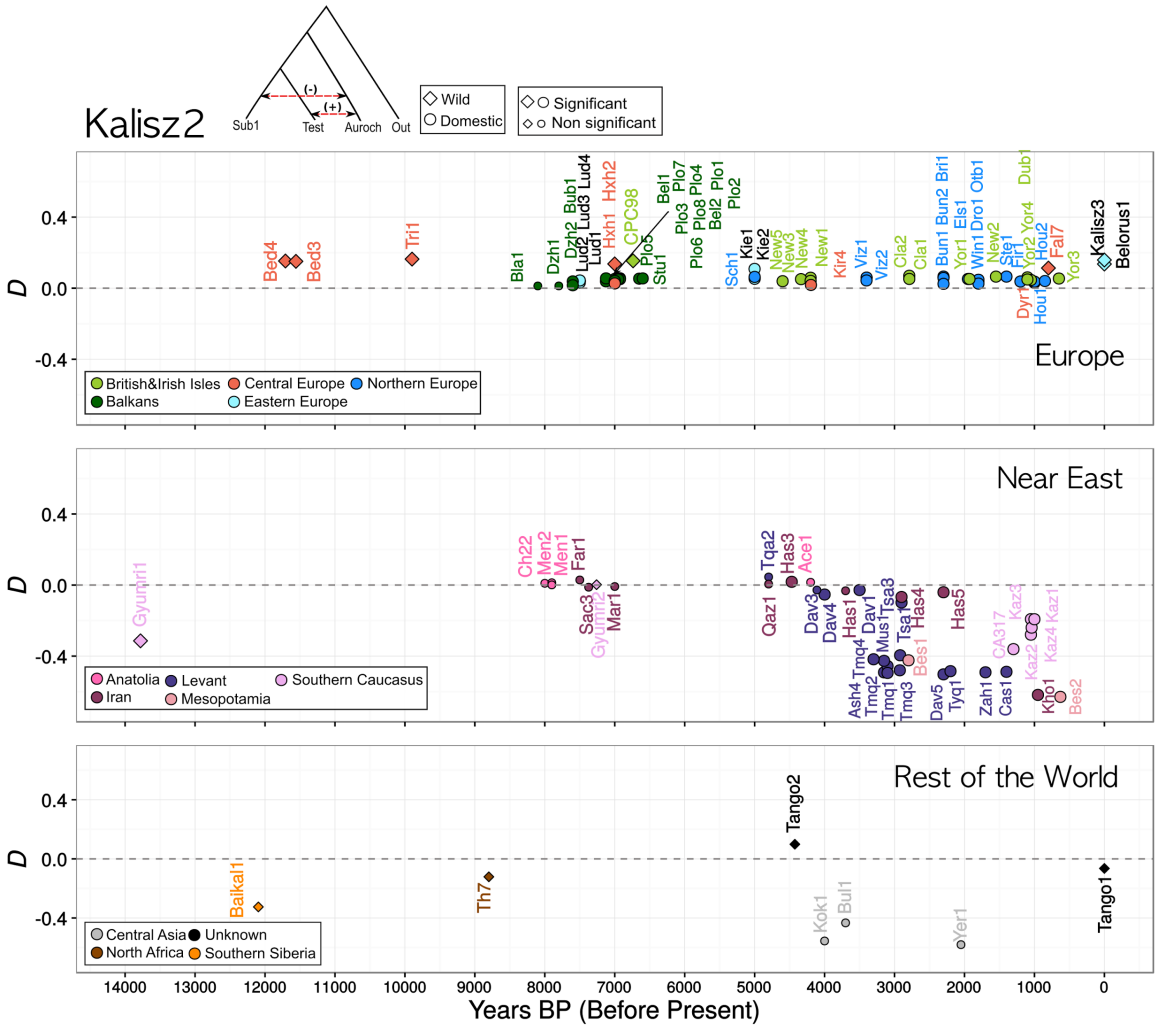


***Figure 5.13 - D(((Sub1,Test),Kalisz2),Yak)**. Plot of D-statistic for Europe (top), Near East (middle) and the rest of the World (Central and East Asia, Africa and unknown location). Positive D values indicate gene flow between Test and the aurochs. Wild individuals are shown as diamonds and domestics as circles. Significance is given by size of points: small points indicate non significant Z score (Z<=\|3\|) and big points indicate significant Z score (Z>=\|3\|). Each region within each continent is coloured differently. Individuals where no dating or archaeological context was available (Tango1, Kalisz2, Kalisz3, Belorus1) were placed at 0 Years BP.*

5.4.9.2 Near Eastern Bos primigenius

Gyumri2 (5036-5076 cal. BC)

The 5036-5076 cal. BC Near Eastern aurochs Gyumri2 was first introduced in Chapter 4 and is here tested in a broader geographical and temporal context. *D*-statistics confirmed no significant gene flow between Gyumri2 and any wild or domestic cattle population from Europe (Figure 5.14). All *Bos primigenius* individuals gave a significantly

negative *D* value, suggesting that the Neolithic Anatolian Sub1 is closer to this Armenian aurochs. With the Upper Paleolithic Armenian, Gyumri1, a significant negative *D* value, suggests that Sub1 shares a higher number of derived alleles with Gyumri2 than Gyumri1 does. This could indicate some gene flow from ancient Near Eastern domestics into Gyumri2.

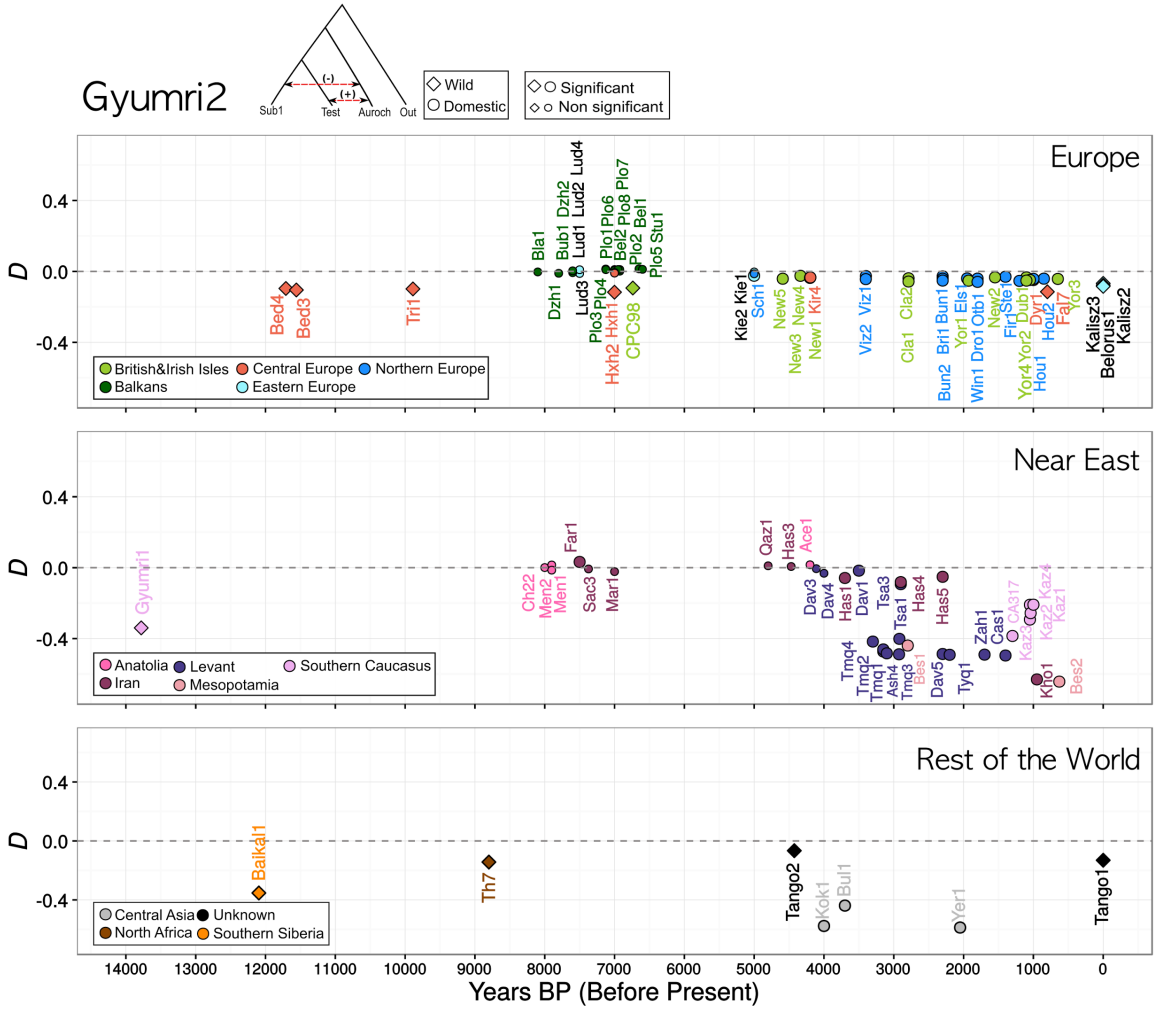


Figure 5.14 - D(((Sub1,Test),Gyumri2),Yak). *Plot of D-statistic for Europe (top), Near East (middle) and the rest of the World (Central and East Asia, Africa and unknown location). Positive D values indicate gene flow between Test and the aurochs. Wild individuals are shown as diamonds and domestics as circles. Significance is given by size of points: small points indicate non significant Z score (Z<=|3|) and big points indicate significant Z score (Z>=|3|). Each region within each continent is coloured differently. Individuals where no dating or archaeological context was available (Tango1, Kalisz2, Kalisz3, Belorus1) were placed at 0 Years BP.*

In Chapter 4, *D*-statistics reported a possible outlier in Neolithic Near Eastern cattle: Far1, from the Iranian Neolithic site of Miyanroud (6000-5500 BC) in the Southern

province of Fars. It suggested non-significant (*Z*=1.6) possible gene flow from Gyumri2. The same statistic using whole genome data (Figure 5.14), is significant (*D*=0.03, Z= 3.08). This is the only positive significant *D*-statistic observed for Near Eastern individuals. Most individuals after ~2000 BC showed a significantly negative *D*-statistic for this test, a likely consequence of influx of zebu during the Bronze age (Loftus *et al.* 1999; Edwards, Baird, *et al*. 2007; Podany 2013; Cunliffe 2015).

Gyumri1 (11,842-11,622 cal. BC)

D-statistics for the Upper Paleolithic Gyumri1 revealed some contrasting results to Gyumri2 (Figure 5.15). A few individuals from the Neolithic Serbian sites of Pločnik and Stubline (Plo2, Plo5, Plo7 and Stu1) yielded significant positive D values, which agree with gene flow from Gyumri1; Gyumri2 shared significant gene flow with these individuals. This signal does not seem to be associated with a specific site, temporal context or genomic coverage. The eight Pločnik individuals overlap chronologically whilst their *D*-statistics differ. It is unclear why there might be some gene flow from this aurochs into some of these Serbian specimens. The younger Armenian aurochs, Gyumri2 gave a positive value (*Z*=5.22), thus supporting gene flow between these two Armenian aurochs. Similarly, Far1 from Neolithic Southwest Iran, revealed significant gene flow from Gyumri1 (*D*=0.04, Z=3.35). Neolithic Iranian samples from Northeast and Northern Iran (Sac3, Mar1) show no significant gene flow from Gyumri1. However, the Iranian Early Bronze Age Has3 result (*D*=0.02; Z=3.63) supports gene flow from this aurochs in contrast to what was reported for Gyumri2. Significant gene flow between Gyumri1 and Baikal1 was reported (*D*=0.43). Furthermore Tango1 and Tango2 also revealed significant gene flow with Gyumri1 in contrast to what was observed for Gyumri2. The Northern African Th7 did not show any indication of gene flow with Gyumri1 (*D*=-0.07, Z=-1.45).

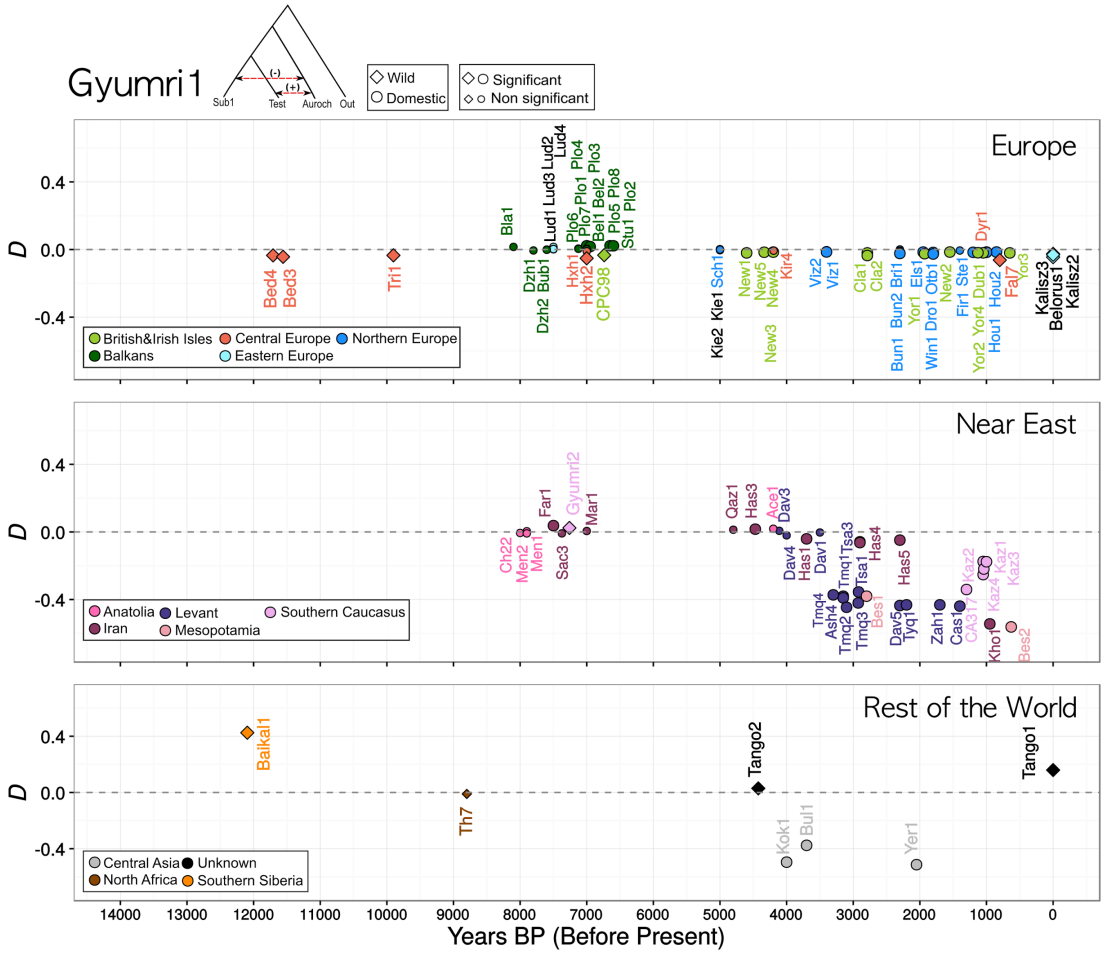


Figure 5.15 - D(((Sub1,Test),Gyumri1),Yak). *Plot of D-statistic for Europe (top), Near East (middle) and the rest of the World (Central and East Asia, Africa and unknown location). Positive D values indicate gene flow between Test and the aurochs. Wild individuals are shown as diamonds and domestics as circles. Significance is given by size of points: small points indicate non significant Z score (Z<=|3|) and big points indicate significant Z score (Z>=|3|). Each region within each continent is coloured differently. Individuals where no dating or archaeological context was available (Tango1, Kalisz2, Kalisz3, Belorus1) were placed at 0 Years BP.*

5.4.9.3. North African Bos primigenius

Th7, a Moroccan auroch from the site Taghit Haddouch and dated to 7051-6801 cal. BC is of extremely low coverage (0.07x)and thus not all combinations passed the threshold number of sites to be included in this analysis (Figure 5.16).

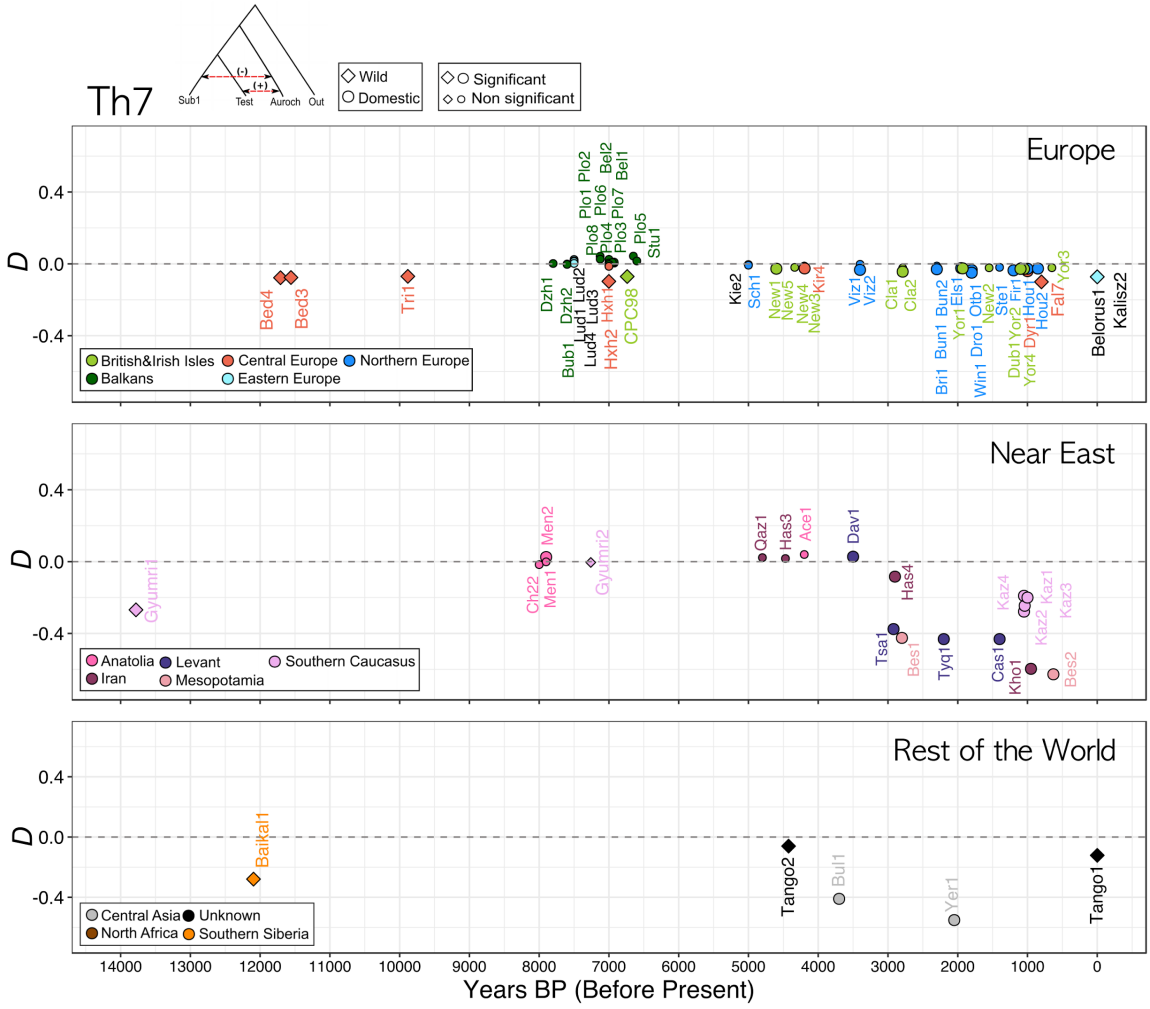


Figure 5.16 - D(((Sub1,Test),Th7),Yak). *Plot of D-statistic for Europe (top), Near East (middle) and the rest of the World (Central and East Asia, Africa and unknown location). Positive D values indicate gene flow between Test and the aurochs. Wild individuals are shown as diamonds and domestics as circles. Significance is given by size of points: small points indicate non significant Z score (Z<=\|3\|) and big points indicate significant Z score (Z>=\|3\|). Each region within each continent is coloured differently. Individuals where no dating or archaeological context was available (Tango1, Kalisz2, Kalisz3, Belorus1) were placed at 0 Years BP.*

Within European cattle it is clear that no significant gene flow could be supported by this statistic. Furthermore, no gene flow between any of the European aurochs and Th7 is evident and all *D* values were significantly negative. The same is the case for all other non European aurochs. Within ancient domestic Near Eastern cattle, one Neolithic (6048-5893 cal. BC) individual from Northeast Anatolia (Men2) reported a significant positive *D* value (*D*=0.03, *Z*=3.07). It is unclear why there is significant support for gene flow, as no

other analyses suggested this to be the case for Men2. In addition, three Bronze Age individuals from Central Anatolia (Ace1), North and Northwest Iran (Qaz1, Has3) returned positive *D* values for this test, albeit with non significant *Z* scores: 2.37, 2.78 and 2.14, respectively.

It is unclear whether the strong African taurine ancestry in Neolithic Israel is due to a local aurochs input or an early genetic backflow from African domestics. The earliest Southern Levantine individual available was Dav1, radiocarbon dated to 1929-1753 cal. BC (Middle Bronze Age). Dav1 yielded a significant positive *D* value (*D*=0.03; Z=3.85). With later Near Eastern samples no gene flow from Th7 is observed, likely influenced by indicine gene flow from the East after the Bronze Age.

5.4.9.4. Tango1

Tango1, with prehistoric west Europeans, gave similar values to those observed in non-European aurochs (Figure 5.17). All German and British *primigenius* animals yielded negative *D*-statistics. By contrast, early Neolithic ancient domestic Europeans from the Balkans and Eastern Europe (Poland) yielded positive *D* values with significant Z scores, suggesting gene flow.

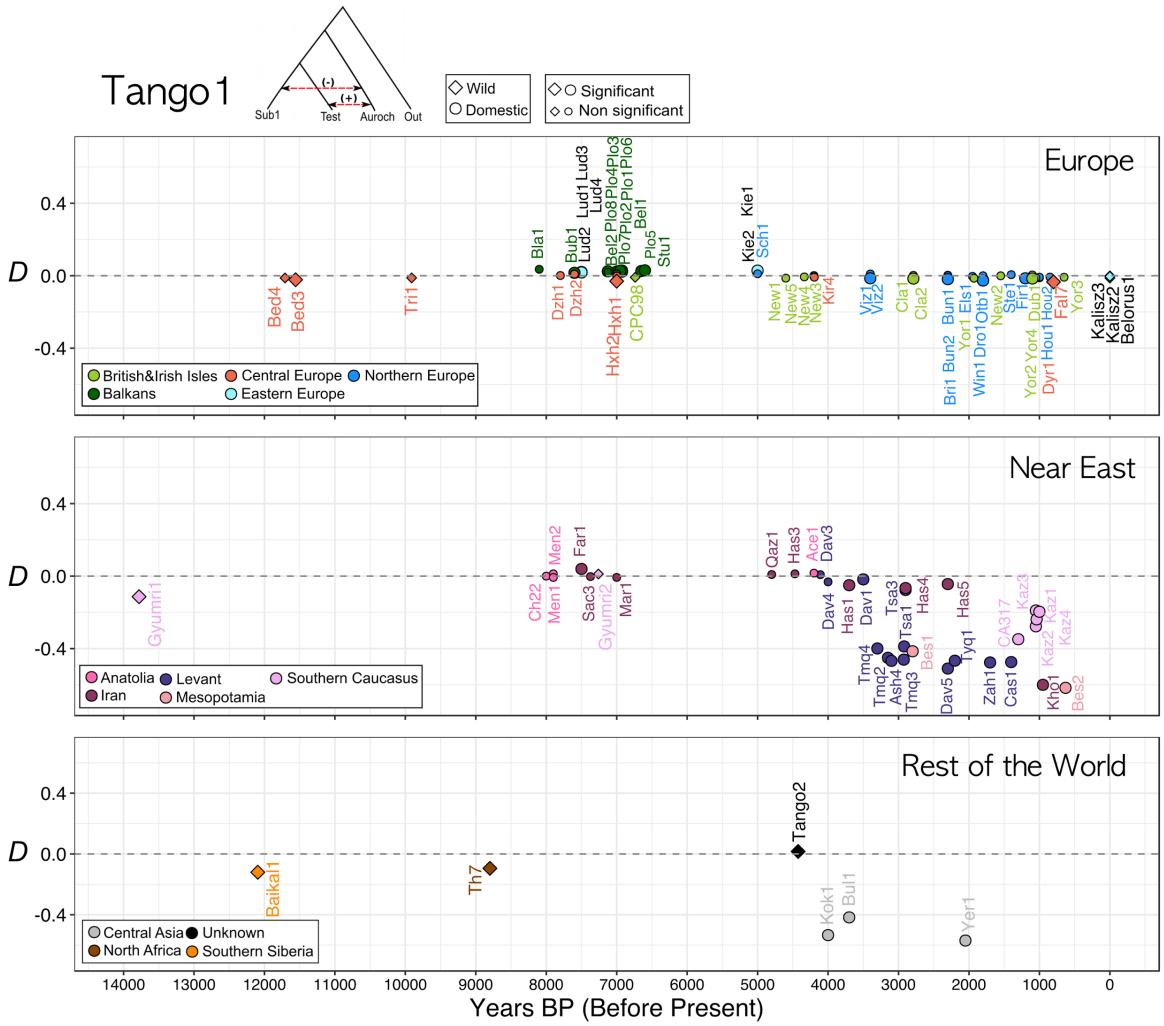


Figure 5.17 - D(((Sub1,Test),Tango1),Yak). *Plot of D-statistic for Europe (top), Near East (middle) and the rest of the World (Central and East Asia, Africa and unknown location). Positive D values indicate gene flow between Test and the aurochs. Wild individuals are shown as diamonds and domestics as circles. Significance is given by size of points: small points indicate non significant Z score (Z<=\|3\|) and big points indicate significant Z score (Z>=\|3\|). Each region within each continent is coloured differently. Individuals where no dating or archaeological context was available (Tango1, Kalisz2, Kalisz3, Belorus1) were placed at 0 Years BP.*

Interestingly, the Eastern European aurochs from Belorussia (Belorus1) and Poland (Kalisz2, Kalisz3) did not significantly deviate from a zero D value, suggesting Tango1 is related to these Eastern European aurochs. The Neolithic Southern Iranian Far1, which reported significant gene flow from both Armenian aurochs (Gyumri2, Gyumri1) (Figures 5.14 and 5.15), shows a positive and significant *D* value (*D*=0.04, Z=3.79).

5.4.9.5. Tango2 (2470-2297 cal. BC)

Tango2 reported a very similar *D*-statistic pattern to the European *Bos primigenius* Bed3 and Kalisz2 (Figures 5.12 and 5.13), which is shown in Figure 5.18.

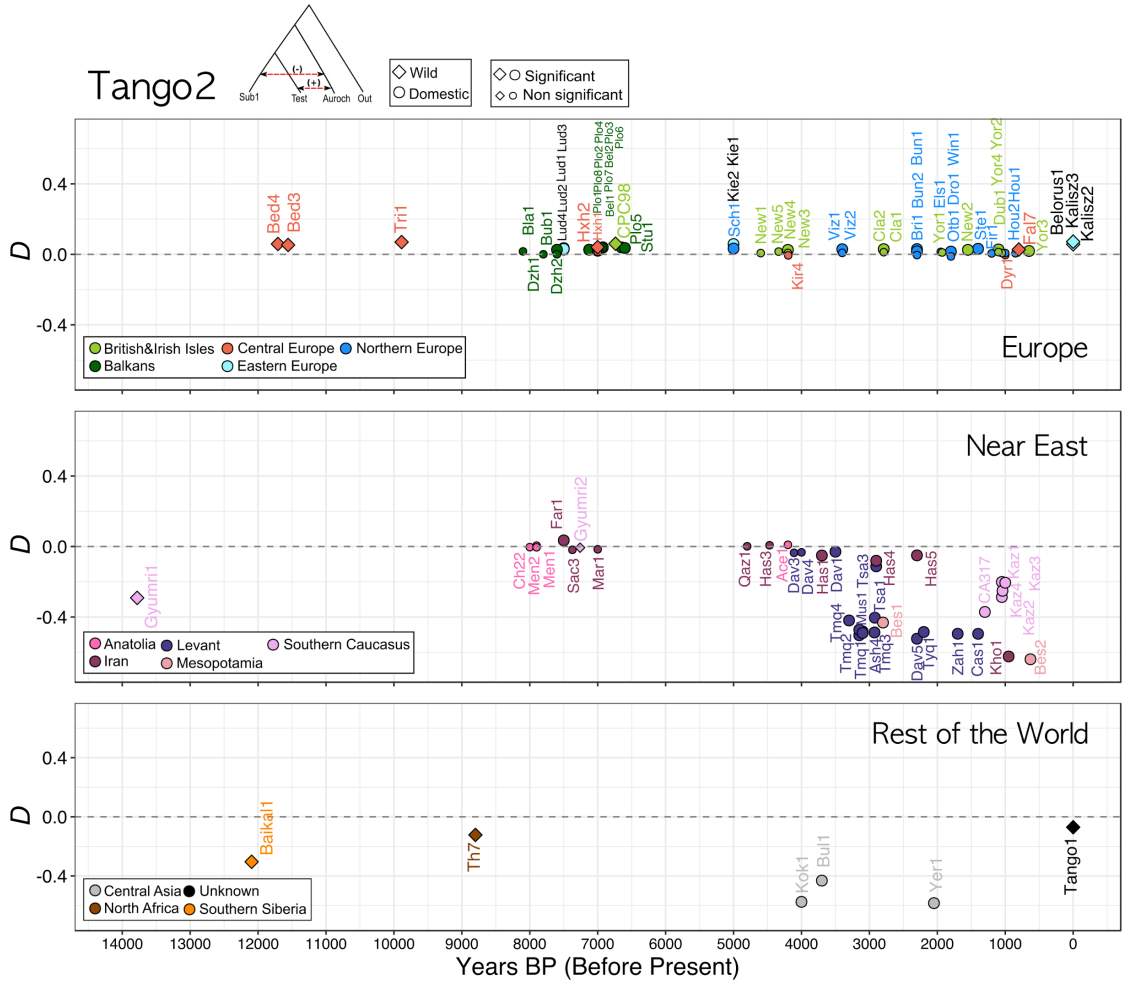


Figure 5.18- D(((Sub1,Test),Tango2),Yak). *Plot of D-statistic for Europe (top), Near East (middle) and the rest of the World (Central and East Asia, Africa and unknown location). Positive D values indicate gene flow between Test and the aurochs. Wild individuals are shown as diamonds and domestics as circles. Significance is given by size of points: small points indicate non significant Z score (Z<=|3|) and big points indicate significant Z score (Z>=|3|). Each region within each continent is coloured differently. Individuals where no dating or archaeological context was available (Tango1, Kalisz2, Kalisz3, Belorus1) were placed at 0 Years BP.*

5.4.9.6. South Central Siberian Bos primigenius

The Russian aurochs from Lake Baikal, Baikal1, dated to 10,431-10,029 cal. BC, revealed no gene flow to ancient Europeans, wild or domestic, with the exception of the

Neolithic Vinča culture Serbian samples Plo5 (4850-4500 cal. BC) and Stu1 (4800-4500 cal BC), from the archaeological sites of Pločnik and Stubline, respectively (Figure 5.19).

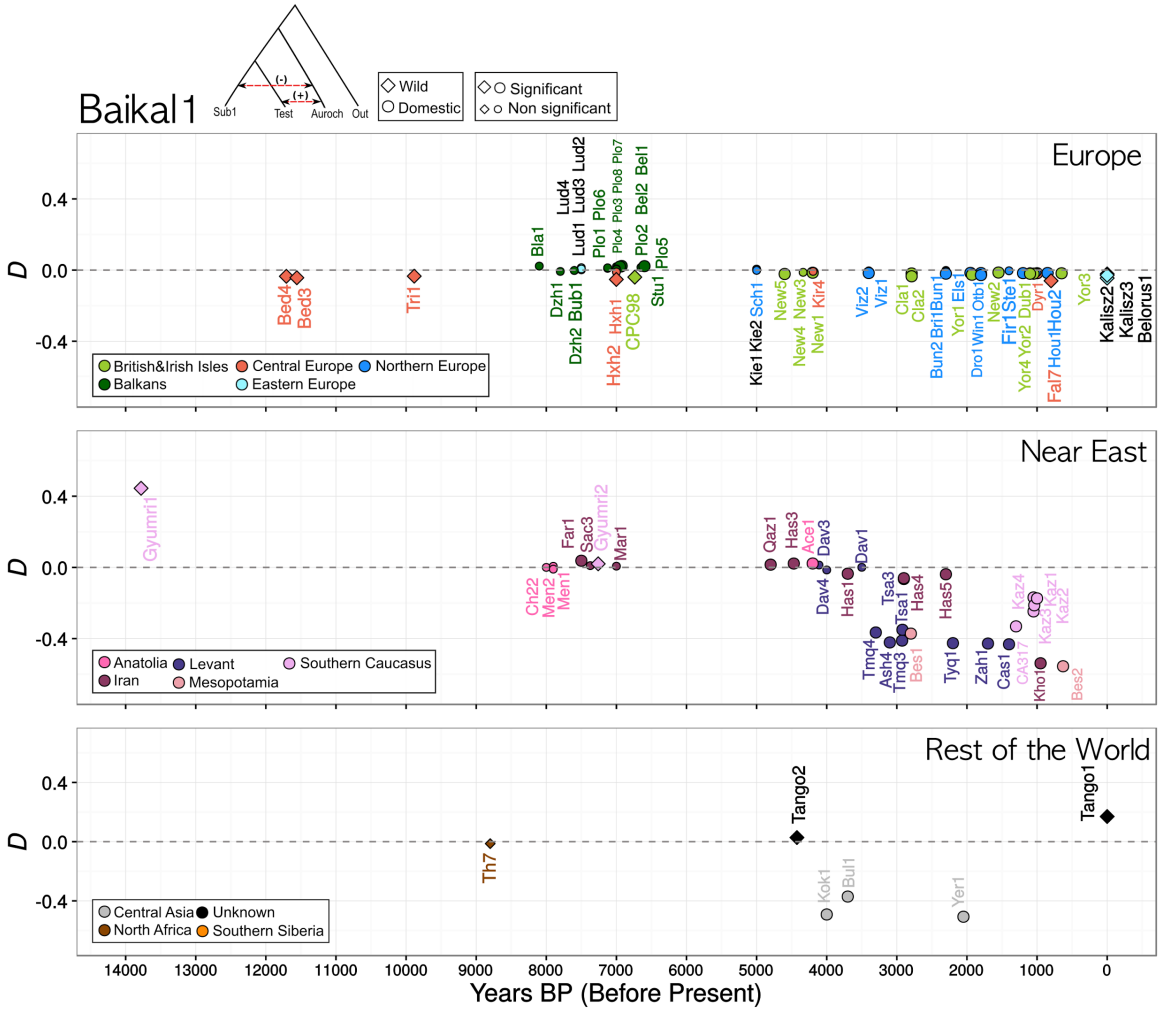


Figure 5.19 - D(((Sub1,Test),Baikal1),Yak). *Plot of D-statistic for Europe (top), Near East (middle) and the rest of the World (Central and East Asia, Africa and unknown location). Positive D values indicate gene flow between Test and the aurochs. Wild individuals are shown as diamonds and domestics as circles. Significance is given by size of points: small points indicate non significant Z score (Z<=|3|) and big points indicate significant Z score (Z>=|3|). Each region within each continent is coloured differently. Individuals where no dating or archaeological context was available (Tango1, Kalisz2, Kalisz3, Belorus1) were placed at 0 Years BP.*

Both Near Eastern aurochs, Gyumri1 and Gyumri2, showed significantly positive *D* values and therefore support for ancestral gene flow with Baikal1. Contrastingly, Neolithic domestics from Anatolia (Ch22, Men1, Men2) did not reveal any significant *D* values, as well as the 5373 cal. BC Sac3 from Tapeh-Sang-e-Caxmaq in Northeastern Iran and the ~5000 BC Mar1 from Maral Tappeh in the North Central Iran. However, the

Southern Iranian Far1 (6000-5500 BC), reported a similar statistic to that observed with Gyumri1 (*D*=0.04, Z= 3.46). Three early Bronze Age individuals from Iran and Anatolia (Qaz1, Has3 and Ace1), also gave positive significant *D* values. From the Middle Bronze Age onwards no significant gene flow from Baikal1 is reported in any Near Eastern samples. Finally, Tango2 and Tango1 revealed significant positive *D* values.

5.4.10. Auroch contribution to Modern populations of cattle 700K

To test the contribution of different aurochs groups to modern cattle populations the *D*-statistic was computed using AdmixTools with the 700K Bovine dataset, for the test *D*(((Test, Sub1), Aurochs), Yak), where Test is each modern cattle population in turn. All *D*-statistics can be found in the Appendix section 9.3.

The North African Epipaleolithic aurochs Th7 is of low coverage (0.07x) and yielded ~8600 SNPs present in all populations. Only three positive *D* values were observed - from the humpless taurine cattle from the African continent, Lagune, N'Dama and Somba. Lagune and N'Dama produced marginal Z scores > 2 standard deviations (Z=2.53 and Z=2.62) (Figure 5.20). This is suggestive that there was an ancient admixture event between a Th7 type population and the ancestors of modern African cattle. African and Asian cattle breeds that have had zebu introgression reported significant negative *D* values: Muturu (Nigeria), Sheko (Ethiopia), Gobra (Senegal), Maure (Mali), Kenana (Ethiopia), Butana (Ethiopia). European taurine breeds also gave negative *D* values; that Sub1 shares more derived alleles with Th7 than any of these modern breeds may be due to their partial ancestry from European aurochs.

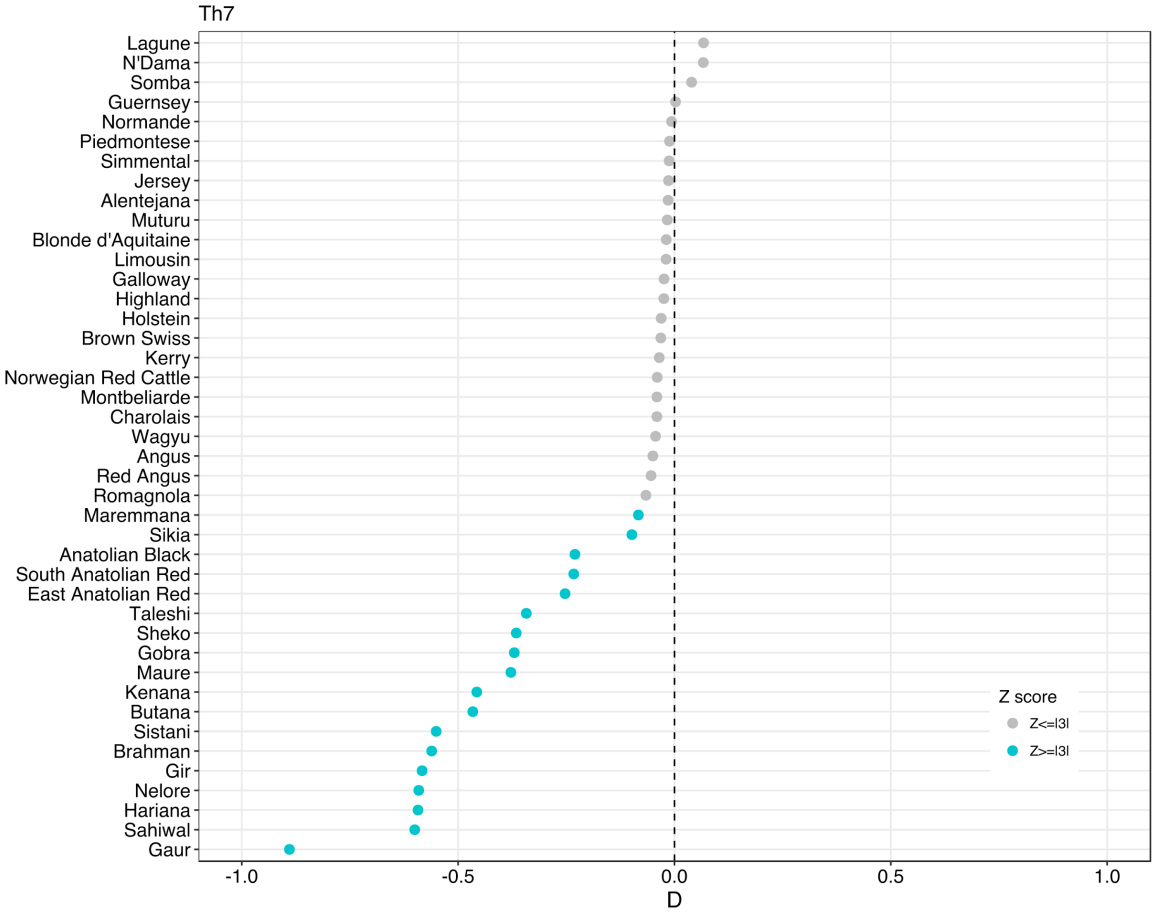


Figure 5.20 - D(((Test,Sub1),Th7),Yak). *Th7 being North African auroch from Morocco (6933 cal. BC) and Test being all modern cattle breed populations from the 700K dataset. Positive D values indicate gene flow either from Th7 to Test or from Yak to Sub1. Statistical significance is coloured: significant (blue), non significant (grey). D-statistics calculated with ~8,600 SNPs.*

A similar *D*-statistic was computed for each of the two West and East Asian aurochs, Gyumri1 and Baikal1. Neither of these aurochs, which pre-date the Neolithic Revolution, contributed genetically to the ancestors of these modern cattle breeds (Figures 5.21 and 5.22).

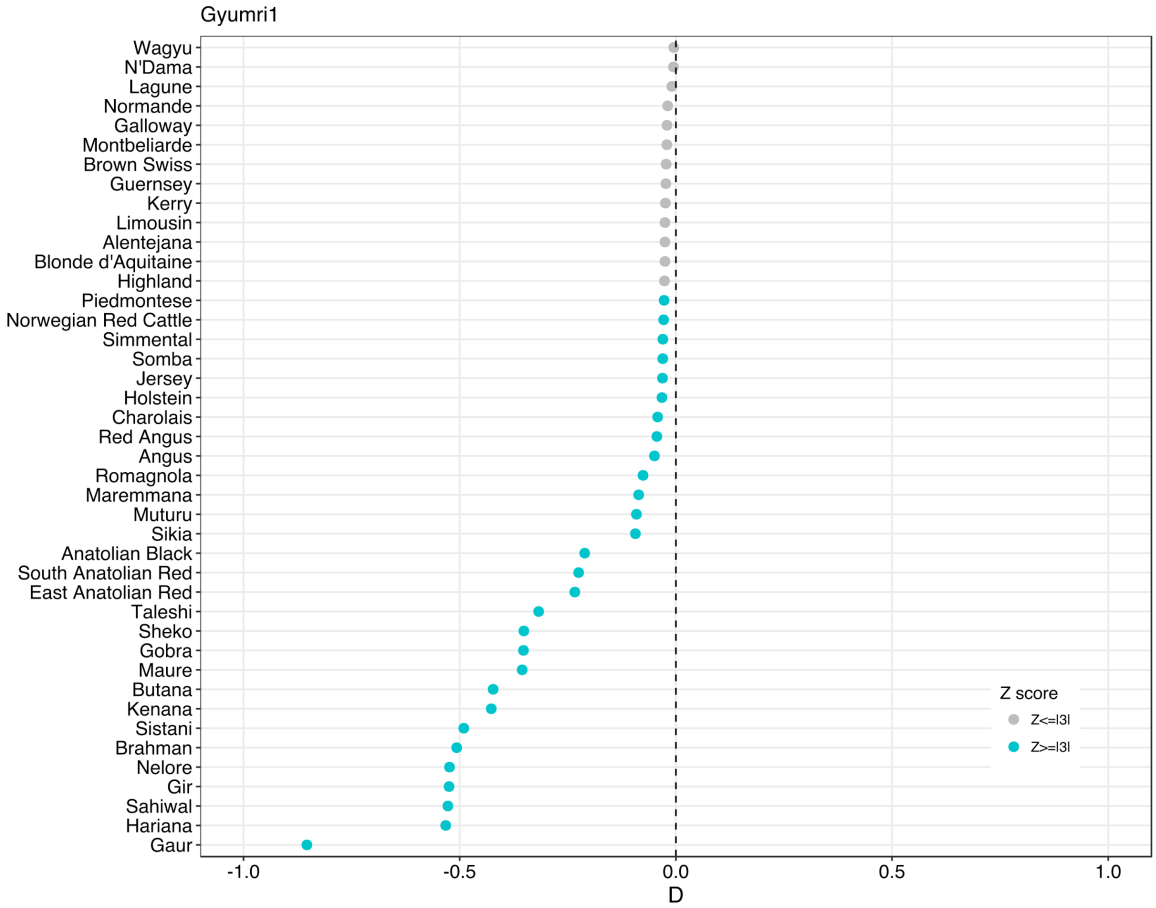


Figure 5.21 - D(((Test,Sub1),Gyumri1),Yak). *Gyumri1 being Near Eastern aurochs from Armenia (11,830 cal. BC) and Test being all modern cattle breed populations from the 700K Bovine dataset. Positive D values indicate gene flow either from Gyumri1 to Test or from Yak to Sub1. Statistical significance is coloured: significant (blue), non significant (grey). D-statistics calculated with ~93,000 SNPs.*

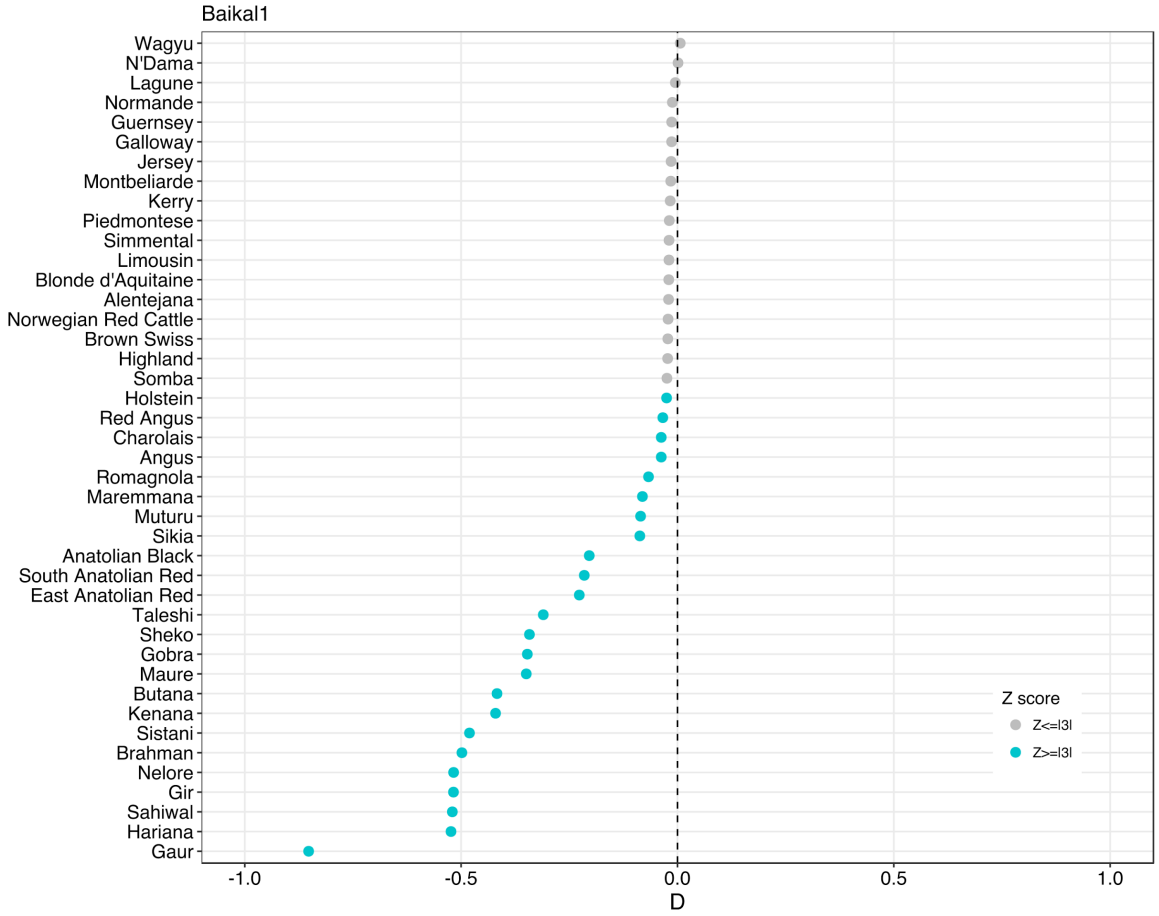


Figure 5.22 - D(((Test,Sub1),Baikal1),Yak). *Baikal1 being South Siberian aurochs from Lake Baikal in Russia (10,145 cal. BC) and Test being all modern cattle breed populations from the 700K dataset. Positive D values indicate gene flow either from Baikal1 to Test or from Yak to Sub1. Statistical significance is coloured: significant (blue), non significant (grey). D-statistics calculated with ~100,369 SNPs.*

D-statistics with modern breeds were computed for Kalisz2 (Figure 5.23) in the interest of comparison to Mesolithic German auroch, Bed3 (Chapter 4, Figure 4.8), and CPC98 (Park *et al.* 2015; Upadhyay *et al.* 2017). Kalisz2 reported the same top three significant positive *D* values as Bed3: Highland, Kerry and Galloway. However, it contrasts with Bed3, in that significant Z scores are observed for the Southwestern breed Alentejana, Italian breed Piedmontese. Also, positive Z scores are observed for French breeds such as Normande, Blonde d'Aquitaine, Limousin, Montbeliarde; for Swiss breeds such as Simmental; and for the Dutch Holstein. This aurochs could be a result of a past admixture event between ancient European *primigenius* and taurine animals, thus sharing

a higher number of derived alleles with these European taurine breeds. This pattern could be compared to the seemingly admixed Fal7 (Appendix Table 9.3.23). Alternatively, it could be typical of Eastern European aurochs.

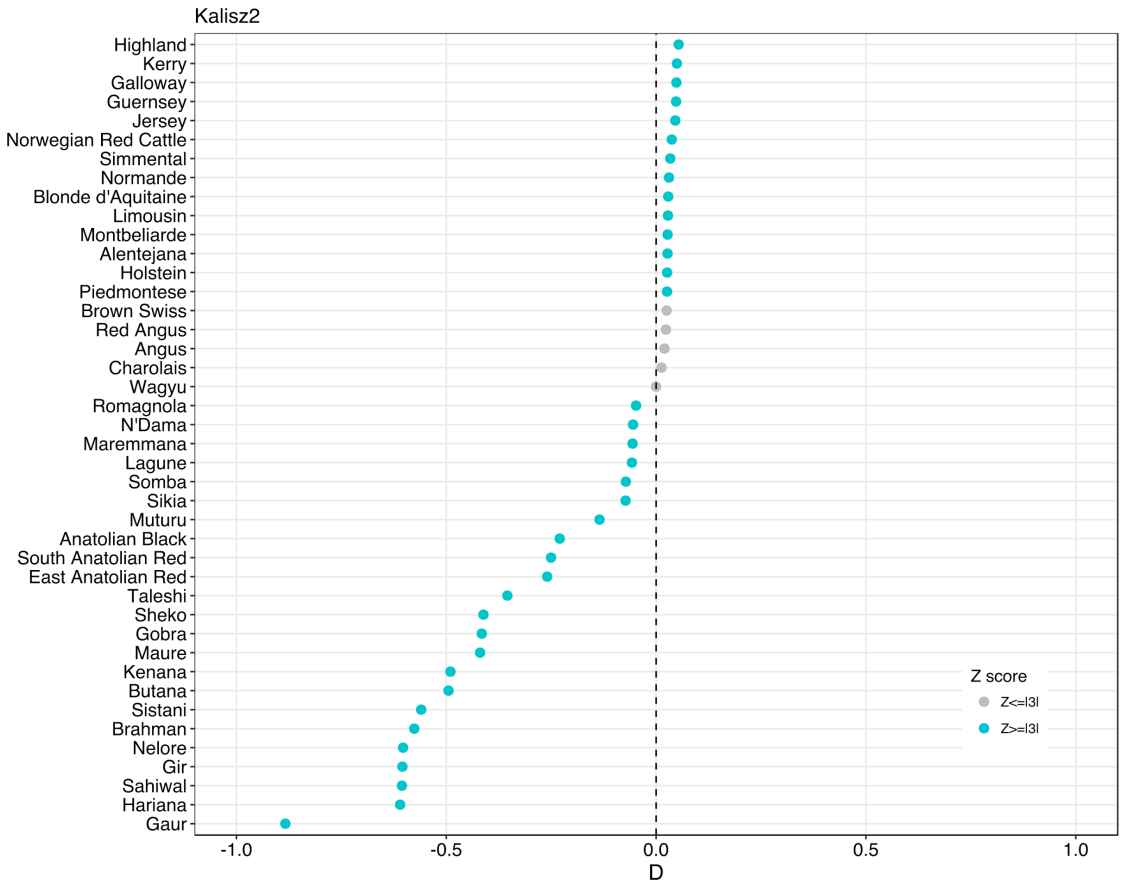


Figure 5.23 - D(((Test,Sub1),Kalisz2),Yak). *Th7 being Eastern European auroch from Kalisz (Poland) and Test being all modern cattle breed populations from the 700K dataset. Positive D values indicate gene flow either from Th7 to Test or from Yak to Sub1. Statistical significance is coloured: significant (blue), non significant (grey).*

Finally, both individuals of unknown archaeological or geographical context were analysed in relation to modern breeds from Europe, Africa and Asia (Appendix Figures 9.5.11 and 9.5.12). Tango1, revealed no positive *D* values for any of the modern populations present in the 700K Bovine SNP dataset, whereas Tango2 shows positive *D* values, albeit non significant, for the Northwestern European (British and Irish) modern breeds: Galloway, Highland, Guernsey and Kerry.

5.4.11. Y chromosomal tree of Bos primigenius

The sequencing of two male Asian *Bos primigenius* and many medium to high coverage ancient domestic bulls provided the opportunity to compare ancient Y chromosomes. Sequencing depths were highly variable among ancient samples and only eight could be included in this analysis (Appendix Table 9.1.6). The NJ tree produced and shown in Figure 5.22, was based on multiple alignment of the MSY1 region of the bovine Y chromosome.

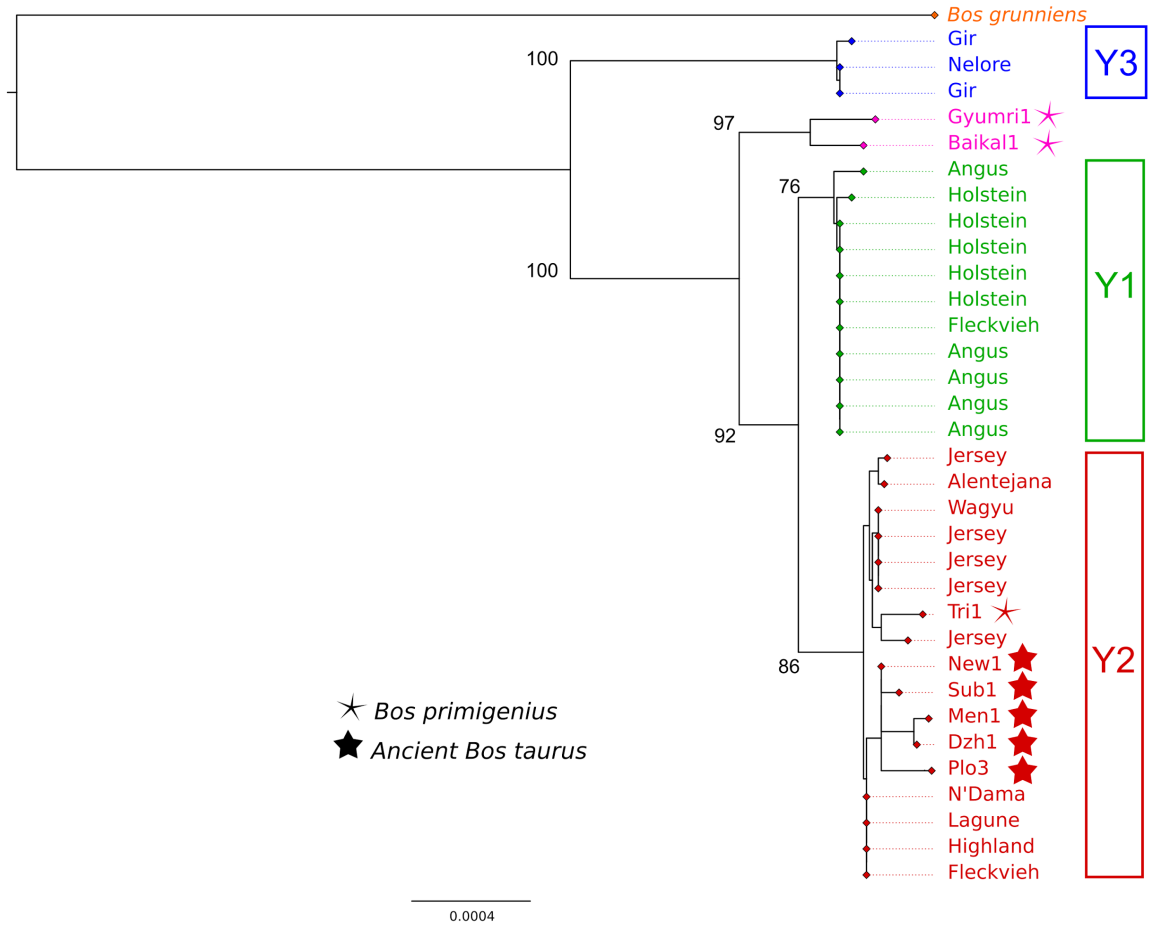


Figure 5.24 - Y chromosome Neighbour-joining tree. *Based on multiple alignment of 25000 base pairs of the MYS1 region of the bovine Y chromosome and 160 SNPs. Stars indicate ancient individuals. Haplogroups defined on previous knowledge from frequency of each haplogroup in modern cattle breeds (Gotherstrom et al. 2005; Edwards et al. 2011). Novel Y haplogroup is coloured in pink and constitutes of the two Asian aurochs Gyumri1 and Baikal1. Bos primigenius and ancient domestics from Europe and ancient domestics from the Near East cluster together carrying Y2 haplotypes.*

This phylogeny used domestic yak as the root and showed a deep bifurcation between *Bos indicus* and *Bos taurus* breeds (Figure 5.24), which is similar to what has been observed in bovine mitochondrial data (Figure 5.3) (Loftus, MacHugh, Bradley, *et al.* 1994; Troy *et al.* 2001; Chen *et al.* 2010), microsatellite data (Loftus *et al.* 1999) and genome wide SNP chip data (Decker *et al.* 2014; Park *et al.* 2015; Upadhyay *et al.* 2017). Previous studies on Y chromosome SNPs, microsatellites and interspersed multilocus satellites have shown a strong phylogeographic structure among modern cattle breeds (Bradley *et al.* 1994; Hanotte *et al.* 2000; Gotherstrom *et al.* 2005; Ginja *et al.* 2009; Ginja *et al.* 2010; Pérez-Pardal, Royo, Beja-Pereira, Chen, *et al.* 2010; Edwards *et al.* 2011). Y haplogroups have been previously defined based on these studies and these are comprised of three major haplogroups for modern cattle: Y1, Y2 and Y3. The first two being associated with taurine cattle and the latter with indicine breeds.

In addition to the indicine cluster, the two ancient Asian aurochs (Baikal1,Gyumri1) branch together away from *Bos taurus* and European *Bos primigenius* (Tri1). Prior research has produced a pattern for the phylogeography of two haplogroups, Y1 and Y2, in modern domestics from Europe with Y1 present at higher frequencies in Northern Europe and some Iberian breeds; and Y2 at higher frequencies in Central, Mediterranean and Iberian breeds (Gotherstrom *et al.* 2005; Edwards *et al.* 2011). This tree reveals two distinct clades for taurine cattle (including ancient and domestic), which are assigned here to the previously defined haplogroups based on prior distribution. Y1 was assigned to the clade that was composed mostly of Northern European cattle breeds: Angus and Holstein (Gotherstrom *et al.* 2005; Ginja *et al.* 2009; Edwards *et al.* 2011). Jersey (Britain), Highland (Britain), Fleckvieh (Germany), Alentejana (Portugal), N'Dama (Guinea) and Wagyu (Japan) have been previously described as carriers of Y2 haplotypes (Gotherstrom *et al.* 2005; Edwards *et al.* 2011; Pérez-Pardal, Royo, Beja-Pereira, Chen, *et al.* 2010).

Interestingly, all ancient domestics from Neolithic Anatolia (Sub1, Men1), Neolithic Serbia and Bulgaria (Plo3, Dzh1), Neolithic Ireland (New1) and a Mesolithic German aurochs (Tri1) seem to fall within the Y2 haplogroup variation.

5.5. Discussion

5.5.1. Ancient mitochondrial DNA confirms new haplogroups in Bos primigenius

Both the mitochondrial genome and Y chromosome are informative loci in population genetics/genomics. Their haploid nature means we can trace back female and male lineages in order to understand past populations events. It also means we can determine if introgression was sex-biased, and in domestic animals this is important as it might reflect husbandry practices (MacHugh *et al.* 1997; Edwards, Baird, *et al.* 2007). Mitochondrial genomes of *Bos primigenius* individuals have shown that mitochondria of wild cattle are diverse and that this might reflect geographical/temporal distribution of subpopulations.

First, a new ancient *Bos primigenius* individual (Baikal1) from Southern Russian Siberia has been observed to carry the C haplogroup previously found in a *primigenius* individual of East Asia (Zhang *et al.* 2013; Brunson *et al.* 2016). In addition, a novel R-sister clade is given by Gyumri1, an ~11,700 cal BC aurochs from Armenia. Additionally, a clear dominance of the P haplogroup in European aurochs was observed (Edwards, Bollongino, *et al.* 2007; Zeyland *et al.* 2013), albeit with one exception, Kalisz3 from Poland, which belonged to the Q haplogroup. The Q haplogroup has been described in extant Egyptian cattle and in ancient domestics from Southeastern, Central/Western Europe, Western Anatolia and Iran (Scheu *et al.* 2015; Olivieri *et al.* 2015). However, since this individual has not been radiocarbon dated nor is there archaeological context it is hard to speculate on whether this is a result of an admixture event or a wider geographical spread for the Q haplogroup.

5.5.2. Asian aurochs reveal a new Y haplogroup

Y chromosomes have been little explored for ancient DNA specimens. The reference sequence for the bovine Y chromosome was not released until 2011 (UCSC Baylor Btau4.6.1_bosTau7) and most modern studies have relied on just a small number of SNPs or microsatellites (Bradley *et al.* 1994; Teale *et al.* 1995; Hanotte *et al.* 1997; Hanotte *et al.* 2000; Gotherstrom *et al.* 2005; Ginja *et al.* 2009; Ginja *et al.* 2010; Pérez-Pardal, Royo, Beja-Pereira, Chen, *et al.* 2010; Edwards *et al.* 2011). Y chromosomes have been useful in identifying zebu introgression in Africa (Bradley *et al.* 1994; Hanotte *et al.* 2000; Pérez-Pardal, Royo, Beja-Pereira, Chen, *et al.* 2010) and in the Near East (Edwards, Baird, *et al.* 2007). Efforts have also been put into typing ancient Y chromosomes from Early Neolithic and Bronze age cultures in Europe from both aurochs and domesticates (Gotherstrom *et al.* 2005; Bollongino *et al.* 2008; Svensson & Götherström 2008). However, confounding results emerged, where one supported admixture between domestic cows and auroch bulls in Europe (Gotherstrom *et al.* 2005) and others did not find the same support in a broader European dataset (Bollongino *et al.* 2008; Kantanen *et al.* 2009).

Here, Y chromosomes of ancient aurochs and domestic cattle have produced four haplogroups from 160 SNPs: Y1, Y2 and Y3, which have been previously defined. A new haplogroup was evident from the early branching off of the clade formed by the two Asian aurochs Gyumri1 (Armenia) and Baikal1 (Southern Siberia Russia). The Mesolithic P aurochs Tri1 from Germany (close to the Luxembourg border) belongs to the Y2 haplogroup. Additionally, Neolithic *Bos taurus* from Anatolia (Men1, Sub1), Bulgaria (Dzh1), Serbia (Plo3) and Ireland (New1) all ostensibly carry Y2 haplotypes, which could support the hypothesis proposed by Gotherstrom *et al.* (2005) that Y2 could have been the haplotype carried by the first domestic cattle in Europe, but not that Y1 was fixed in European aurochs.

5.5.3. A time transect through European Bos primigenius

The first evidence of *Bos primigenius* in Europe comes from Spain, 700,000 years ago (Van Vuure 2005; Wright 2013). Population sizes of aurochs seem to have oscillated with episodes of climate change during the Pleistocene (Wright & Viner-Daniels 2015). In this chapter, European *Bos primigenius* specimens have been explored in the European context but also in relation to other wild specimens from different continents, with overlapping time depths. Genome-wide SNP data and mitochondrial DNA analyses have revealed these to be a somewhat homogenous population. They cluster together in projection PCA analyses and in whole genome IBS analyses, and all but one have the P mtDNA haplogroup (Troy *et al.* 2001; Edwards, Bollongino, *et al.* 2007). European aurochs have shown gene flow into ancient domestic cattle from Europe from as early as ~5000 BC in Serbia, just 1000 years after the introduction of domestics from the Near East (Tresset & Vigne 2011), continuing for thousands of years. Additionally, no evidence was observed for gene flow from these aurochs into ancient domestic Near Eastern or Central Asian populations, nor into Near Eastern, African or Siberian aurochs.

Park *et al.* (2015) explored the genetic contribution of a British Mesolithic aurochs (CPC98) to the ancestors of modern European cattle using *D*-statistics. This was also explored for Bed3, a Mesolithic aurochs from Germany and the Polish Kalisz2, which showed the highest and significant *D* values with northwestern European breeds Highland, Kerry and Galloway; thus supporting previous studies showing the genetic contribution of European aurochs to modern cattle breeds from Britain and Ireland (Park *et al.* 2015). Kalisz2, however, revealed other modern European breeds from Switzerland, France, the Netherlands, Portugal and Northwest Italy to have received significant gene flow from this Eastern European aurochs. It could be however, suggested, that like Fal7, Kalisz2 is either a recent wild-domestic cattle mix or that it represents and Eastern European aurochs. This should be tested in the future.

In conclusion, a survey of the nuclear and mitochondrial genomes revealed the population of aurochs living in the European continent to be relatively homogenous. As aurochs distributions have been suggested to vary with climatic events during the Pleistocene, this could have been a result of a population bottleneck following the Last Glacial Maximum. A consensus for introgression between ancient wild and domestic cattle when tested across different European aurochs from Central, Northern and Eastern Europe is that admixture events seem to have been frequent across Europe from as early as ~1000 years after the introduction of cattle from the Near East (Tresset & Vigne 2011). Therefore, European aurochs have significantly contributed to the ancestors of modern European domestic breeds through introgression with ancient domestics. Whether this gene flow was due to chance, resulting from absence of modern day-like enclosures (Clutton-Brock 1999), or on purpose to improve/increase breeding stock it is still not clear. Furthermore, the Southwestern region of Portugal and Spain is understudied (Anderung *et al.* 2005). Even though modern day primitive Iberian breeds have shown gene flow with the British Mesolithic aurochs as a proxy, it is still unclear of whether Iberian aurochs would present a similar population to the wild Northern and Eastern European population (Upadhyay *et al.* 2017).

5.5.4. Bos primigenius across the Asian continent

Four new aurochs genomes from Western Asia (Gyumri1, Gyumri2, Kor1) and Northern Asia (Baikal1), with an average genome coverage of 2x, were analysed here. These genomes span a period of around 7,000 years of prehistory, overlapping the appearance of taurine domestic cattle in the Near East and they were compared to other aurochs specimens from North Africa and Europe. It was demonstrated that Gyumri1 (11,842-11,622 cal. BC) and Baikal1 (10,431-10,029 cal. BC) likely belonged to the same aurochs population.

These two individuals carried matrilines and Y chromosome haplotypes which were each divergent outgroups to the diversity observed in European aurochs and domestic taurine cattle. PCA and IBS analysis revealed a clear clustering of these two individuals and ADMIXTURE suggested equiproportional structure for the three main components (indicine, European taurine, African taurine). This is not observed for any other aurochs. The clustering of these two is not perfect: the Mesolithic aurochs (Bed3, Bed4, Tri1), Neolithic Anatolian Sub1, Tango1 and Gyumri2, all seem to share higher number of derived alleles with Gyumri1 than with Baikal1.

Contrastingly, Gyumri2 (5036-5017 cal. BC), the younger Armenian aurochs which post-dates the domestication of taurine cattle in the Near East revealed more taurine ancestry in PCA and ADMIXTURE, which could be indicative of a past admixture event with ancient taurine domestics or could be a sampling of a wild individual closer to the immediate ancestors of *Bos taurus*. Moreover, the higher number of shared derived alleles between Gyumri2 and Gyumri1 than with Baikal1 or Sub1, in addition to the high shared drift between Gyumri2 and Sub1, might suggest Gyumri2 to be a mixture of Gyumri1 and an early Neolithic domestic like Sub1. This could be tested in the future with f_3 statistics. The clear difference in population structure between Gyumri1 (~11,800 cal. BC) and Gyumri2 (~5000 cal. BC) could also be explained by intervening migration.

A survey for admixture involving each aurochs and a much larger ancient dataset also revealed that Baikal1, Gyumri1 and Gyumri2 showed relatively similar patterns of admixture into ancient domestics. For European ancient domestics gene flow is not observed from any of these individuals with the exception of a few Neolithic Serbian ancient cattle that reported significant gene flow from Gyumri1 and Baikal1 (Figure 5.15 and 5.19). However, it is unclear why this might be the case. For Neolithic Anatolian individuals no gene flow was reported from any of these Near Eastern aurochs. However, it seems that ancient cattle in the Westernmost archaeological sites in Iran, Miyanroud in the South (Fars Province), Hasanlu and Qazvin in the Northwest, have had some contact

with wild aurochs. Gene flow is observable from ancestors resembling Baikal1 and Gyumri1 into Neolithic and Early Bronze age Far1, Has3 and Qaz1. This contrasts with more Eastern Neolithic/Chalcolithic individuals like Sac3 (Semnan) and Mar1 (Maral Tappeh), which do not seem to have had any such influence. In addition, an Early Bronze Age individual from Central Anatolia (Ace1) has also revealed similar gene flow. Therefore, there seems to have been auroch introgression at least in the most Western regions of Iran and Central Anatolia following along the Turkish-Iranian plateau, as early as ~5500 BC in Southwest Iran (Far1) and as late as the Early Bronze Age Northeast Iran (Has3) and Bronze Age (c.2200 BC) Central Anatolia (Ace1) from a population related to Baikal1 and Gyumri1. From the Middle Bronze Age onwards no gene flow is detectable from any of these Asian aurochs into populations from the Levant, Iran, Georgia and Central Asia, which likely reflects masking of this signal by domestic zebu coming from the East (Loftus *et al.* 1999; Matthews 2002; Edwards, Baird, *et al.* 2007). Finally, *D*-statistics on modern domestics revealed no gene flow from this Asian aurochs population into the ancestors of any modern domestic breeds. Still, it is important to note that Asian modern breeds are clearly underrepresented in comparison to European modern breeds in the 700K dataset.

In conclusion, the Southern Siberian Baikal1 seems to be an outgroup to all other aurochs populations presented in this chapter. It seems to cluster on a genome-wide level with the other Late Pleistocene individual from West Asia, Gyumri1 (~11,800 cal. BC), and there is support for gene flow between these aurochs, likely belonging to a population that was spread across the Asian continent and that were distinct from those in Europe and North Africa. They seemed to have contributed to the genetic pool of early domestics from Western Iran, although more data is needed from this region to fully understand the extent in a broader temporal and spatial background.

5.5.6. Bos primigenius from an important Near Eastern site of early exploitation of cattle

Körtik Tepe is a Pre-Pottery Neolithic A site (~9300 cal. BC), located in the southeast of Anatolia (modern day Turkey) on the foothills of the Taurus Mountains and adjacent to the Tigris river (Arbuckle & Özkaya 2006). At around 16%, *Bos* comprise the third most common of faunal remains, after sheep/goat and red deer. Logarithimic size index (LSI) - a measure for body size using a standard animal (Arbuckle *et al.* 2014) - identified most cattle remains to be at least as big as the standard auroch used for comparison (Arbuckle & Özkaya 2006). It is therefore most likely that *Bos* specimens found at Körtik Tepe are *primigenius*. Kor1 has revealed a T2 mitochondrial haplogroup and clusters with an Early Neolithic individual from Anatolia (Sub1) (Figure 5.3). T2 has also been previously found in a Bronze Age aurochs from Maral Tappeh (Iran) and PPNB Syrian *Bos (Edwards et al. 2004; Edwards, Bollongino, et al. 2007)*; and is present at higher frequency in the Near East but present at lower frequencies elsewhere (Troy *et al.* 2001; Edwards *et al.* 2004; Scheu *et al.* 2015). The presence of another and earlier *Bos primigenius* specimen with a T haplogroup (Edwards *et al.* 2004; Edwards, Bollongino, *et al.* 2007) further supports the origin of this haplogroup in the Near East and does not support the evidence for a separate domestication in Europe (Beja-Pereira *et al.* 2006; Bonfiglio *et al.* 2010; Hristov *et al.* 2017). It also revealed clustered in PCA analysis with modern Iranian breeds Taleshi from Northern Iran, not with other Near Eastern aurochs (Gyumri1, Gyumri2) or Anatolian *Bos* (Ch22). A similar tripartite structure in ADMIXTURE further supports this individual as *Bos primigenius* specimen. However, its population structure contrasts to the other two Near Eastern aurochs (Gyumri1 and Gyumri2) in that it presented the highest fraction of indicine observed for all the aurochs.

5.5.7. North African Bos primigenius

The question of whether there was a separate domestication event for cattle in Africa has been explored using mitochondrial DNA, Y chromosomes, nuclear microsatellite data and genome wide SNP data (Bradley *et al.* 1994; MacHugh *et al.* 1997; Troy *et al.* 2001; Anderung *et al.* 2007; Hanotte *et al.* 2002; Decker *et al.* 2014; Kim *et al.* 2017). The North African *Bos primigenius* Th7 presents a unique opportunity to delve into the genetics of prehistoric African cattle as no aurochs from this continent has been subjected to population genetic analyses. The poor preservation of bone remains from this individual yielded low percentage of endogenous DNA and thus has limited the nuclear genomic coverage obtained (0.07x). Nevertheless, whole mitochondria were retrieved to place this individual confidently on a mtDNA phylogeny. Surprisingly, this aurochs belonged to the R haplogroup (Figure 5.3); so far only described in extant Italian breeds (Agerolese, Cinisara, Romagnola, Marchigiana) and clustered in a sub-haplogroup (R2) found in Italian Romagnola cattle (Achilli *et al.* 2009; Bonfiglio *et al.* 2010). Previous research has found the restricted geography of this haplogroup in modern breeds and the complete absence from European *Bos primigenius* individuals as suggestive of an independent domestication event and/or admixture with wild aurochs in Italy (Achilli *et al.* 2009; Bonfiglio *et al.* 2010). Furthermore, the estimated early divergence of this haplogroup (~143 KYA) was suggested as an indication that this haplogroup came from a wild population that had become geographically confined to the south of the Alps during the LGM (Taberlet *et al.* 1998; Bonfiglio *et al.* 2010). The results presented challenge this view in that this haplogroup is observed in an extinct wild population in the Epipaleolithic (7051-6801 cal. BC) Northern Africa.

Additionally, Th7 places away from all other aurochs in PCA, and is closer to extant African breeds than any other aurochs (Figure 5.4). Moreover, its location on the PCA is similar to what was observed for Neolithic, Chalcolithic and Early Bronze age Israel.

This was reflected in ADMIXTURE where Th7 revealed a tri-component genetic structure composed of mainly taurine ancestry. It revealed a similar fraction of the indicine component in relation to European aurochs of similar age, but contrasted in that the African taurine component comprised the highest fraction over the European fraction (Figure 5.5, Table 5.4). This population structure did not resemble any other extinct or extant population. Furthermore, IBS analysis (Figure 5.6) suggested Th7 to cluster with Asian aurochs, however *D*-statistics formally rejected the inclusion of Th7 in the pre-Agricultural Asian clade of Gyumri1/Baikal1 clade. The same statistics also confirm Th7 as an outgroup to European aurochs, Near Eastern aurochs and ancient domestics (Sub1, Ch22).

Additionally, computed *D*-statistics to test admixture between Th7 and extinct wild and domestic cattle have revealed no significant gene flow in Europe or Asia, with two exceptions; the 6048-5893 cal. BC Anatolian Men2 and the 1929-1753 cal BC Israeli Dav1 (Figure 5.12). It is unclear why there would be gene flow in an early domestic from Northwest Anatolia from a North African aurochs, which should be investigated further for a possible spurious positive signal of gene flow. Unfortunately, due to the extremely low coverage obtained for most Neolithic Southern Levantine specimens and Th7 alike, these did not yield sufficient data for this analyses. Nevertheless, Dav1, revealed a significant *D* value, supporting admixture from Th7 with this Southern Levantine Middle Bronze Age individual. Notably, such evidence for gene flow has only been observed for Th7 out of all other *Bos primigenius* specimens. Given the similar positioning on the PCA for other Southern Levantine individuals observed in Chapter 4, we can surmise that these have similar affinity, although more data is pivotal to formally test this. This is suggestive of a male-mediated African aurochs gene flow given that the T1 mtDNA haplogroup is most common in African extant cattle (Troy *et al.* 2001), and present at high frequency in ancient Southern Levantine cattle (Chapter 4, Figure 4.12); and the R haplogroup observed in Th7 is absent from the ancient Levant, and the Near East.

In conclusion, it could be suggested that the ancestors of African taurine cattle were imported into the African continent from the Fertile Crescent, with humpless taurine cattle being the first taxa of domesticated cattle in African (Epstein & Mason 1971; Payne 1991). They could have subsequently admixed with local aurochs bulls, which from archaeological record would have inhabited the Nile region (Gautier 2002) and which has been suggested from 50K genome-wide SNP data (Decker *et al.* 2014) and from 700K SNP data (Section 9.3.10). These results do not support a separate and secondary domestication event in Italy (Bonfiglio *et al.* 2010). The R haplogroup in Italy could reflect the Mediterranean route of domestic cattle spread with early North African contact with wild aurochs along the Mediterranean coast (Gautier 2002; Zeder 2008; Tresset & Vigne 2011; Felius *et al.* 2014; Cunliffe 2015). On the other hand, it could also be a legacy of the Roman empire, which reached Northern Africa (Cunliffe 2015).

5.5.8. Complex genetic prehistory of a Late Neolithic domestic from a German cave

Kir4 (2894-2670 cal. BC) was identified as a possible mtDNA outgroup to the R haplogroup and here forms a clade with the oldest aurochs in this collection, Gyumri1 (11,842-11,622 cal. BC). However, these individuals are distinct in their nuclear genomes. PCA analysis revealed that Kir4 clusters with modern day European taurine breeds and with ancient individuals from Southeastern and Eastern Europe; whereas Gyumri1 clusters with *Bos primigenius* from Southern Siberia (Figure 5.4). Moreover, in ADMIXTURE analyses Kir4 did not show a tripartite structure characteristic of aurochs (Park *et al.* 2015) and instead revealed a genetic structure like contemporary European taurine cattle. It was hypothesized that Kir4 could be a result from a past admixture event during migration from the Russian steppe to the west of Europe around ~3100 BC by the Yamnaya (Cunliffe 2015; Haak *et al.* 2015; Jones *et al.* 2015). No support was found for gene flow when testing with *D*-statistics involving the Mesolithic aurochs Bed3.

However, gene flow was observed from the Polish Kalisz2, the German Neolithic Hxh2 and the Mesolithic British CPC98. The Polish individual provides an interesting result giving that it could represent a more Eastern and somewhat different sub-population of aurochs. Whether this is a legacy from the Yamnaya migrations, remains to be verified.

5.5.9. From genomes to bones: unraveling the origins of Tango2 and Tango1 with genomics

The two *Bos primigenius* specimens of unknown geographical origin or archaeological context pose a challenge to interpret. Inferences solely on genetic ancestry can be misleading without a geographical and temporal context. One of these samples, however, has been radiocarbon dated to 2470-2297 cal. BC, thus indicating a post-domestication of cattle temporal context for Tango2. For Tango1, no radiocarbon date is available as of yet. Tango1 and Tango2 both carry the T3 mtDNA, which is present at highest frequency in modern European breeds (Troy *et al.* 2001). Although, it has been observed in aurochs from Italy and in the Near East (Edwards *et al.* 2004; Beja-Pereira *et al.* 2006; Edwards, Bollongino, *et al.* 2007). Based on the skeletal remains (Figure 5.2) it is evident that these individuals are beyond doubt *Bos primigenius* and not domestics. Tango2 clusters closer to European *Bos primigenius* than to any other aurochs groups, whereas Tango1 sits in a PCA space that is not occupied by any modern cattle breeds or ancient individuals (Figure 5.4). In ADMIXTURE Tango2 resembles European aurochs, albeit with a slightly higher fraction of the African taurine component than typical. Tango1, on the other hand, did not show a very similar structure to any other aurochs presented. Additionally, the whole genome NJ tree positioned Tango1 seemingly within the grouping of Asian/African *Bos primigenius*, whereas Tango2 placed basal to the European clade of aurochs (Figure 5.6). *D*-statistics did not support Tango1 as part of the Gyumri1/Baikal1 clade nor did it form a clade with the North African Th7.

Similarly, *D*-statistics did also not support Tango2 as part of the European aurochs clade. Looking at possible introgression patterns with ancient domestics, Tango2 revealed a similar pattern for the computed *D*-statistics as the European aurochs Bed3 and Kalisz2. Whereas, Tango1 revealed similar patterns of gene flow to those observed in Baikal1 and Gyumri1, with also the only significant gene flow observed into the Southeastern Iranian Far1.

Finally, these individuals seem to be quite well preserved, Tango1 reporting 45% endogenous DNA content and Tango2 reporting 49%. Such high percentages are typically associated with higher latitudes, although exceptions have been observed, for example the Epipaleolithic Gyumri1 from Armenia (53%). Thus, Tango1 seems to belong to an Asian population of aurochs perhaps from Western Russia. Tango2, on the other hand could belonged to an European population of aurochs, but perhaps from Eastern Europe. Also, its T3 mitochondrial haplogroup might indicate that these aurochs are admixed, or the presence of two T3 aurochs could indicates that this haplogroup was more common in European *Bos primigenius* than previously thought.

5.5.10. Conclusion and future prospects

In this chapter, a new Y haplogroup has been observed, along with two new mitochondrial haplogroups. Furthermore, a first comprehensive look into whole nuclear genomes of extinct aurochs from the Near East, Asia, Europe and North Africa has given new insights into cattle prehistory. Gene flow between different aurochs populations have been reported as well as gene flow between wild and domestics, showing different patterns for different continents and time depths. It has also been possible to start to disentangle the complex prehistory of these wild individuals although more sampling across East and South Asia would be pivotal to further understand their population prehistory. The Southwestern side of Europe is undeniably understudied and it is a clear gap in the current knowledge.

Furthermore, although the origin of indigenous African cattle is still debatable, Th7 has clearly revealed to be an essential piece in that it challenges a previously proposed hypothesis for a secondary domestication of Italian aurochs based on mitochondrial lineages (Achilli *et al.* 2009; Bonfiglio *et al.* 2010). It has also revealed, gene flow into Middle Bronze Age Southern Levant, which is the only and earliest evidence for such a past admixture event.

6. When *taurus* met *indicus*: admixture events in ancient Near Eastern cattle

"Man selects only for his own good: Nature only for that of the being which she tends.(...)He often begins his selection by some half-monstrous form; or at least by some modification prominent enough to catch the eye or to be plainly useful to him."

Charles Darwin, The Origin of Species

6.1. Introduction

6.1.1. The nature of taurine and indicine cattle

Domestic cattle comprise two subspecies or taxa, *Bos taurus* (humpless) and *Bos indicus* (zebu or humped); they have the same number of chromosomes and can produce fertile offspring upon interbreeding (Magee *et al.* 2014; Melletti & Burton 2014). They have a series of morphological and biological differences. These include in zebu the presence of a muscular fatty hump, a more pronounced dewlap and drooping ears, a tolerance to ticks and intestinal parasites (Roberts & Gray 1973; Murray *et al.* 1982), and adaptation to dry climates with lower basal metabolic rate and, consequently, decreased needs for the intake of water and nutrients (Magee *et al.* 2014). Furthermore, the spread of these two different taxa to different parts of the world has led to specific breeds adapting to local environments, like tolerance to trypanosoma by West African taurine breeds, or adaptation to colder climates with an insulating hair coat in breeds like Scottish Galloway (Melletti & Burton 2014).

6.1.2. Archaeology and genetics of Bos indicus domestication

The most widely held view is that *Bos indicus* were domesticated in South Asia from a genetically and morphologically distinct *Bos primigenius* which gave rise to *Bos taurus*.

Evidence from osteological measurements of cranial elements have shown zebu cattle to be more similar to the aurochs *Bos primigenius namadicus* (Falconer 1859) than to the Eurasian *Bos primigenius primigenius* (Bojanus, 1827) (Grigson 1980; Loftus, MacHugh, Bradley, *et al*. 1994).

The earliest archaeological evidence for the domestication of *Bos indicus* comes from the site of Mehrgarh in Baluchistan (Pakistan) in the Indus River Valley (Meadow 1993). The diminution in size of cattle in addition to their increase in faunal records, the presence of zebu figurines and of bifurcated vertebra at this site all support the appearance of domestic cattle (*indicus*) in this region by ~5000 BC (Meadow 1993; Matthews 2002; Fuller 2006). The domestication of zebu cattle in Baluchistan from the local wild aurochs, which were widespread during the Pleistocene and Holocene (Van Vuure 2005), is thought to have followed the earlier introduction of domesticated crops such as wheat and barley from West Asia (~7000 BC) (Meadow 1993; Fuller 2006). Farming settlements spread from this region into neighbouring regions of the Indus Valley, with main urban sites like Mohenjo-Daro and Harappa (c.4000-3000 BC) (Cunliffe 2015). This became known as the Indus Valley or Harappan civilization, which had well established trade routes across the Iranian plateau, in the search of raw materials such as lapis-lazuli or turquoise from Afghanistan and Iran; or gold and tin from Northeastern Iran and Central Asia, respectively. On the other hand these ancient communities were exporting other goods like carnelian beads into Iran and Mesopotamia, for example (Asthana 1993). Furthermore, the Harappan seal for example, shows how central cattle were to these economies, depicting a clearly zebu animal, showing the typical hump and marked dewlap. The collapse of this civilization came around ~1900 BC although the reasons are unclear. It is unknown whether it was due to climatic and/or environmental factors, or connected to the Late Bronze Age collapse in the Near East that likely ruptured trade connections with the East.

Genetic evidence for the deep divergence between taurine and indicine, and thus support for a separate domestication of *Bos indicus* from a highly divergent wild ancestor, has built up consistently over many decades, based on mitochondrial DNA (Loftus, MacHugh, Bradley, *et al.* 1994; Bradley *et al.* 1996; Troy *et al.* 2001; Bollongino *et al.* 2006; Edwards, Bollongino, *et al.* 2007; Magee *et al.* 2007; Achilli *et al.* 2008; Achilli *et al.* 2009; Bonfiglio *et al.* 2010; Chen *et al.* 2010), Y chromosome (Bradley *et al.* 1994; Teale *et al.* 1995; Bradley *et al.* 1996; Hanotte *et al.* 1997; Hanotte *et al.* 2000; Edwards, Baird, *et al.* 2007; Pérez-Pardal, Royo, Beja-Pereira, Chen, *et al.* 2010), autosomal markers (MacHugh *et al.* 1997; Loftus *et al.* 1999; Murray *et al.* 2010) and high-density SNP data (Bovine HapMap Consortium *et al.* 2009; Porto-Neto *et al.* 2013; Decker *et al.* 2014; Upadhyay *et al.* 2017). The two main haplogroups (T and I) of taurine and indicine cattle have been estimated to have diverged more than 200,000 years ago (Loftus, MacHugh, Ngere, *et al.* 1994; Bradley *et al.* 1996; Troy *et al.* 2001; Achilli *et al.* 2008) with similar estimates for nuclear autosomal markers (MacHugh *et al.* 1997; Murray *et al.* 2010). Therefore, this means that introgression can be easily detectable between the two subspecies.

6.1.3. Zebu cattle in the Near East

The Bronze Age was a highly significant period in prehistory, with socio-economic changes that saw the rise and fall of city states across Mesopotamia. From the 4th millennium BC up to the Late Bronze age (2nd Millennium BC), the Near East saw the development of great civilizations like Uruk, Akkad, Ur and Babylonia. These developing complex societies saw increased exploitation of raw materials which consequently gave rise to new trade routes for gold, silver and copper; as well as lapis lazuli, wood, fabrics among many other raw materials (Asthana 1993; Cunliffe 2015; Podany 2013). In Bronze Age Anatolia, an increase in cattle archaeological assemblages has been observed, which could reflect intensification of agriculture as a product of these complex societies and economies (Arbuckle 2014).

Evidence of zebu cattle presence and importance in Mesopotamia comes from seals, amulets, figurines and painted pottery motifs depicting zebu cattle (Matthews 2002). Such Indus Valley objects were also found in the Makran coast (Baluchistan) after ~2500 BC, which probably connected with the south of Mesopotamia via the Persian Gulf (Matthews 2002; Cunliffe 2015). Furthermore, figures and painted pots are found ~ 3000 BC in Southwestern Iran; as well as zebu bones at high frequency in the Bronze Age urban centre of Shahr-i Sokhta (Iran) (c.2900-2500 BC) and a probable source of precious stones, metals and exotic animals (Matthews 2002; Cunliffe 2015). In Anatolia, zebu seem to be underrepresented and not commonly depicted in the Bronze Age, but are present from the Iron Age into the Byzantine empire (Arbuckle 2012a; Matthews 2002). However, there is little archaeozoological evidence that corroborates the archaeological artifacts described, especially since zebu and taurine faunal remains are hard to differentiate and rely on a few skeletal differences like v-shaped vertebra (Matthews 2002). However, zebu cattle are thought to have been introduced into Mesopotamia at the end of the Late Bronze Age (end of the 2nd millennium BC). Notwithstanding, an earlier introduction is also possible around the end of the Middle Bronze age (mid-3rd millennium BC), and these animals might have only reached the Levant and Syria by the end of Late Bronze Age (Matthews 2002).

The question of secondary zebu introgression in the Near East has been explored in modern day Near Eastern breeds, from nuclear microsatellite data (Loftus *et al.* 1999; Freeman *et al.* 2005) to mitochondria and Y chromosomes (Edwards, Baird, *et al.* 2007). Also, taurine introgression into South Asian cattle as also been explored in cattle from the Indian subcontinent, where taurine influence was reported (Kumar *et al.* 2003), and modelling demographic history on autosomal sequences has suggested admixture (Murray *et al.* 2010). In summary, modern Near Eastern cattle are admixed with zebu, and present an east to west decrease in the frequency of zebu alleles.

6.2. Aims and context

In this chapter a collection of 67 individuals from 37 different archaeological sites from the Near East, Europe and Asia is presented (Figure 6.1). The large time range and geographical area is used to investigate admixture processes between the two taxa of domestic cattle in the Near East. Since modern breeds have shown some degree of admixture between *Bos taurus* and *Bos indicus* animals the starting hypothesis is that there was introgression in the Near East (Loftus *et al.* 1999; Edwards, Baird, *et al*. 2007); and that this likely happened during the Bronze age, a time of climatic and socio-economic change (Matthews 2002). This chapter aims to pinpoint the time of admixture by looking directly at ancient cattle from the Near East. It makes use of low endogenous DNA samples, and consequently low coverage genomes on the basis that the deep divergence between taurine and indicine cattle allows for an easy detection of increase in indicine alleles. For this purpose, PCA, ADMIXTURE, *D*-statistics and *F*-statistics (F3) should detect admixed ancient individuals (or populations) between *taurus* and *indicus*. In addition, F_4-ratios should give admixing proportions for each ancient individual and a first look into how these might have varied through time and space. It is also the aim of this chapter to understand whether this gene flow was male mediated, similar to what has been shown for the African continent (Bradley *et al.* 1994; Teale *et al.* 1995; MacHugh *et al.* 1997; Hanotte *et al.* 2000; Pérez-Pardal, Royo, Beja-Pereira, Chen, *et al.* 2010) and for the Near East (Loftus *et al.* 1999; Edwards, Baird, *et al.* 2007). Whole mitochondria and Y chromosome phylogenies should indicate any sex-bias in zebu admixture. Moreover, an east to west decrease in zebu admixture has been described in modern cattle breeds from the Middle East (Edwards, Baird, *et al.* 2007). Thus, we aim to understand whether this pattern of introgression is apparent in the ancient Near East. Finally, we try to link possible human events like the rise and fall of Mesopotamian and Harappan civilizations, as well as climate events that could have played a role in the influx of zebu animals from the East.

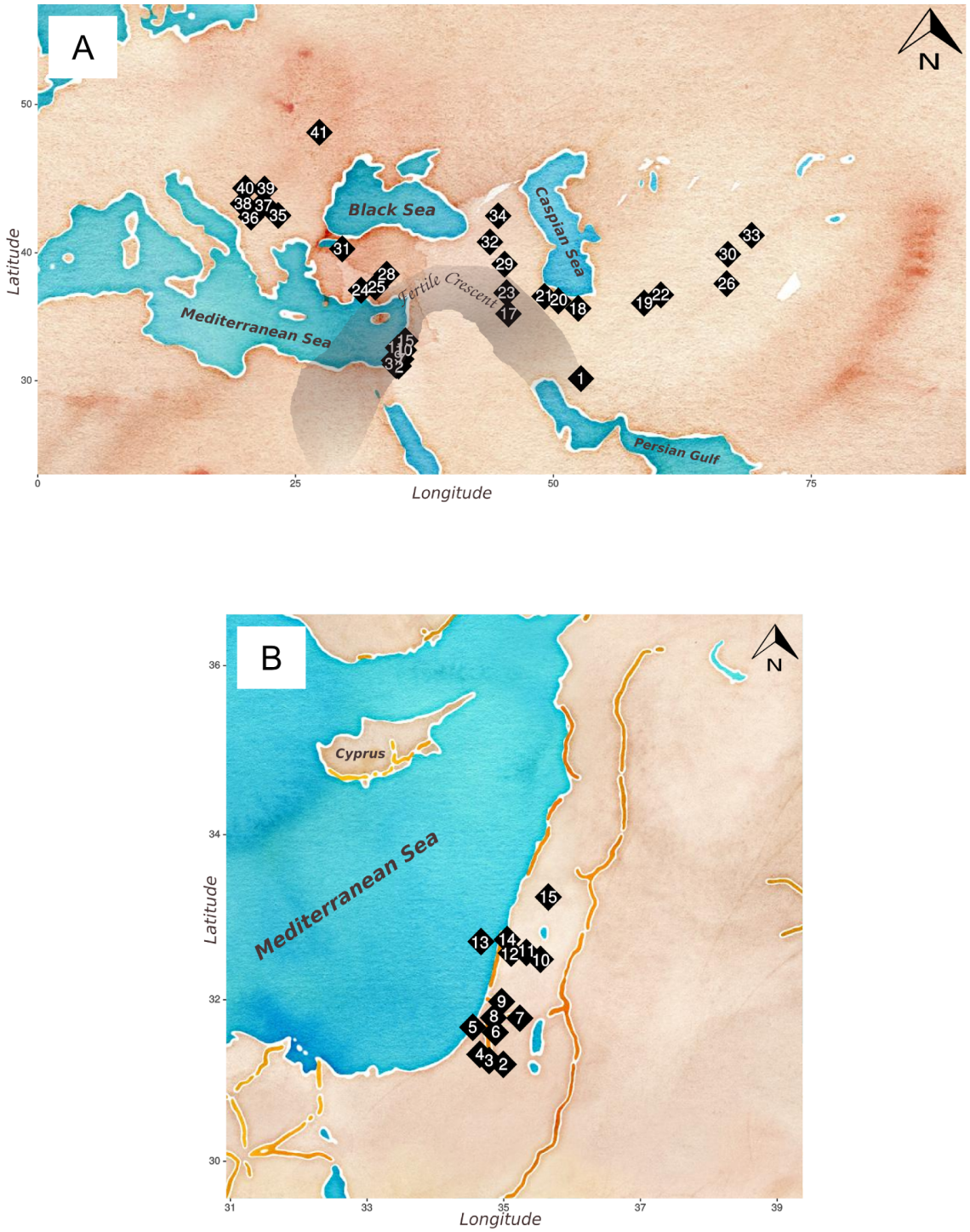


Figure 6.1- (A) Location of archaeological sites. (B) Zoom of archaeological sites located in the Southern Levant. *(1) Miyanroud; (2) Tel Masos; (3) Nahal Tillah; (4) Gilat; (5) Tel Ashqelon; (6) Tel Es-Safi; (7) Jerusalem; (8) Tel-Miqne; (9)Tel-Dalit; (10) Tel Zahara; (11) Castra; (12) Tel Yoqneam; (13) Tel-Hreiz (submerged); (14) Tel es-Qassis; (15) Tel Dan; (17) Bestanşur; (18) Maral Tappeh; (19) Nishapur Qohandez; (20) Tepe Shizar; (21) Tapeh-Sang-e-Caxmaq; (22) Monjukli Depe; (23) Hasanlu; (24) Suberde; (26) Tilla Bulak; (28) Acemhöyük; (29) Kültepe; (30) Kok Teppe; (31) Menteşe; (32) Gyumri; (33) Yerqorqan; (34) Tamara Fort; (36) Plocnik; (37) Bubanj; (38) Blagotin; (39) Belovode- Veliko; (40) Stubline; (41) Birnova/Byrnova Luka.*

Table 6.2- Summary of archaeological samples for DNA analyses. *Archaeological details for each specimen. Samples marked with (*) were processed by Andrew Hare (Trinity College Dublin); samples marked with (^) were processed by Kevin Daly (Trinity College Dublin); samples marked with (") lab work was done by Valeria Mattiangeli (Trinity College Dublin).*

ID	Bone	Country	Site	Archaeological Context	Date
Ace1	petrous	Turkey	Acemhöyük	Early Bronze Age	c. 2200 BC
Ash4	petrous	Israel	Tel Ashqelon	Early Iron I	1200–1000 BC
Azer1*	petrous	Iran	Kültepe	Late Chalcolithic	4260-4050 cal. BC
Bel1	petrous	Serbia	Belovode-Veliko	Late Neolithic	5050/4925-4900/4800 cal. BC
Bel2	petrous	Serbia	Belovode-Veliko	Late Neolithic	5050/4925-4900/4800 cal. BC
Bes1	petrous	Iraq-Kurdistan	Bestansur	Iron age	911–609 BC
Bes2	petrous	Iraq-Kurdistan	Bestansur	Medieval	1292-1399 cal. AD
Bir1	tooth	Moldova	Birnova/Byrnova Luka	Cucuteni-Trypillian	c. 5200 - 3500 BC
Bir2	astralagus	Moldova	Birnova/Byrnova Luka	Cucuteni-Trypillian	c. 5200 - 3500 BC
Bir3	astralagus	Moldova	Birnova/Byrnova Luka	Cucuteni-Trypillian	c. 5200 - 3500 BC
Bla1	petrous	Serbia	Blagotin	Early Neolithic Starčevo	6200-6000 cal. BC
Bla2	petrous	Serbia	Blagotin	Early Neolithic Starčevo	6200-6000 cal. BC
Bub1	petrous	Serbia	Bubanj	Neolithic	c. 6000-5600 BC
Bul1	petrous	Uzbekistan	Tilla Bulak	Late Bronze Age	2000-1700 cal. BC
CA317"	non petrous	Georgia	Tamara Fort	Medieval	AD 651-766
Cas1"	petrous	Israel	Horvat Castra	Byzantine	AD 324-638
Dan1"	petrous	Israel	Tel Dan	PN-Early Bronze	3500-3000 BC
Dav1^	petrous	Israel	Jerusalem	Middle Bronze Age II A-B	1929-1753 cal. BC
Dav2	petrous	Israel	Jerusalem	Middle Bronze Age II	2200-2000 BC
Dav3	petrous	Israel	Jerusalem	Middle Bronze Age II	2200-2000 BC
Dav4	petrous	Israel	Jerusalem	Middle Bronze Age II	2200-2000 BC
Dav5"	petrous	Israel	Jerusalem	Early Hellenistic	332-167 BC

Far1	petrous	Iran	Miyanroud	Late Neolithic	waiting for Azadeh to answer
Gil1	petrous	Israel	Gilat	Chalcolithic	c.4300–3300 BC
Has1	petrous	Iran	Hasanlu	Middle Bronze	1900-1600 BC
Has3	petrous	Iran	Hasanlu	Early Bronze II	2470 cal. BC
Has4	petrous	Iran	Hasanlu	Iron II	1050-800 BC
Has5	petrous	Iran	Hasanlu	Achaemenid/Seleuco-Parthian	550-275 BC
Kaz1	petrous	Georgia	Tamara Fort	Medieval	AD c.950
Kaz2	petrous	Georgia	Tamara Fort	Medieval	AD c.900
Kaz3	petrous	Georgia	Tamara Fort	Medieval	AD c.900
Kaz4	petrous	Georgia	Darialiti Fort	Medieval	AD c.910
Kho1	petrous	Iran	Nishapur Qohandez	Parthes-Islamic	300 BC- AD 1300
Kok1	petrous	Uzbekistan	Kok Teppe	Iron Age	1500-3000 BC
Mar1	scapula	Iran	Maral Tappeh	Chalcolithic/Bronze Age	c.5000 BC
Men1	astragalus	Turkey	Mentese	Neolithic	c.6000-5500 BC
Men2	petrous	Turkey	Mentese	Neolithic	6048-5893 cal. BC
Mon1	petrous	Turkmenistan	Monjukli Depe	Chalcolithic	5100-4500 cal. BC
Mus1^	petrous	Israel	Tel Masos	Iron Age I	1200-1000 BC
Nah1	petrous	Israel	Nahal Tillah	Early Bronze I	3300-3050 BC
Plo1	petrous	Serbia	Plocnik	Neolithic	5275/5125-5100/5000 cal. BC
Plo2	petrous	Serbia	Plocnik	Neolithic	5025/4950-4850-4650 cal. BC
Plo3	petrous	Serbia	Plocnik	Neolithic	5100/5000-5025/4950 cal. BC
Plo4	petrous	Serbia	Plocnik	Neolithic	5100/5000-5025/4950 cal. BC
Plo5	petrous	Serbia	Plocnik	Neolithic	4850/4650-4600/4500 cal. BC
Plo6	petrous	Serbia	Plocnik	Neolithic	5275/5125-5100/5000 cal. BC
Plo7	petrous	Serbia	Plocnik	Neolithic	5100/5000-5025/4950 cal.

					BC
Plo8	petrous	Serbia	Plocnik	Neolithic	5100/5000-5025/4950 cal. BC
Qaz1	petrous	Iran	Tepe Shizar	Middle Bronze Age	2880-2830 cal. BC
Sac3	non petrous	Iran	Tapeh-Sang-e-Caxmaq	Late Neolithic	5373 cal. BC
Stu1	petrous	Serbia	Stubline	Neolithic	4800-4500 cal. BC
Sub1	petrous	Turkey	Suberde	Neolithic	6221-6024 cal. BC
Tda1	petrous	Israel	Tel-Dalit	Early Bronze Age II	3050 BC
Thr1	petrous	Israel	Tel Hreiz	Pottery Neolithic	5100-4300 BC
Tmq1	petrous	Israel	Tel Miqne-Ekron	Iron Age IA	1200-1150 BC
Tmq2	petrous	Israel	Tel Miqne-Ekron	Iron Age IA	1200-1150 BC
Tmq3	petrous	Israel	Tel Miqne-Ekron	Late Bronze IIA	1000-925 BC
Tmq4	petrous	Israel	Tel Miqne-Ekron	Late Bronze/Iron Age	1400-1200 BC
Tqa1	petrous	Israel	Tel es-Qashish	Early Bronze Age 3	3150-2200 BC
Tqa2	petrous	Israel	Tel es-Qashish	Early Bronze Age 3	3150-2200 BC
Tqa3^	petrous	Israel	Tel es-Qashish	Early Bronze Age 3	3150-2200 BC
Tsa1^	petrous	Israel	Tel es-Safi	Iron Age II	925-720 BC
Tsa2	petrous	Israel	Tel es-Safi	Iron Age I	1200-1000 BC
Tsa3	petrous	Israel	Tel es-Safi	Iron Age II	925-720 BC
Tyq1^	petrous	Israel	Tel Yoqneam	Early Hellenistic	332-167 BC
Yer1	petrous	Uzbekistan	Yerqorqan	Achaemenid	c.50 BC
Zah1″	petrous	Israel	Tel Zahara	Islamic	c. 63 BC - AD 330

6.3. Methods

6.3.1. Radiocarbon dating

Samples of key geographical, archaeological context and of good DNA preservation were chosen. Calibration curve plots produced by OxCal (Ramsey 2009) can be found in the Appendix Section 9.5.

6.3.2. Principal Component Analysis

Principal component analysis was done on the basis of Procrustes analysis using LASER (Version 2.03), as described in 3.1.1.

6.3.3. ADMIXTURE

To look at genetic structure among these ancient individuals unsupervised ADMIXTURE (Alexander *et al.* 2009a) was run using the 700K bovine SNP dataset, as described in section 3.2. The final input dataset for ADMIXTURE had a total genotyping rate of 0.93 and 119,323 variants and 857 cattle. For the purpose of this chapter K=2 was chosen in order to differentiate between *Bos taurus* and *Bos indicus*.

6.3.4. D-statistics - AdmixTools

To formally test admixture events in this collection of ancient individuals *D*-statistics were calculated for the test *D*(((Test,Limousin),Sahiwal),Yak), in which Yak served as the Outgroup, Sahiwal as the putative *B.indicus* introgressor population, and Limousin as an non-admixed *Bos taurus* individual from Europe forming a clade with the *B.taurus* ancient individuals being tested. The 700K bovine dataset was used with the AdmixTools package (Patterson *et al.* 2012), with transitions removed and individuals as pseudo-diploids. Finally, samples in which analysis was performed on less than 1000 variants were removed.

6.3.5. D-statistics - ANGSD

The test applied to the ancient data was *D*(((Highland, Test), Sahiwal), Yak). The coverage and origin of the modern cattle genomes used in this test are summarized in Appendix Table 9.1.3. For this test, ancient samples that had less than 81 total number of ABBA+BABA sites counted by ANGSD were removed. ANGSD was run as described in section 3.3.2.

6.3.6. f_3-statistics

In this chapter, the f_3-statistic was computed using the AdmixTools package (Patterson *et al.* 2012) with 700K Bovine SNP data, with transitions removed. The test was set up as f_3(Target; Sahiwal, Neolithic Anatolia), with source populations being *Bos indicus* population Sahiwal and Neolithic Anatolians (Sub1, Men1, Men2); and Target being of ancient populations: Neolithic European (Serbia and Moldova), Neolithic Near East (Levant, Iran), Bronze Age Near East (Anatolia, Iran, Levant), Iron Age Near East (Levant, Iraq, Iran), Post Iron Age Near East (Iraq, Georgia, Levant, Iran) and Central Asia (Uzbekistan and Turkmenistan). A list of ancient samples and the population they have been assigned to can be found in Table 9.4.7 in the Appendix.

6.3.7. f_4-ratio

To estimate the proportion of zebu ancestry in each ancient individual f_4-*ratio* was computed using the AdmixTools package (Patterson *et al.* 2012) for the test f_4 (Sahiwal,Yak; ancient, Limousin)/(Sahiwal,Yak; Gir,Limousin). The test was computed as described in 3.4.1.

6.3.8. Mitochondrial genomes capture

Whole mitochondrial sequences were obtained by shotgun sequencing and processed as explained in section 3.5. Given that in this chapter mitochondrial genome coverages were sometimes too low, some samples have been subsequently captured in order to obtain complete mtDNA genomes. Mitochondrial capture involved indexing PCR prior to pooling; and enrichment was performed using a previously designed custom RNA capture (Mycroarray, 5692 Plymouth Road, Ann Arbor, MI 48105) and used as per manufacturer's instructions. A final PCR amplification step followed the enrichment with 15 cycles. Captured mitochondrial sequences were then sequenced on an Illumina® MiSeq at TrinSeq, the Trinity Genome Sequencing Laboratory, located in the Institute of Molecular Medicine (IMM).

A neighbour joining (NJ) mitochondrial DNA (mtDNA) tree was drawn following the pipeline described in section 3.5.

6.3.9. Y chromosome phylogeny

Y chromosome reads were processed as described in section 3.6. For the VCF generated a filter for missingness was applied and 10,904 out of a possible 1,350,000 sites were kept, using 32 ancient and modern individuals, including a *Bos grunniens* (domestic yak) individual and NJ tree was drawn with 160 SNPs with 1000 replicates.Y chromosome coverages for all samples can be found in Appendix Table 9.1.6.

6.4. Results

6.4.1. Screening and radiocarbon dating the ancient dataset

A total of 155 samples from 51 archaeological sites were screened. Samples with a minimum endogenous DNA of 0.1% aligning to the *Bos taurus* (UMD 3.1.) reference genome were sequenced and coverages obtained are presented in Table 6.3. Some specimens were originally sampled by Kevin Daly and Andrew Hare at TCD, and these are clearly identified in the table. Radiocarbon dating was done on well preserved samples of interest (Table 6.4). The total final dataset thus comprised of 67 ancient samples.

The sequencing strategy for this chapter was based on the minimum coverage tested that would still show a zebu admixture signal. The high coverage samples that had shown a high influx of indicine admixture were downsampled in coverage in steps up to 0.001x in order to test whether the signal of indicine admixture would be retained. For this experiment, both PCA and ADMIXTURE analysis were computed and controls of various levels of admixed and non admixed individuals (including Moderns) were used as controls. Since the signal was consistent, even with a very low number of SNPs, or very low coverages, all samples with endogenous DNA greater than 0.05 % were then included in the sequencing strategy. Endogenous DNA percentages ranged from 0.05% to 62%; nuclear DNA coverages ranged from 0.0002x to 14x; and mitochondrial DNA coverages ranged from 0.04x to 1344x.

Table 6.3- Screening and final sequencing results. *Species, endogenous DNA content, coverages for nuclear and mitochondrial genomes, and sexing for each sample used in this chapter. Endogenous DNA percentage is given for each specimen based on the calculation: (number of reads q25 x100/ number of total reads). Whole genome average coverage and mitochondrial genome coverage were calculated using Qualimap (García-Alcalde et al. 2012). Bone samples marked with (^) have been originally sampled by Kevin Daly and one marked with (*) by Andrew Hare at TCD. Specimens that could represent Bos primigenius individuals based on archaeological evidence have been marked with a question marked.*

ID	Species	% DNA	Coverage	Mitochondria	Sex
Ace1	*Bos taurus*	29	0.1	21	Female
Ash4	*Bos*	2	0.01	1	Male
Azer1*	*Bos*	0.3	0.001	0.4	Female
Bel1	*Bos taurus*	21	0.09	12	Female
Bel2	*Bos taurus*	28	0.1	25	Male
Bes1	*Bos taurus*	35	2	149	Female
Bes2	*Bos taurus*	39	14	609	Male
Bir1	*Bos taurus*	0.3	0.002	1	Female
Bir2	*Bos taurus*	0.05	0.001	4	Female
Bir3	*Bos taurus*	1	0.004	2	Female
Bla1	*Bos taurus*	14	0.019	4	Male
Bla2	*Bos taurus*	17	0.005	1	Male
Bub1	*Bos taurus*	38	0.4	53	Female
Bul1	*Bos taurus*	24	0.05	14	Male
CA317	*Bos primigenius?*	9	0.02	7	Male
Cas1	*Bos*	38	0.07	10	Female
Dan1	*Bos*	0.1	0.0002	0.04	Female
Dav1^	*Bos*	16	5	946	Female
Dav2	*Bos*	5	0.004	2	Female
Dav3	*Bos*	7	0.02	4	Male
Dav4	*Bos*	6	0.02	12	Male
Dav5	*Bos*	0.22	0.004	1	Female
Far1	*Bos*	8	0.03	5	Female
Gil1	*Bos*	0.2	0.0007	0.2	Female
Has1	*Bos*	22	0.03	5	Male

Has3	*Bos*	43	1	174	Male
Has4	*Bos*	24	1	150	Male
Has5	*Bos*	13	0.03	13	Female
Kaz1	*Bos*	58	3	157	Female
Kaz2	*Bos*	57	0.3	28	Female
Kaz3	*Bos*	62	0.5	37	Female
Kaz4	*Bos*	54	0.5	29	Female
Kho1	*Bos*	51	0.2	21	Female
Kok1	*Bos*	6	0.01	2	Male
Mar1	*Bos primigenius?*	3	0.04	4	Male
Men1	*Bos*	13	3	334	Male
Men2	*Bos*	20	2	88	Female
Mon1	*Bos taurus*	8	0.001	0.1	Female
Mus1^	*Bos*	2	0.003	2	Female
Nah1	*Bos*	0.3	0.0004	0.2	Male
Plo1	*Bos taurus*	44	0.1	10	Female
Plo2	*Bos taurus*	36	0.4	36	Female
Plo3	*Bos taurus*	57	3	153	Male
Plo4	*Bos taurus*	54	3	154	Male
Plo5	*Bos taurus*	31	0.08	13	Male
Plo6	*Bos taurus*	26	0.1	8	Male
Plo7	*Bos taurus*	32	0.1	19	Female
Plo8	*Bos taurus*	29	0.2	14	Female
Qaz1	*Bos*	48	2	193	Female
Sac3	*Bos*	4	0.02	3	Female
Stu1	*Bos taurus*	33	0.15	10	Male
Sub1	*Bos*	40	14	1344	Male
Tda1	*Bos*	0.3	0.001	0.3	Male
Thr1	*Bos*	0.3	0.001	0.2	Male
Tmq1	*Bos*	0.5	0.003	2	Female
Tmq2	*Bos*	0.7	0.004	1	Female
Tmq3	*Bos*	7	0.02	3	Female

Tmq4	*Bos*	17	0.02	3	Female
Tqa1	*Bos*	0.6	0.003	0.8	Male
Tqa2	*Bos*	4	0.005	0.6	Female
Tqa3^	*Bos*	4	0.004	3	Female
Tsa1	*Bos*	38	1	160	Female
Tsa2^	*Bos*	0.3	0.002	1	Female
Tsa3	*Bos*	4	0.02	3	Female
Tyq1^	*Bos*	29	0.05	11	Male
Yer1	*Bos*	46	0.02	7	Female
Zah1	*Bos*	20	0.03	3	Male

Table 6.4- Radiocarbon dating. *Measured radiocarbon dates in C14 BP with error; Calibrated dates in BC and BP based on 2-sigma calibration (95% probability).*

Sample ID	Conventional C14 age (BP)	Calibrated Date BC/AD (cal.BC/AD) 95% probability	Calibrated Date BP (cal.BP) 95% probability
Bes2	629+/-25	1292-1399 (AD)	658-551
Dav1	3520+/-30	1929-1753	3879-3703
Qaz1	4170+-30	2880-2830	4830-4780

6.4.2. Principal Component Analysis

Principal components for all samples were calculated and are shown in the Procrustes Projection PCA in Figure 6.2 (Appendix Table 9.4.1), where PC1 accounts for most of the variability, separating *Bos taurus* from *Bos indicus*; and PC2 separates European taurine from African taurine ancestry. The most striking results are those for Southern Levant ancients in which two main distinct clusters are observed. One includes early Neolithic to Early Bronze Age individuals, while the other includes Late Bronze Age, Iron Age and later individuals. There is a clear increase in indicine ancestry after the

Bronze Age. These post Bronze Age individuals cluster close to modern Turkish and Iranian breeds (South Anatolian Red, East Anatolian Red, Taleshi).

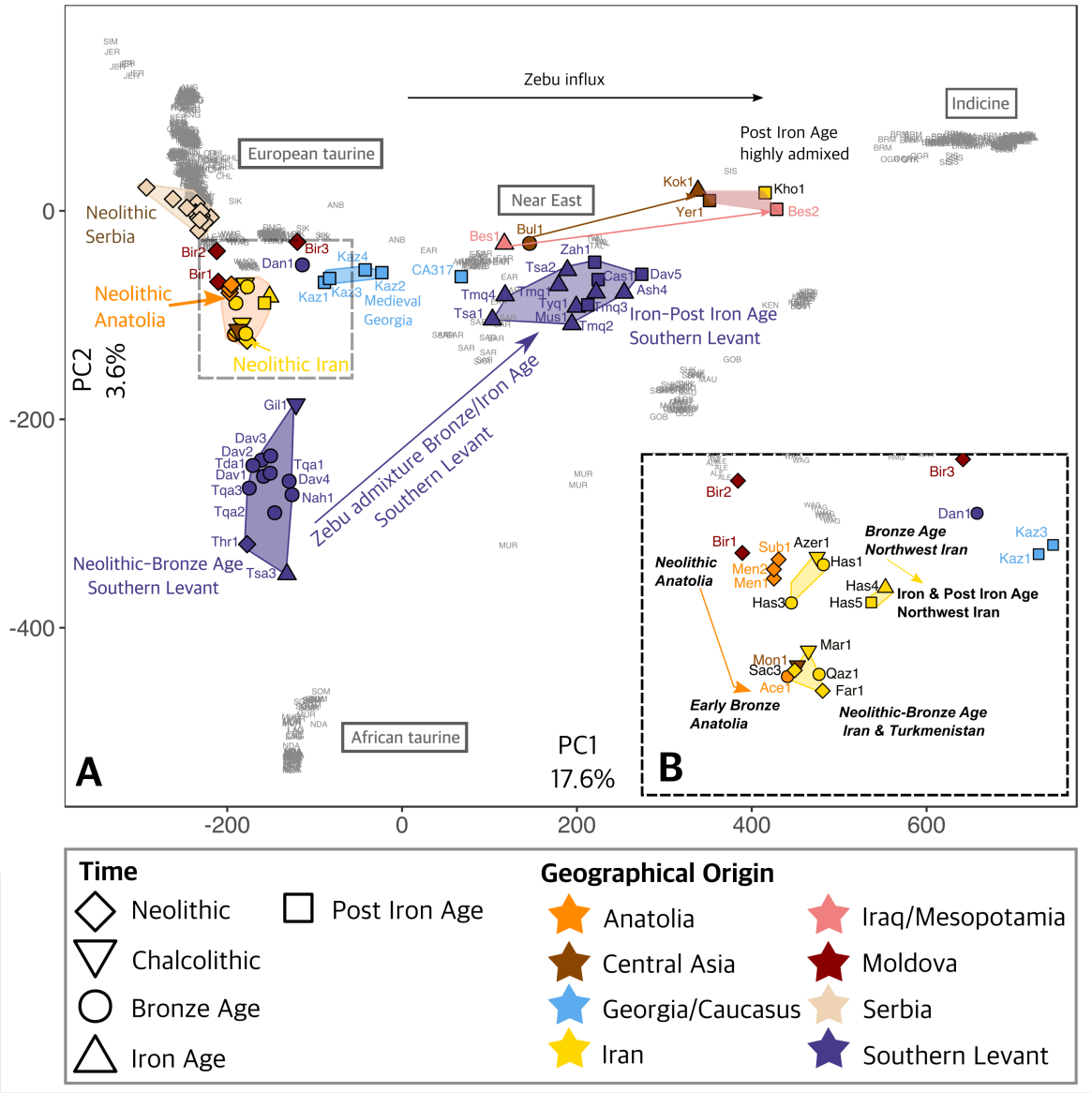


Figure 6.2 - Principal Components analysis. *Computed with Laser and projected onto Bovine 700K SNP chip Data. Modern dataset (grey text) shows cattle breeds clustering into 4 main groups: European taurine, African taurine, Near Eastern taurine and indicine. Geographical origin is given by colour and time depth by symbols.* ***(A)*** *PCA for all samples.* ***(B)*** *Zoom of ancient Anatolia and Iran.*

In addition, early Neolithic Anatolians cluster tightly. These samples, Sub1, Men1 and Men2 are also close to samples from the Chalcolithic and Bronze Age in the Iranian Northwestern province of Azerbaijan (Azer1 and Has1) (Figure 6.2B). A shift in the Bronze Age Anatolian, Ace1, seems to be apparent and clusters with Sac3, from Late Neolithic Northern Iran Semnan Province, and Mon1 from Chalcolithic Monjukli Depe in

Turkmenistan. This group is more closely related to the Early Neolithic and Bronze Age Levantine samples than early Neolithic Anatolians. Iran seems to form three geographical and temporal clusters. The first is comprised of Late Neolithic (Far1, Sac3) and Chalcolithic (Mar1) samples, excluding any of the sites from the Northwestern Province of Azerbaijan (Hasanlu, Kültepe). The latter divides into two clusters, one comprising only Chalcolithic/Bronze Age samples and another of Iron Age (1050-800 BC) and Achaemenid/Seleuco-Parthian Empire (550-275 BC) individuals. A major influx of zebu alleles is observable in the later 300 BC-1300 AD sample from Khorasan (Kho1) in Eastern Iran (Kho1). It clusters with Medieval Iraqi (Bes2), Iron Age and Later Uzbekistan (Kok1, Yer1) as well as showing higher genetic affinity to modern day indicine cattle breeds (Sistani, Brahaman, Gir, Nelore, Sahiwal). Iron Age Iraq (911–609 BC) and Bronze Age Uzbekistan (2000-1700 cal. BC), Bes1 and Bul1, respectively, cluster with modern Eastern Anatolia Red cattle. Post Bronze/Iron Age samples from the same regions (Bes2, Kok1, Yer1) cluster closely to modern day *Bos indicus*.

Medieval (AD 800 - 1000) Georgian samples from the site of Tamara Fort in Kazbegi, cluster together halfway between the Iranian and Anatolian clusters and the modern Turkish cattle breeds (East Anatolian Red). A clear outlier to this cluster is the individual CA317, which is a possible *Bos primigenius* specimen from Tamara fort (AD 651-766), although it cannot be archaeologically confirmed (Marjan Mashkour, personal communication). Finally, the Serbian and Moldovan Neolithics cluster with modern day European taurine breeds, with the exception of Bir1, which shows higher genetic affinity to early Neolithic Near Eastern Anatolians.

6.4.3. ADMIXTURE

The two-population model (K=2) has been shown previously to distinguish between indicine and taurine coefficients and to be able to identify admixed modern cattle breeds and reflecting the predomestication divergence (Bovine HapMap Consortium *et al.* 2009; Park *et al.* 2015). Results are shown separately for ancient (Figures 6.3 and 6.4) and modern cattle (Figure 6.5), although ADMIXTURE was run on both modern and ancient datasets together (Appendix, Tables 9.4.2, 9.4.3., 9.4.4).

Neolithic cattle from the Near East and Europe present a clear dominance of the taurine component and most individuals reported coefficients of 99-100%. Two exceptions are observed in the Moldovan individual Bir3 (86% taurine), which has been suggested to likely represent a *Bos primigenius* individual (Chapter 4); and also the Southern Levantine Thr1 (5100-4300 BC) (92% taurine). During the Chalcolithic and Bronze Ages in the Near East zebu admixture is not typical, with exception of a few samples in the Chalcolithic Southern Levantine Gil1 (c.4300–3300 BC); Early Bronze Age Levantine Nah1 (3300-3050 BC) (Figure 6.4); and the Late Bronze Age Central Asian Bul1 (2000-1700 BC) (Figure 6.3) . It is clear that by the Iron Age zebu admixture has occurred in Mesopotamia (Bes1), Northwestern Iran (Has4) and the Southern Levant. The highest fraction of the indicine component (62%) was observed in the Central Asian Kok1 sample (1500-3000 BC); followed by Southern Levantine animals of similar age from Tel Miqne-Ekron Tmq2 (56%) and Ash4 (55%) from Tel Ashqelon. In fact, most individuals from Iron Age Israel reported an indicine coefficient of ~50% (Figure 6.4). In the Northwestern part of Iran (Hasanlu) a time transect through this archaeological site showed the highest percentage observed for the indicine coefficient was 8% in the Iron Age (Has4). In Post Iron Age Iran, the Eastern Iranian site of Khorasan Kho1 (300 BC-1300 AD) reported a percentage of indicine coefficient of 72%.

Furthermore, modern day Iranian breeds also show a East to West decrease in indicine coefficients (Figure 6.5), with the Southeast breed Sistani being >90% indicine and the Northwest Taleshi being ~50% indicine (Appendix Table 9.4.4).

This Post Iron Age peak of zebu admixture was also observed in Central Asia, the Levant and Iraq, where the indicine component fraction is by then dominant over the taurine component. This was also true for the Iraqi-Kurdistan samples Bes1 and Bes2 from the site Bestanṣur, in which a shift in dominant component from taurine to zebu is observed from the Bronze Age (Bes1) to the Iron Age (Bes2) (Figure 6.3). Bes1 reported 39%, whereas Bes2 reported 73% indicine coefficients.

Finally, the Medieval Ages Southern Caucasus showed some level of admixture ranging from 15-33% indicine component. Moreover, similar fractions of taurine and zebu were observed in modern day breeds from Eastern Anatolia such as East Anatolian Red (Figure 6.5).

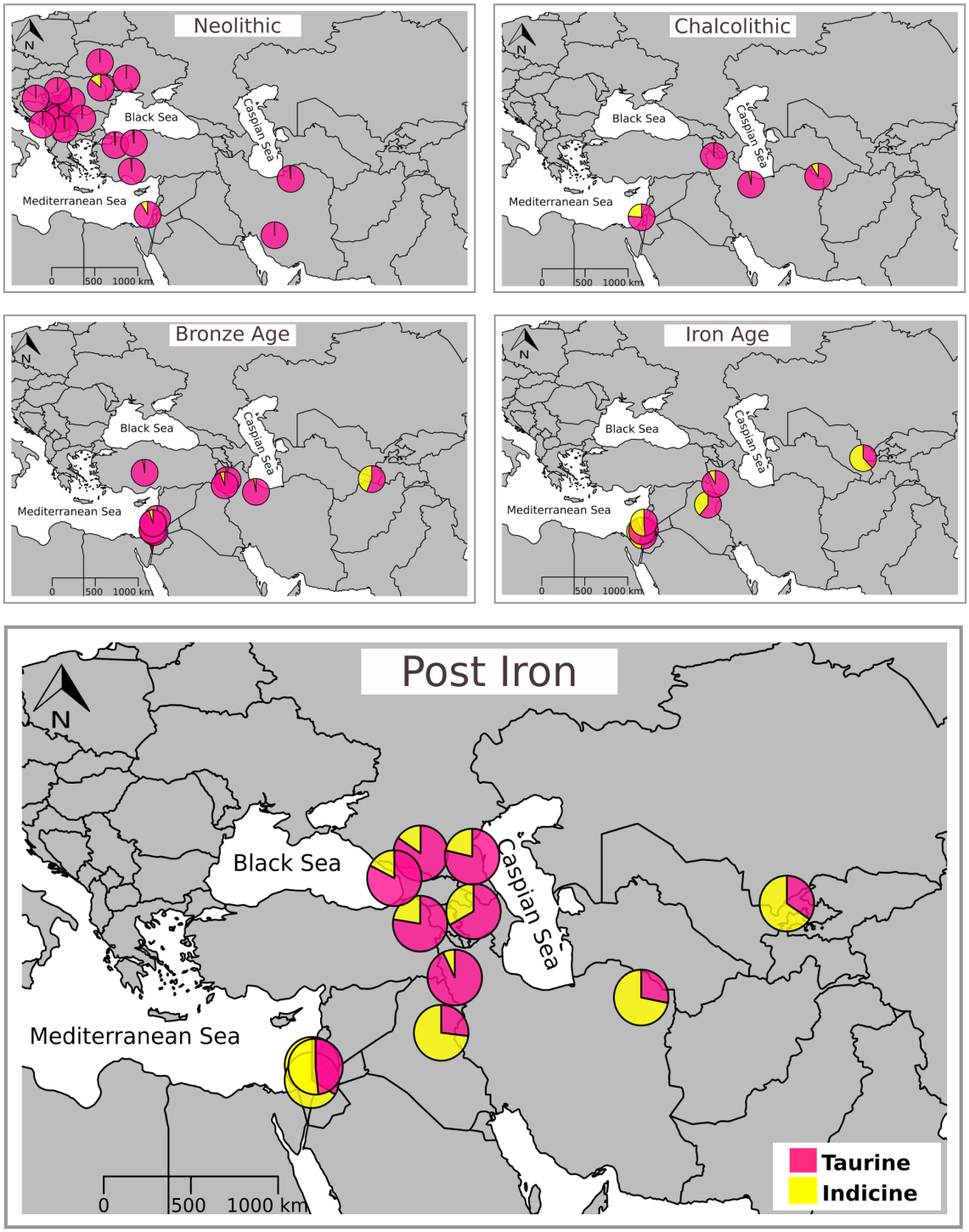


Figure 6.3 - ADMIXTURE maps for ancients only. *Each map showing a different time period and each pie chart representing a single individual from a given archaeological site. Taurine=pink; Indicine=yellow. Samples are grouped by archaeological context for a simpler representation of the data, although BC dates for these will vary between regions. Approximate geographical locations are shown for some cases for easier visualization.*

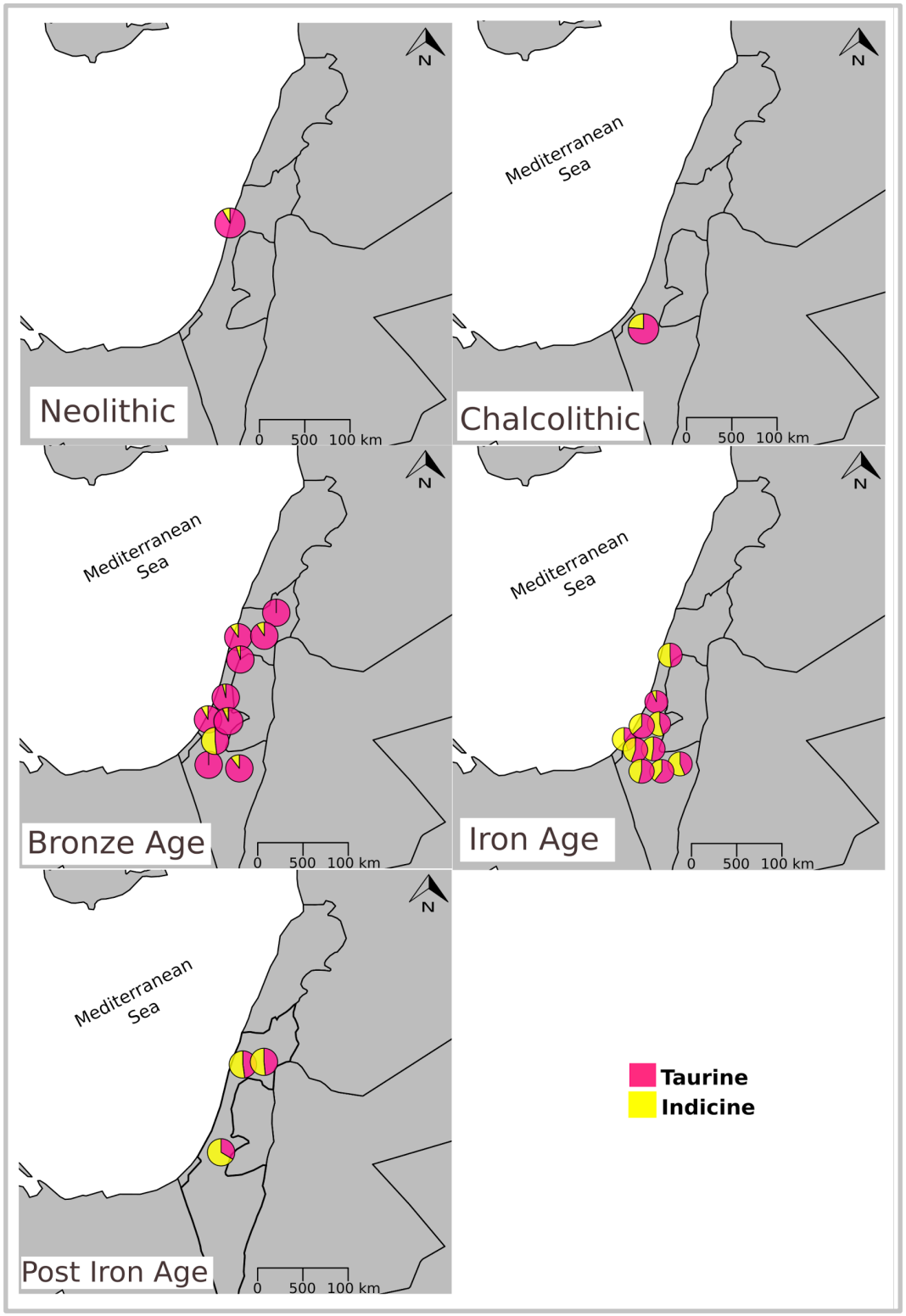


Figure 6.4 - Admixture maps of the Southern Levant. *Each map showing a different time period and each pie chart representing a single individual from a given archaeological site. Taurine=pink; Indicine=yellow. Samples are grouped by archaeological context for a simpler representation of the data, although BC dates for these will vary between regions. Approximate geographical locations are shown for easier visualization.*

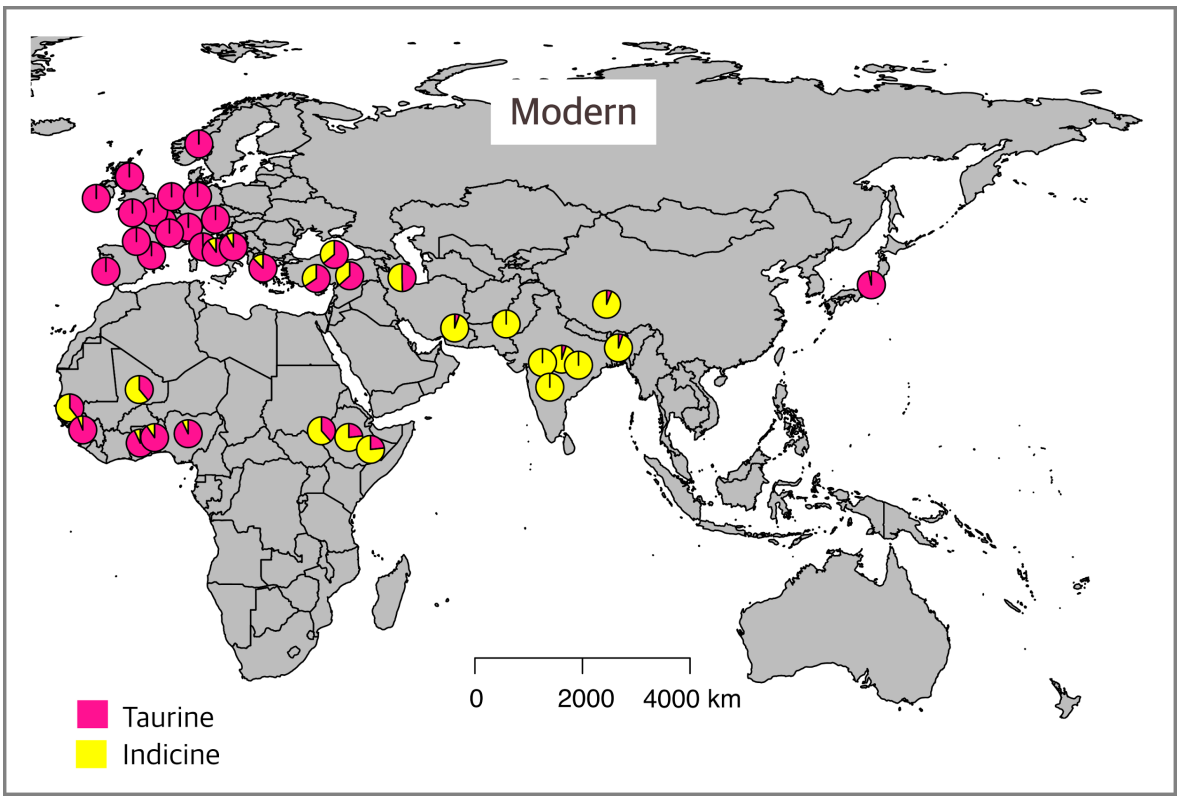


Figure 6.5 - Admixture maps of Modern breeds (K=2). *Modern cattle breeds from the 700K dataset are shown, where each pie chart corresponds to the median value for each component, across a group of individuals belonging to the same breed. Admixture components are represented by colours: Taurine (pink) and indicine (yellow). Individuals are plotted by approximate geographical location to allow for better display of data. Computed values from ADMIXTURE for each breed (median) and for each individual can be found the in Appendix in tables 9.4.3 And 9.4.4.*

6.4.4. D-statistics

The test *D*(((Test,Limousin),Sahiwal),Yak) was computed using the AdmixTools package and the 700K bovine dataset (Figure 6.6; Appendix Table 9.4.5) and *D*(((Highland,Test,Sahiwal),Yak) was computed using ANGSD whole genomes (Figure 6.7; Appendix Table 9.4.6). Due to our modern whole genome dataset not including a Limousin, a Highland was picked for the latter instead. After filtering for poor data based on number of sites as described in the methods, AdmixTools analysis included a 47 out of 67 samples; and ANGSD a total of 67 out of 67 samples.

Early Neolithic Near East (Anatolia, Levant, Iran) and Europe (Serbia and Moldova) reported no gene flow from *Bos indicus*.

Gene flow from *indicus* is not detected until more than ~4000 years after the domestication of *Bos taurus* in the Near East and more than ~2000 years after the domestication of *Bos indicus* in the Indus Valley, with Has3, an Early Bronze Age (2470 cal. BC) individual reported the earliest gene flow using AdmixTools (D=0.0255; Z=3.1) (Figure 6.6) but not with ANGSD (Figure 6.7) (D=-0.0057; Z=-1.20).

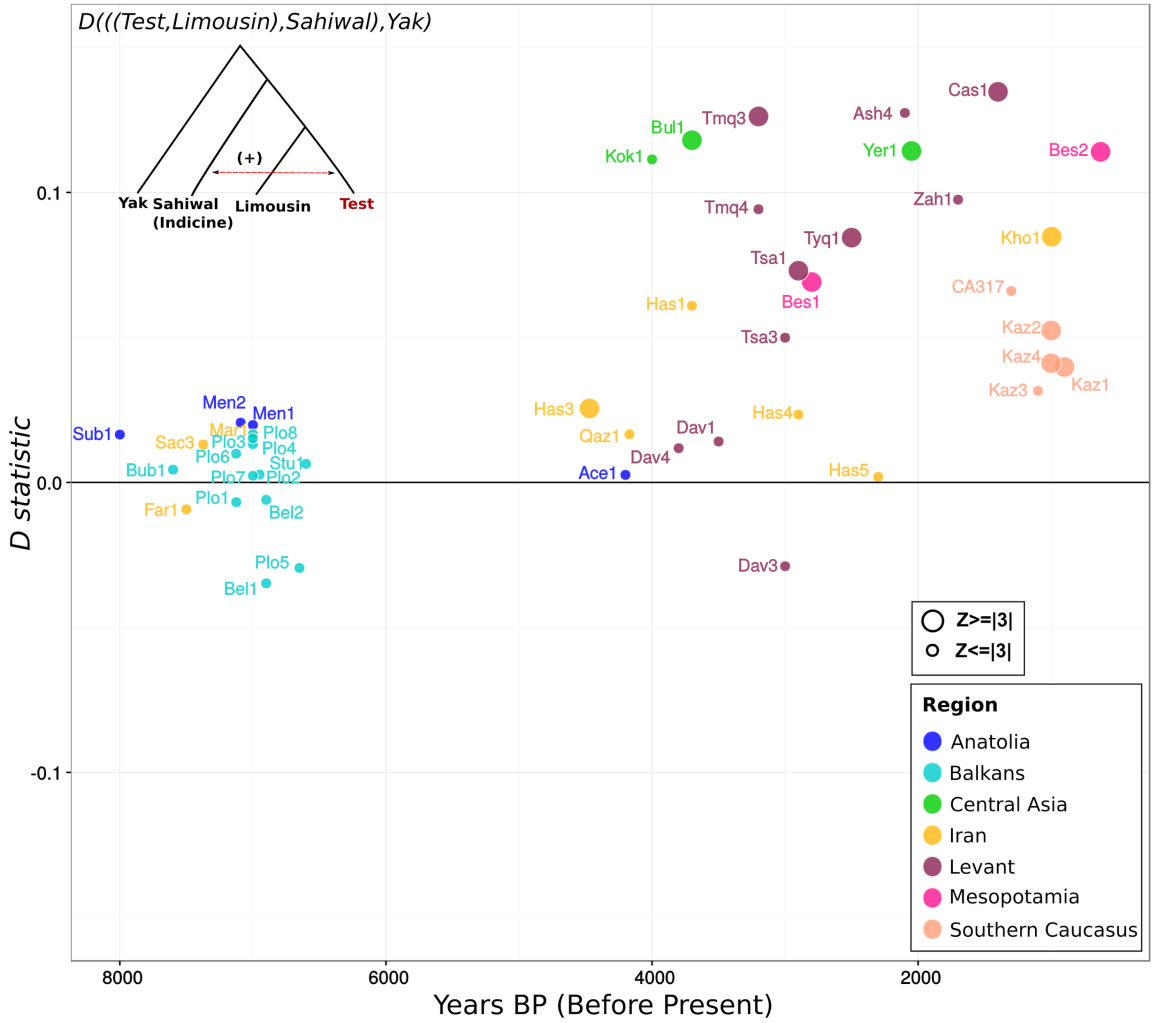


Figure 6.6 - D statistic (((Test,Limousin),Sahiwal),Yak). *Dates BP are approximate for samples that have not been dated. Significant Z scores are shown as smaller circles (non significant Z<=\|3\|) or bigger circles (significant >=\|3\|). Significant negative D value indicates no gene flow between the Test and indicus. Significant positive D value indicates admixture between test and indicus. Zebu admixture is observed in the Near Post Bronze Age.*

Has4 and Has5 also show contrasting results in Z scores between the two methods, which in AdmixTools show nonsignificant D values (D=0.0234, Z=2.9; D=0.0019, Z=0.059; respectively). This contrasts with ANGSD, where significant D values

for zebu admixture were reported for Has4 (D=0.04, Z=6.8) and for Has5 (D=0.04, Z=4.1).Nevertheless, both methods a clear shift after ~2000 BC is observed in which there is a significant influx of zebu, reported by significant positive D statistics for Central Asia and the Near East (Levant, Iraq, Iran and Georgia).

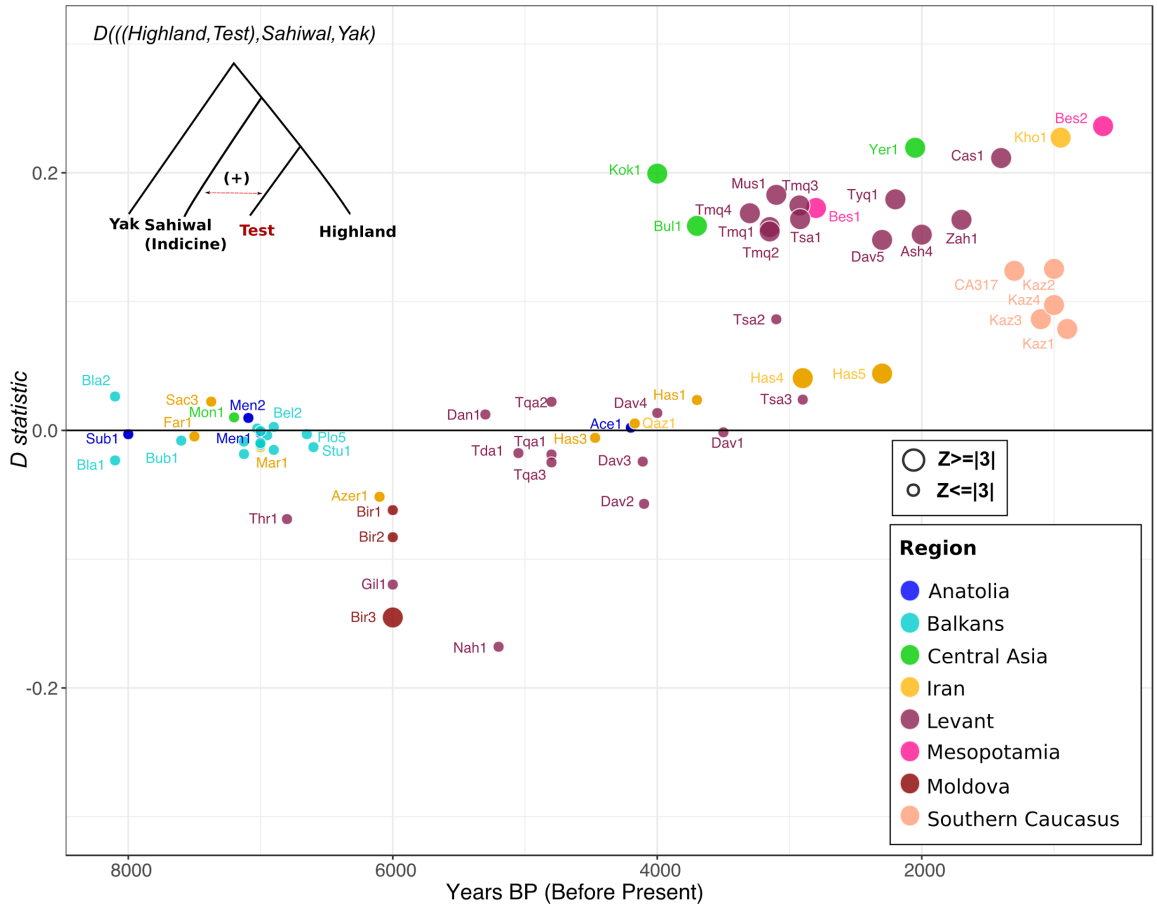


Figure 6.7 - D statistic (((Highland,Test,Sahiwal),Yak) ANGSD. *Each represent a single individual's genome and not a population. Dates BP are approximate for samples that have not been dated. Significant Z scores are shown as smaller circles (non significant Z<=|3|) or bigger circles (significant >=|3|). Significant negative D value indicates no gene flow between the Test and indicus. Significant positive D value indicates admixture between test and indicus. Zebu admixture is observed from the Iron Age until Medieval times in the Near East.*

6.4.5. f_3-statistic - three-population test

To further test admixture a f_3-statistic was computed based on the tree shown in Figure 6.8. f_3-statistics are expected to present a negative score if the Target population is the result of an admixture between the two source populations (Table 6.5). Significant negative f_3 mean values for both Iron Age (F_3=-0.08, Z=-31) and Post Iron Age (F_3=-0.11, Z=-49) Near Eastern populations were observed; as well as for Central Asia population (Uzbekistan and Turkmenistan) (F_3=-0.13, Z=-6) (Figure 6.9).

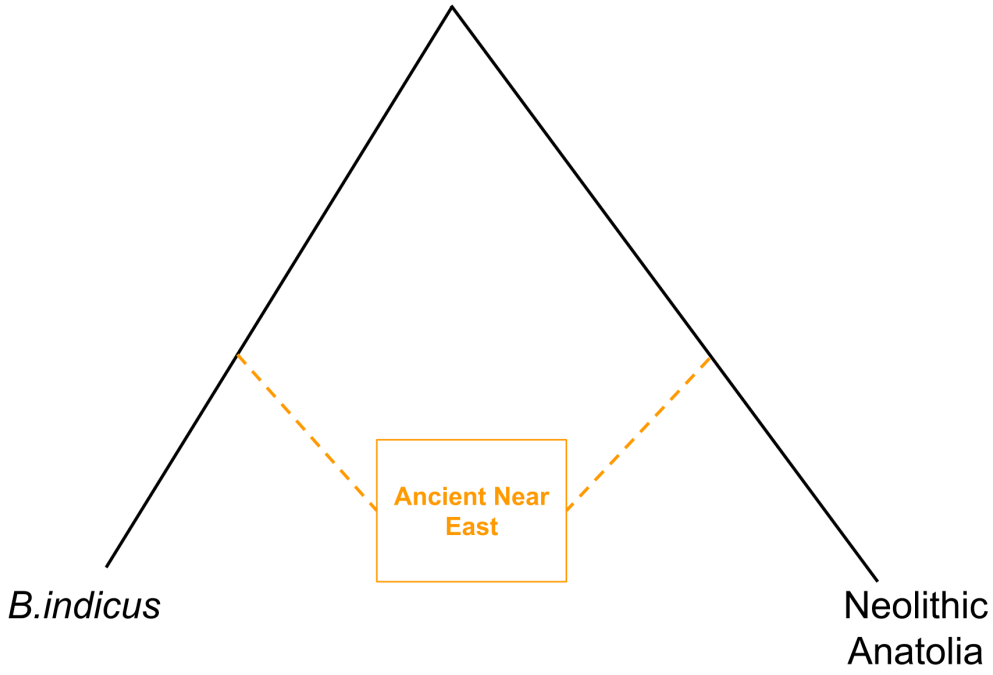


Figure 6.8 - f_3-statistic phylogenetic tree. *Showing the proposed f_3-statistic test for ancient admixture. Ancient Near Eastern (Target) individuals formed by admixture between Bos indicus (Source 1) and Bos taurus early domestics (Neolithic Anatolia- Source 2).*

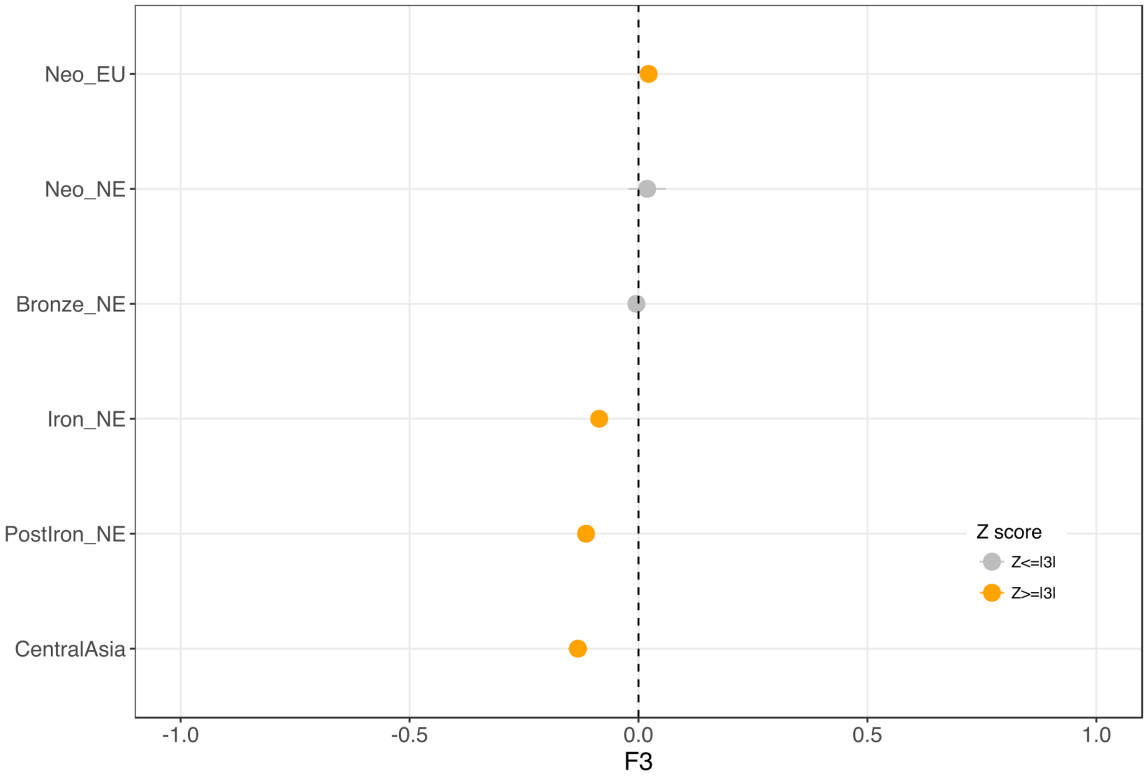


Figure 6.9 - f_3-statistic for ancient cattle populations. *Neo_EU: Neolithic European Bos taurus (including Serbia and Moldova); Neo_NE: Neolithic Near East (including Levant, Iran, excluding Anatolia); Bronze_NE: Bronze Age Near East (including Anatolia, Iran, Levant); Iron_NE: Iron Age Near East (including Levant, Iraq, Iran); PostIron_NE: Post Iron Age Near East (including Iraq, Georgia, Levant, Iran); Central Asia: Chalcolithic,Iron and Post Iron (Uzbekistan and Turkmenistan). F3 with negative mean confirms Target population as a mixture of Early Neolithic Anatolia and Bos indicus. If F3 yields a non-negative mean we consider the Target population to be non-admixed.*

Table 6.5 - f_3-statistic values for Figure 6.9. *F_3-statistic with negative mean confirms Target population as a mixture of Early Neolithic Anatolia and Bos indicus. If F_3 yields a non-negative mean we consider the Target population to be non-admixed. Source population Sahiwal was comprised of a total of 10 individuals; Source population Neolithic Anatolia comprised a total of 3 individuals.*

Source1	Source2	Target	Number Individuals/ Population	F_3	Standard Error	Z
SAH	Neolithic Anatolia	**Neo EU**	17	0.02	0.00	8.52
SAH	Neolithic Anatolia	**Neo NE**	4	0.02	0.04	0.47
SAH	Neolithic Anatolia	**Bronze NE**	16	0.00	0.00	-1.95
SAH	Neolithic Anatolia	**Iron NE**	11	-0.09	0.00	-31.36
SAH	Neolithic Anatolia	**Post Iron NE**	12	-0.11	0.00	-49.06
SAH	Neolithic Anatolia	**Central Asia**	4	-0.13	0.02	-6.29

6.4.6. F4-ratio

F4-ratios were computed in order to estimate the admixture proportions of *Bos indicus* (Sahiwal) into Near Eastern ancient individuals (Figure 6.10). Admixture proportions of Neolithic Near East and Europe were observed to be very low and nonsignificant.

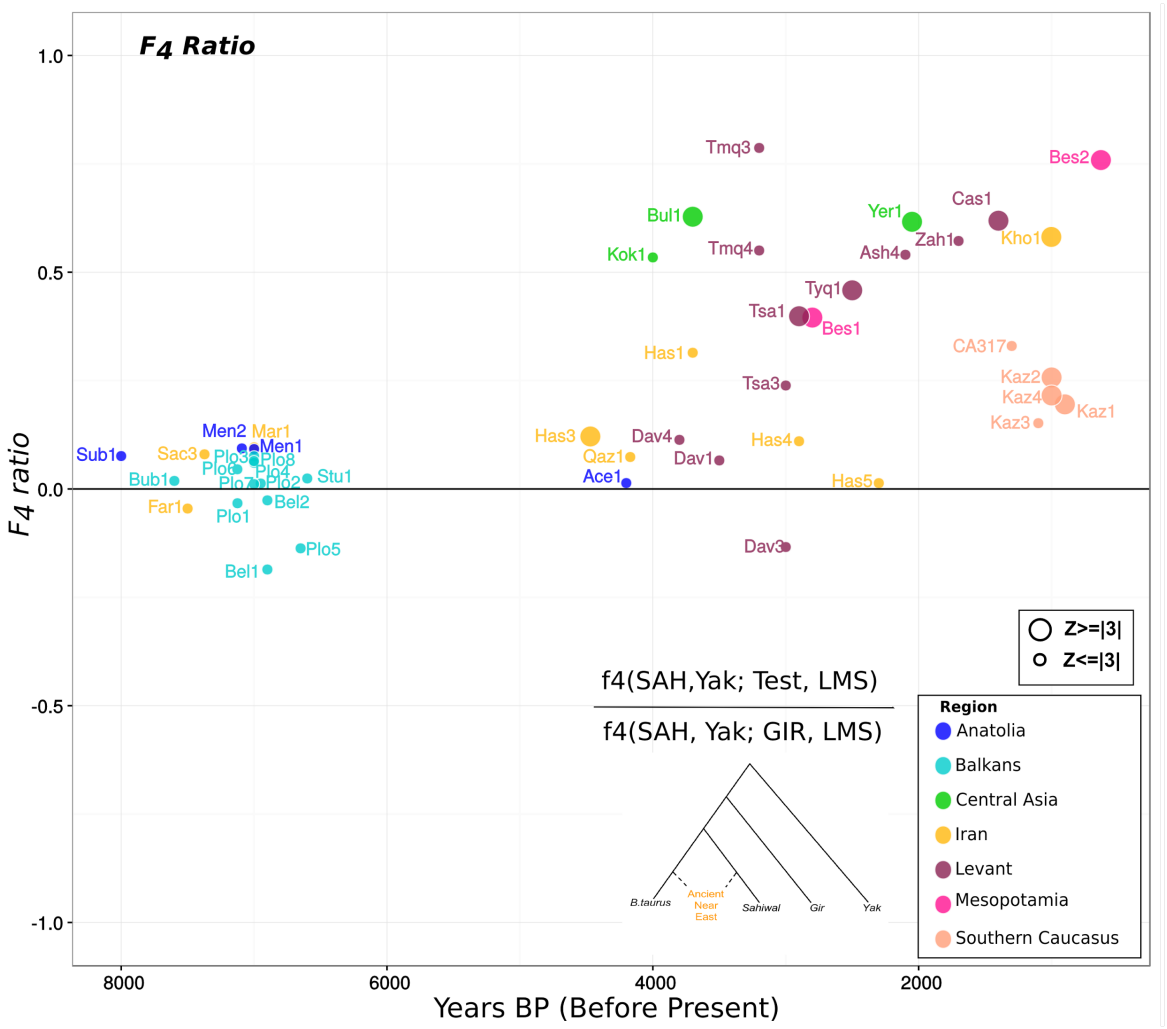


Figure 6.10 - F4-ratios. f4(SAH,Yak; ancient, LMS)/(SAH,Yak; Gir,LMS). *Dates BP are approximate for samples that have not been dated. Significant Z scores are shown as smaller circles (non significant Z<=|3|) or bigger circles (significant >=|3|). Samples are coloured by region of origin.*

These results showed an increase in admixture proportions from the Late Bronze Age onwards in Central Asia and the Near East. Moreover, an increasing in the admixture proportions of zebu was observed, with a series of samples showing a majority of indicine ancestry, like for example from the Medieval (1292-1399 cal. AD) Iraqi-Kurdistan sample Bes2 (F_4=0.75; Z=18), the Eastern Iranian Kho1 (300 BC- AD 1300) (F_4=0.58; Z=7.3) and the Byzantine (324-638 AD) Southern Levantine Cas1 (F_4=0.62; Z=6.3).

6.4.7. Mitochondrial diversity

The Near East is dominated by a diversity of taurine mitochondrial haplogroups (Q,T) from the Neolithic until after the Iron Age (Figure 6.11). T3 seemed to dominate in ancient European cattle followed by Q and T2; similar to Neolithic Anatolia. Q was present at higher frequencies in Neolithic Iran and haplogroup T2 seemed to dominate during the Bronze Age, in Anatolia, Iran and Central Asia. The Southern Levant is dominated by the T1 haplogroup from the Neolithic until the Iron Age, where more mitochondrial taurine diversity is observed, with the appearance of Q, T2 and T3. Only one indicine haplotype is observed in an individual from Khorasan Eastern Iran from the Parthian/Islamic empire (Kho1) (Figures 9.11 and 9.12). The Near East was still dominated by taurine matrilines in the Post Iron age, with the dominance of T3 sub-haplogroup in Georgia, Iran and Central Asia (Figure 6.11). The Post Iron Age Southern Levant seemed to still show greater mitochondrial diversity than the rest of the Near East.

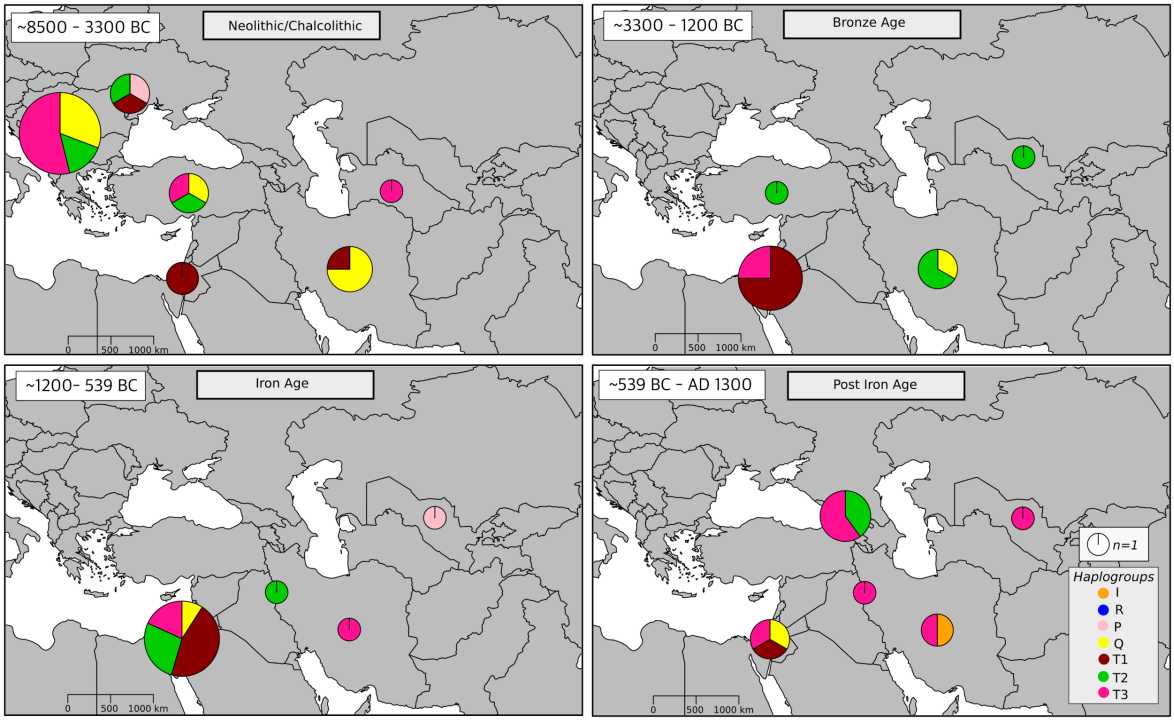


Figure 6.11. Mitochondrial diversity of the ancient Near East through time and space. *Sizes of pie charts reflect number of ancient samples and colours reflect haplogroup assignments. Samples for which haplogroup was uncertain, were not included. Near East clearly dominated by taurine matrilines for more than 8000 years, with the single I haplogroup individual reported in the Post Iron age. List of mitochondrial haplogroups for each individual can be found in Appendix Table 9.1.5.*

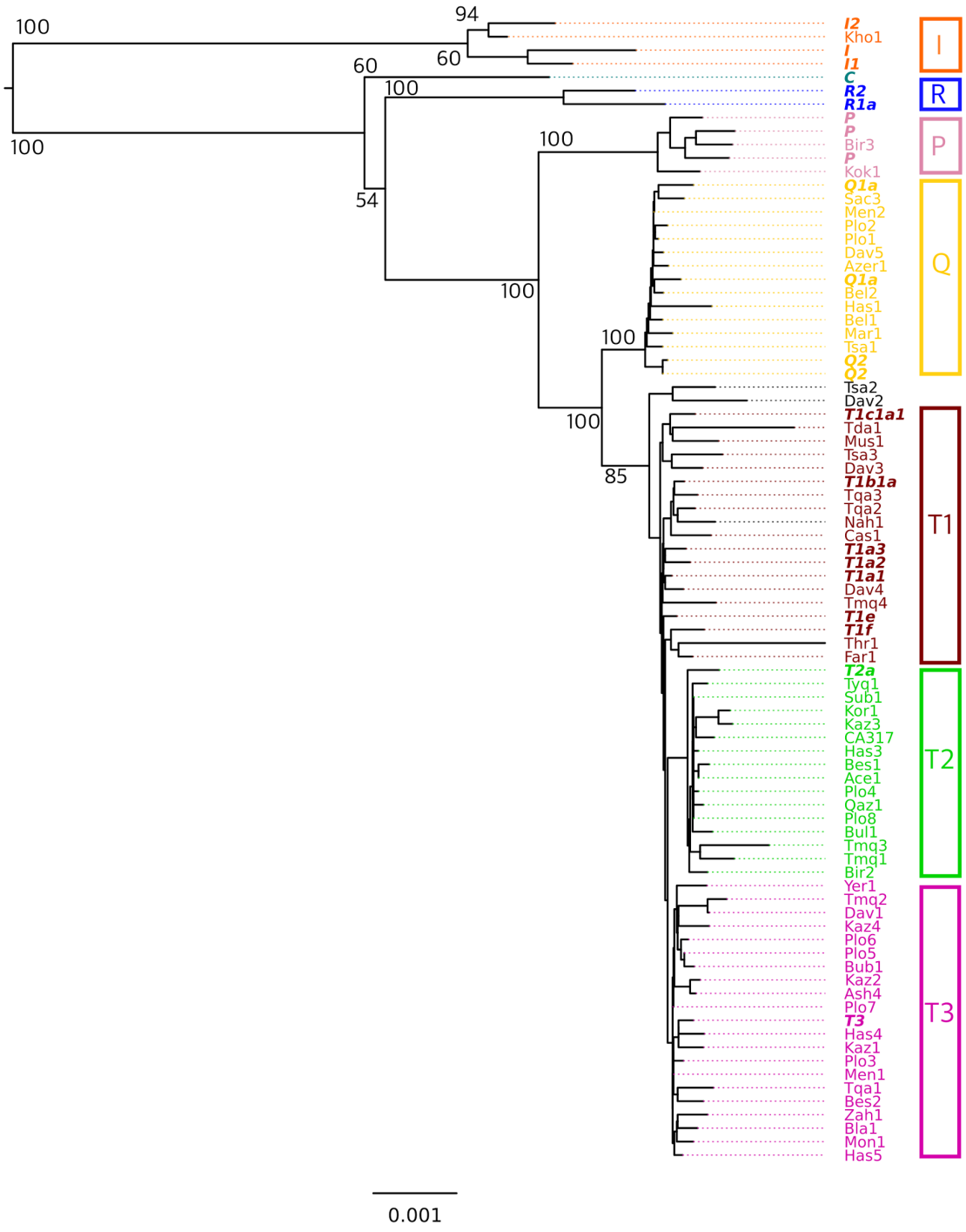


Figure 6.12- Mitochondrial phylogeny of the ancient Near East. *Modern samples are shown in bold and italic. Each colour representing a different haplogroup or sub-haplogroup. Clear higher frequency of taurine matrilines is shown in the Near East, with only one ancient Iranian sample carrying an indicine matriline (Kho1), with dominance of T1 from the Neolithic until the Iron age. Boostrap values are only shown for the macrohaplogroups of taurine and indicine cattle.*

6.4.8. Y chromosome phylogeny

Only four ancient Near Eastern domestic Y chromosomes retrieved enough data for producing a phylogeny. Three revealed a typical taurine Y chromosome: the Early Neolithic Anatolian Sub1, the Early Bronze Age Has3 and the Iron Age Has4 from Hasanlu in Northwestern Iran. These seemed to cluster within the taurine Y haplogroup Y2. Only one individual revealed to have an indicine Y chromosome (Bes2), clustering with *Bos indicus* individuals and belonging to the Y3 haplogroup (Figure 6.13).

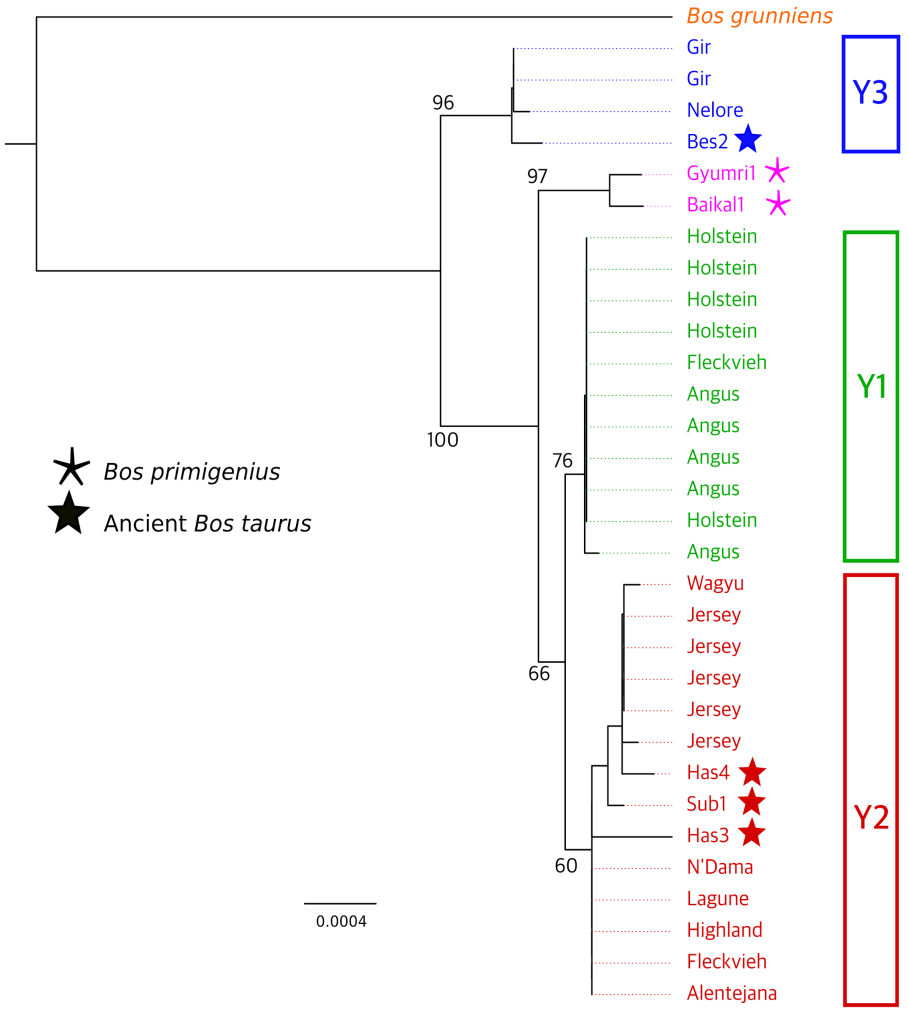


Figure 6.13 - Y chromosome Neighbour-joining tree. *Based on multiple alignment of 10904 base pairs of the MSY1 region of the bovine Y chromosome and 160 SNPs. Stars indicate ancient individuals. Haplogroups defined on previous knowledge from frequency of each haplogroup in modern cattle breeds (Gotherstrom et al. 2005; Edwards et al. 2011). Showing three Near Eastern ancient belonging to Y2 and only one ancient carrying a Y3 (indicine) haplotype from Medieval Iraq-Kurdistan.*

6.5. Discussion

6.5.1. Zebu admixture in the Near East

Cattle genetic studies on extant cattle have previously shown, using a survey of nuclear microsatellite data, that Near Eastern breeds carry indicine alleles at relatively high frequencies (Loftus *et al.* 1999), which support a secondary introgression of zebu cattle into the Near East. Moreover, a west to east increase in admixture has been reported (Loftus *et al.* 1999; Edwards, Baird, *et al.* 2007; Karimi *et al.* 2016).

In this ancient Near Eastern dataset a striking introduction of zebu cattle in the Late Bronze Age/Early Iron age was observed. One remarkable example is the Southern Levant. From the Early Neolithic until the Late Bronze Age, individuals showed greater genetic affinity to modern African taurine breeds in PCA analysis. In Chapter 5 it was possible to confirm gene flow from an African aurochs (Th7) into a Bronze Age individual from the Southern Levant (Dav1), which likely explains this clustering. Moreover, the majority of Southern Levant until the Late Bronze Age/Iron Age (~1400-1200 BC) showed very small indicine component fractions in ADMIXTURE and no significant gene flow was observed using *D*-statistics. Two exceptions, the Levantine Chalcolithic and Early Bronze age samples, Gil1 and Nah1, showed a higher fraction of the zebu component in ADMIXTURE analysis. There could be several possible reasons for this discrepancy. First, that the dating of these samples is not correct and they belong to a later archaeological context and are truly indicine admixed individuals. Second, the relatively higher zebu fraction could be an indication of these individuals either being *Bos primigenius* from the Levant or admixed with wild bovine. The latter seem to be the most plausible scenarios since *D* and F_4-ratio did not support gene flow from *Bos indicus*.

A major influx of zebu alleles was observed in the Iron Age, when ancient Levantine individuals in PCA analysis cluster closely to modern day breeds from the Near East (South Anatolian Red, East Anatolian Red) and Post Iron Age individuals cluster closely to modern day Iranian breeds (Taleshi). Considering that these modern

breeds are known to have been admixed with zebu, it strongly suggested the presence of zebu alleles in these ancients (Loftus *et al.* 1999; Freeman *et al.* 2005; Edwards, Baird, *et al.* 2007; Karimi *et al.* 2016) and gene flow was suggested by ADMIXTURE analysis and formally tested using *D*-statistics and f_3-statistics. This is consistent with LD decay estimates that have proposed an older admixture event for Near Eastern populations in comparison to North Africa (Freeman *et al.* 2005).

The same was observed for other regions of the Near East such as Anatolia, Iran, Iraq and Georgia, and also for Central Asia (Turkmenistan and Uzbekistan). In all of these regions, although a complete transect through time was not available, it is clear that *taurus* and *indicus* admixture has happened and it is observable in the Iron age at significantly high proportions. f_3-statistics have also clearly demonstrated this major influx, where the Bronze Age Near East population showed no support for being admixed, in contrast to Iron Age and Post Iron age Near Eastern populations.

In ancient Anatolia a shift in the Bronze Age site of Acemhöyük is apparent with Ace1 clustering in the PCA, away from Neolithic Anatolia, with Far1 and Qaz1, Late Neolithic Southwest Iran and Bronze Age Northern Iran, respectively. Acemhöyük in the Early Bronze Age was a major urban centre, where cattle were present at higher frequency (Arbuckle 2012b; Arbuckle 2014), and this clustering with these Iranian individuals could represent an import from Iran or an admixed individual due to the trade connections between Mesopotamia and Central Anatolia involving the old Assyrian colonies (Podany 2013; Cunliffe 2015).

In ancient Iran, a less pronounced influx of zebu alleles was observed in the Northwestern region of Azerbaijan (Hasanlu); however significant gene flow was still detected for Iron and Post Iron age individuals. Therefore, the modern structure for Iranian breeds (Karimi *et al.* 2016) seems to be a legacy from past population movement and introgression events, and perhaps reflecting improvement of cattle to the different climates in Iran, where taurine breeds would thrive in more temperate/cold and humid

northeastern regions and indicine would be more well adapted to the western arid parts of the country (Matthews 2002; Yousefi *et al.* 2017). However, there are some discrepancies in the *D*-statistics for a few ancient Iranian samples. The most striking, Has3 from Hasanlu Bronze Age Northwest Iran (2700-2200 BC) sits halfway between the Early Neolithic Anatolian cluster and the Late Neolithic Iran/Central Asia/Bronze Age Anatolia cluster in the PCA. Admixture was not suggested by PCA or ADMIXTURE analysis for this individual, however, gene flow from *indicus* was detected in the AdmixTools computation of *D*, which contrasted with the ANGSD result. Given that the first *D* result is inconsistent with the rest of the genetic evidence of no admixture, it is probable that this is a spurious signal, considering that this individual previously reported significant gene flow from an Armenian aurochs (Figure 5.11). These same issues also apply to the F_4-ratio computations and ANGSD whole genome calculations seemed to have produced the results that are most consistent with the rest of the analyses.

Furthermore, a geographical cline from east to west in increasing ADMIXTURE fractions of zebu and admixture proportions was also observed, which is in agreement with previous research on modern day Near Eastern cattle breeds (Loftus *et al.* 1999; A. R. Freeman *et al.* 2006; Edwards, Baird, *et al.* 2007; Karimi *et al.* 2016). Bes2, the Medieval specimen from the site of Bestanşur (Iraq-Kurdistan) is the ancient individual left-most on the PCA and highest F_4-ratio, suggesting its high genetic affinity with modern day indicine breeds and thus, this suggests a high level of admixture. It had a taurine mitochondrial genome (T3) with an indicine Y haplogroup (Y3). Therefore, there is no doubt this presents a highly admixed individual. This implies a dramatic shift in Mesopotamian zebu admixture from the Iron Age (Bes1) to Medieval Ages (Bes2). This contrasts with modern day Kurdish breeds, which are still admixed but predominantly taurine, which suggests a later secondary introgression of taurine in more recent times (Loftus *et al.* 1999; Freeman *et al.* 2005; Edwards, Baird, *et al.* 2007). This site is very close to the Iranian border and sitting on the piedmont of the Zagros Mountains and would have

been an important passage for trade into the Iranian highlands. Moreover, the main road of the modern village of Bestanşur is still connected to one of the main trade routes in the present day (Elliott *et al.* 2015). It has been proposed that the spread of zebu during the Bronze Age in the Near East was a result of climatic changes, particularly three major aridification phases occurring around 3000, 2200 and 1300 BC. The semi-arid environment of Iraqi-Kurdistan would have favoured zebu adaptation to such climates (Matthews 2002; Elliott *et al.* 2015).

In conclusion, Early Neolithic Anatolia, Levant, Iran and Europe (Balkans, Moldova) report no gene flow from *Bos indicus*, which is consistent with a separate domestication centre for zebu that then spread to Western Asia at a later point in time (Loftus, MacHugh, Bradley, *et al.* 1994; Loftus *et al.* 1999; Matthews 2002; Chen *et al.* 2010; Felius *et al.* 2014). The time for the zebu introduction into the Near East likely precedes the Iron Age and was perhaps a result of expansion of civilizations in Mesopotamia. With this came hierarchical societies that contributed to an expansion of trade of luxury goods, as well as raw materials, such a copper, tin and gold, across Mesopotamia with extensive trade routes connecting to the Indus Valley Civilization (Matthews 2002; Podany 2013; Cunliffe 2015). Moreover, sites that have been associated with trade like Bestanşur (Iraq-Kurdistan), or particularly important sites for raw materials like Nishapur Qohandez (Khorasan, Iran) for its turquoise stones, have shown the highest admixture proportions (Bes2, Kho1) (Meadow 1993; Cunliffe 2015). Furthermore, in this ancient dataset zebu admixture proportions seem to increase with time from the Bronze Age onwards and they also seem to increase in a East-West South-North fashion and thus, the transport of indicine cattle from the Eastern Indus civilization to these major centres of commerce in the Near East would have likely involved many animals and span thousands of years with Western and East Asia connections maintained from the Bronze Age, through the Roman empire, the Arab conquests and the Mongol conquests (Loftus *et al.* 1999; Cunliffe 2015).

6.5.2. Uniparental genetic variation and sex-biased gene flow

Regarding mitochondrial variation in the Near East, it is worth mentioning the high frequency of T1 haplogroup in Southern Levant for at least ~6000 years, since the Pottery Neolithic (Thr1) up until the Byzantine Empire (Cas1). A recent study has suggested that T1 frequency in the Southern Levant increases from the Late Bronze Age to the Iron Age (Meiri *et al.* 2017). However, this study lacked data from Neolithic/Chalcolithic and Early to Middle Bronze Age. In contrast, high frequency of T1 since the Neolithic, through the Early Bronze Age, up until the Post Iron Age was observed. An increase in mtDNA haplotype variation is detected in the transition from the Bronze Age to the Iron Age, which could also be linked to trade among Iron Age Near Eastern states such as the Anatolian Hittites, Egypt, Elam, Babylonia, Assyria and Mitanni; or the later Neo-Assyrian Empire (c.900-612 BC) (Cunliffe 2015).

No *indicus* typical mtDNA haplogroups were observed in the Near East until 300 BC - AD 1300, in a single sample from Khorasan in Northeastern Iran (Kho1) belonging to the I2 clade, which has been reported in extant cattle from the Near East but it is most common across South Asia (Magee *et al.* 2007; Chen *et al.* 2010; Magee *et al.* 2014). Due to the significant lower coverage of genomes generated, the Y chromosome was not retrievable for most male samples. However, comparisons between different geographical and temporal points across the Near East, with different amounts of introgression were possible. The four ancient Near Eastern samples tested presented a majority of taurine Y2 haplotypes, even for the admixed sample Has4, from the Iron Age, in Hasanlu Northwestern Iran. Only one indicine Y3 haplotype was observed out of two significantly admixed samples, Bes2 from Medieval Iraq, which also carries a taurine matriline. In conclusion, admixture of zebu and taurine cattle in the Near East does not seem to be female mediated, as taurine matrilines dominated the ancient dataset. However, we cannot completely reject the hypothesis of a male-mediated gene flow.

6.5.3 The use of low coverage ancient data to answer past population questions

This chapter demonstrated the power of low coverage ancient DNA to pick up signals of ancient admixture in very poorly preserved samples. Using projection procrustes PCA methods all samples were useful in the analysis. However, it is important to mention that very low coverage samples can produce dubious results. One such example is the the Bronze Age (3500-3000 BC) sample Dan1, from the Southern Levant site of Tel Dan in Upper Galilee. This sample's placement on the PCA did not fit with contemporaneous ancients from the Southern Levant. Moreover, its coverage is the lowest presented in this thesis (0.0002x) and yielded only 127 loci for projection and a procrustes similarity value of 0.85. The latter reflects how well a sample is projected onto the reference dataset, *i.e.* a measure of accuracy (Wang *et al.* 2015). For Dan1 this value is remarkably lower than the rest, even when compared to samples of similar coverage (Gil1 and Nah1).

To conclude, inclusion of low coverage data from poorly preserved specimens has increased the ancient dataset seventeen-fold. It is however important to consider that this might not be applicable to more fine-tuned questions and that results should always be validated and reproducible with different methods.

6.5.4. Conclusion and future directions

The most obvious gap in this ancient dataset is temporal, since the majority of regions did not comprise a good time transect. Also, there are still many areas that have not yet been well sampled, for example the southern regions of Iran. Furthermore, some discrepancies between methods used for *D*-statistics and F_4-ratios have demonstrated that genomic coverage and choice of modern animals to perform such tests of admixture can influence results. Nevertheless, the power of low coverage ancient DNA for determining the first spread of zebu from the East into the Near East has been demonstrated. Such introduction likely occurred during the Late Bronze Age and Iron Age transition as a

result of well established trade routes across the Near East, likely involving the movement of significant numbers of animals and spanning thousands of years. It is unclear, however, whether the obvious preference for taurine-zebu crossbreds were due to cultural, socioeconomic, religious or climatic changes (Loftus *et al.* 1999; Matthews 2002; Edwards, Baird, *et al.* 2007). More time depth is thus necessary at these ancient sites in order to perhaps understand if there were several waves of of zebu introduction or if it was a continuing process over several millennia.

7. Conclusion. aDNA: a reservoir for past population events and genetic diversity

7.1. Introduction

This chapter summarizes the main findings in this thesis and tries to pinpoint key gaps in the current knowledge as well as discussing future analyses.

7.1.1. Ancient DNA preservation and Latitude

The aDNA field has taken great leaps into generating larger amounts of data with: decreasing sequencing costs; higher retrieval of nuclear DNA molecules with the discovery of the *pars petrosa* as an extraordinary source for ancient molecules; and the implementation of better extraction techniques as well as aDNA-targeted computational pipelines (Stoneking & Krause 2011; Gamba *et al.* 2014). It is generally accepted that ancient remains from higher latitudes will have a higher chance of containing higher percentages of endogenous DNA, in comparison to temperate and tropical climates (O'Connor 2008; Campos *et al.* 2012). Given the ancient sample size (122) for this thesis and the broad geographical and temporal context, it presents a unique opportunity to test this assumption. Regression analysis on percentage of endogenous DNA versus latitude agrees with this premise, however it did not fully explained the variation observed in the data. We conclude that DNA content, although having higher chances of better preservation in samples from higher latitudes, also might depend on specimens age, pre-sampling treatments done at excavation sites, as well as handling and storing of samples thereafter, for example. Future analyses, could involve regression analyses incorporating time and bone element (petrous versus long bone/teeth).

7.1.2. A Near Eastern origin for Bos taurus

Genome wide analyses from ancient cattle from the Near East have revealed a complete dominance of the mtDNA QT clade, with clear higher frequency of the macro-haplogroup T, supporting previous studies (Troy *et al.* 2001; Achilli *et al.* 2009) for a Near Eastern origin of these two haplogroups. Furthermore, ancient European cattle showed a higher frequency of T3 haplogroup in Central and Northern Europeans, while ancient Neolithic Balkanic animals resembled mtDNA diversity present in Anatolia, which is in agreement with what is observed in extant cattle from Southern Europe (Achilli *et al.* 2009; Scheu *et al.* 2015). The I and Y3 haplogroups, characteristic of zebu cattle, in mtDNA and Y chromosomes were also completely absent in ancient individuals from the Neolithic Near East and Europe. Moroever, the mtDNA and Y chromosome phylogenies showed a deep bifurcation in the two main domestic taxa, which further supports the centre of domestication of *Bos taurus* to be separate from *Bos indicus*. Furthermore, genomewide data analyses, on the 700K SNP dataset, revealed a stepping-stone clustering of ancient cattle with a south to north cline in ancient Europeans, which mimics the genetic variation of modern European cattle (Figure 7.1).

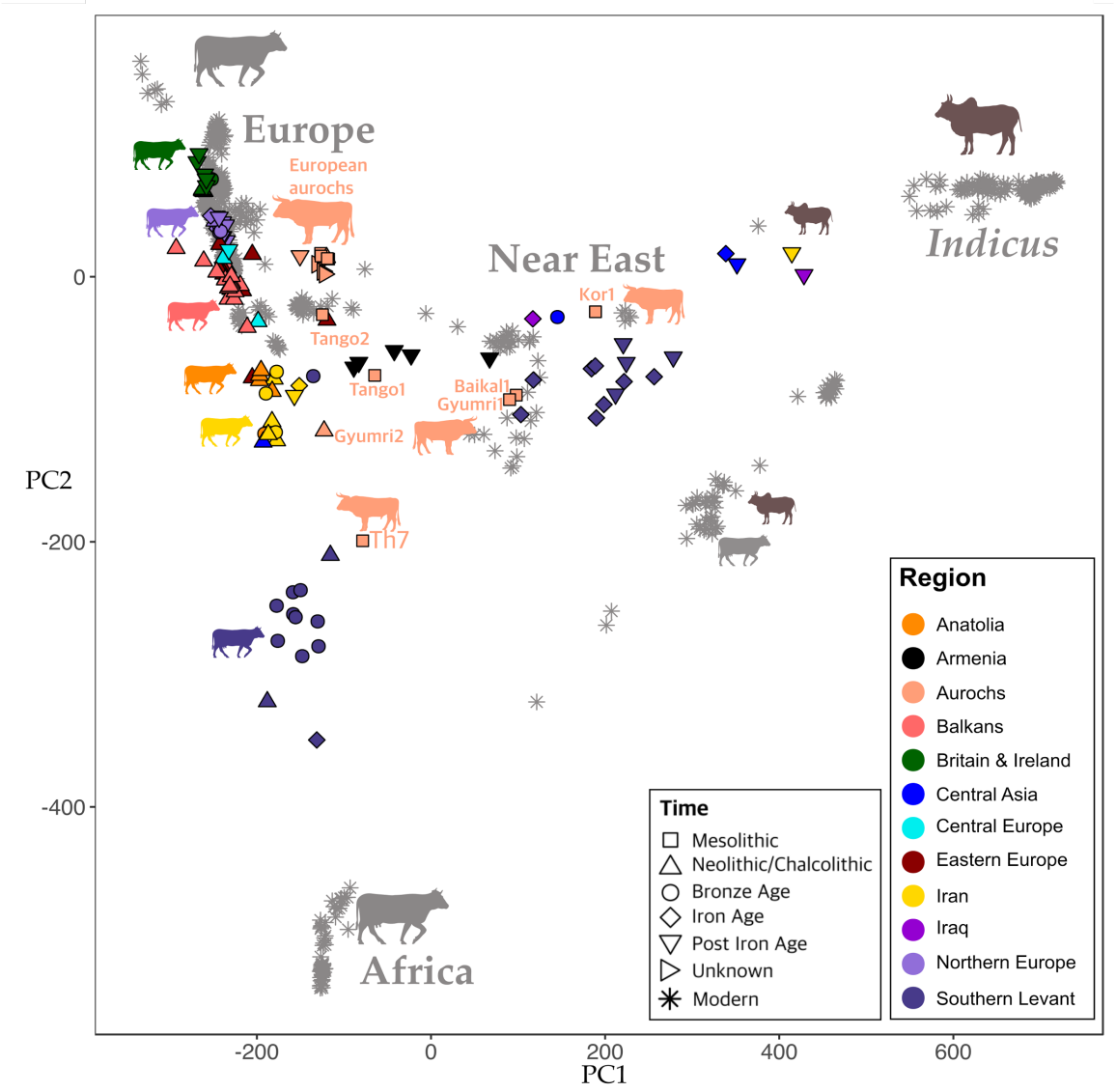


Figure 7.1 - PCA of all ancient samples. *Ancient samples projected on 700K background introduced in Chapter 4. Time is given by symbols and region by colours. PC1 separating Bos taurus from Bos indicus individuals and PC2 separating African Bos taurus and European Bos taurus.*

7.1.3. Local aurochs contribution to the ancient domestic genetic pool in different continents

Previous genetics studies have suggested that introgression between wild cattle and early domestics could have happened in North Africa (Bradley *et al.* 1996; MacHugh *et al.* 1997) and in Europe (Gotherstrom *et al.* 2005; Achilli *et al.* 2009; Park *et al.* 2015;

Upadhyay *et al.* 2017). It was shown by *D* statistics that European aurochs have significantly contributed with gene flow to early ancient domestics from Europe from as early as early as ~5000 BC the Balkan Peninsula, just 1000 years after the introduction of domestics from the Near East (Tresset & Vigne 2011). This seems to have continued to occur for thousands of years and gene flow seems to have been consistent in northern and central Europe (Britain, Ireland, Netherlands, Germany) from the Neolithic to Roman times. Evidence for gene flow was also reported from an Asian population of aurochs genetically similar to the Late Pleistocene Southern Siberian and Armenian aurochs (Baikal1, Gyumri1) into early domestics from the Near East, along the Turkish-Iranian plateau, as early as ~5500 BC in southwestern Iran until the Bronze Age in Anatolia. However, more data from these regions is needed to confirm the extent of this contribution. Finally, a North African aurochs is presented here for the first time in the context of other *primigenius* and ancient domestics. This revealed gene flow from a population of African aurochs into Middle Bronze Age Southern Levantine ancient domestic cattle. PCA (Figure 7.1) and ADMIXTURE analyses supported gene flow to have occurred prior to that, although insufficient data in earlier samples has hindered *D* statistic analyses for the time being.

7.1.4. Genetic diversity of wild aurochs

Five Asian aurochs, from Armenia, Anatolia and Southern Russia have exposed the diverse genetic variation present in wild aurochs prior to their domestication. They have revealed two novel mitochondrial haplogroups in Near Eastern aurochs: V in Gyumri1 and G in Gyumri2; and a novel Y chromosomal haplogroup in Pre-Agricultural Asian aurochs (Y4) (Figure 7.2). Baikal1 (10,431-10,029 cal. BC), from Southern Siberia, has supported the C haplogroup as likely typical of East/North Asian aurochs since it has only been previously found in one other ancient *Bos* individual from China (Zhang *et al.* 2013).

Furthermore, Th7, the Epipaleolithic North African aurochs, has reported a R haplotype similar to those observed in extant Italian cattle (Achilli *et al.* 2009; Bonfiglio *et al.* 2010). This result argues against a secondary domestication event in Italy and suggests that rather the presence of R haplogroup in modern Italian cattle is either due to early contact with North African aurochs population via the Mediterranean route of cattle introduction into Europe or a legacy of the Roman empire with later admixture (Gautier 2002; Zeder 2008; Tresset & Vigne 2011; Felius *et al.* 2014; Cunliffe 2015).

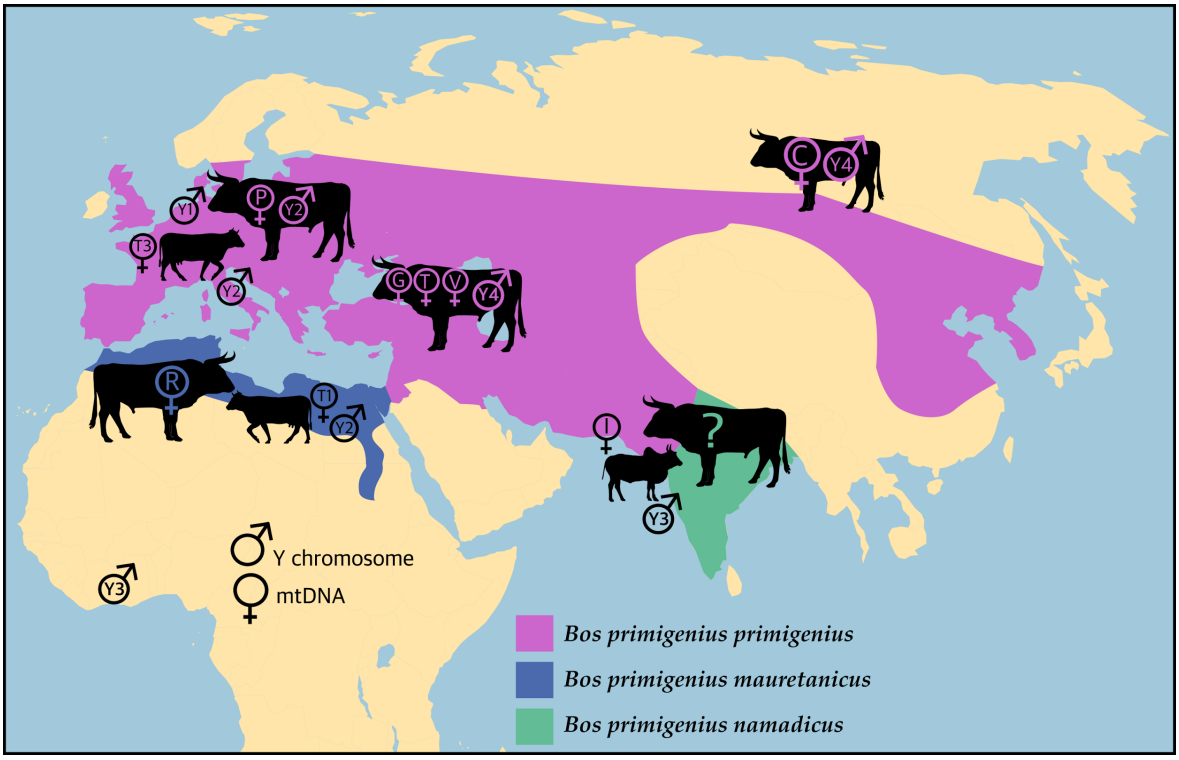


Figure 7.2 - Bos primigenius mtDNA and Y chromosome diversity across Africa and Eurasia*. Map only summarizes results presented in this thesis and not from previously published research. Most common mtDNA haplogroup found in European aurochs is P. Near Eastern aurochs show two new mitochondrial haplogroups: V (Gyumri1) and G (Gyumri2); as well as T in Kor1 and Ch22. C haplogroup is observed in a Southern Siberian aurochs from Lake Baikal (Baikal1) and the R haplogroup is observed in a Moroccan aurochs (Th7). New Y chromosome haplogroup (Y4) is observed in (Gyumri1 and Baikal1); while Y2 is observed in an European Mesolithic aurochs (Tri1). Colours show the distribution of each aurochs subspecies (Grigson 1980). Most common domestic haplogroup for both mtDNA and Y chromosome are also shown for African taurine, European taurine and Indicine cattle.*

In addition, genome-wide data also revealed a greater diversity in other regions than what had been observed so far from European aurochs (Park *et al.* 2015). European aurochs revealed form a quite homogenous population, but clearly distinct from

European domestics. The Russian aurochs, Baikal1 has shown to be an outgroup to all other aurochs populations but clustering on a genome-wide level with the Western Asian Gyumri1 (11,842-11,622 cal. BC), which suggests they belonged to a widespread interbreeding Asian population, distinct from European aurochs. Moreover, the North African aurochs (Th7) revealed to be closer to extant African breeds than any other aurochs and to cluster with Southern Levantine ancient cattle (Figure 7.1). It was also demonstrated that Th7 is not part of the Late Pleistocene clade formed by Gyumri1 and Baikal1 and that it is also an outgroup to European and Near Eastern aurochs.

7.1.5. Zebu admixture in the Near East

Using low coverage data from across the ancient Near East, spanning around 8,000 years of domestic cattle prehistory it was established that zebu introduction from the East likely occurred during the Late Bronze Age and Iron Age transition. With the expansion of the Mesopotamian and Indus Valley civilizations, came the establishment of routes across the Iranian plateau for trading metals (copper, tin, gold, silver), precious stones (lapis-lazuli, turquoise) and animals (Figure 7.3) (Matthews 2002; Podany 2013; Cunliffe 2015). Many zebu animals would have likely been involved in this process, and our data supports gene flow to have continued for thousands of years from the Bronze Age, through the Roman empire and the Arab conquests (Loftus *et al.* 1999; Cunliffe 2015). Moreover, an east to west increase in ADMIXTURE fractions of zebu and F_4-ratios supported previous research on modern day Near Eastern cattle breeds (Loftus *et al.* 1999; Freeman *et al.* 2006; Edwards, Baird, *et al.* 2007; Karimi *et al.* 2016). A temporal increase is observed in admixture proportions was also observed, peaking in the post Iron Age (for this dataset). If there is subsequent increase or decline after that it is not possible to infer from this data. Finally, support for a female-mediated gene flow was not found, however, male-mediated admixture could not be excluded due to insufficient numbers of Y chromosomes for comparison of the two haploid markers.

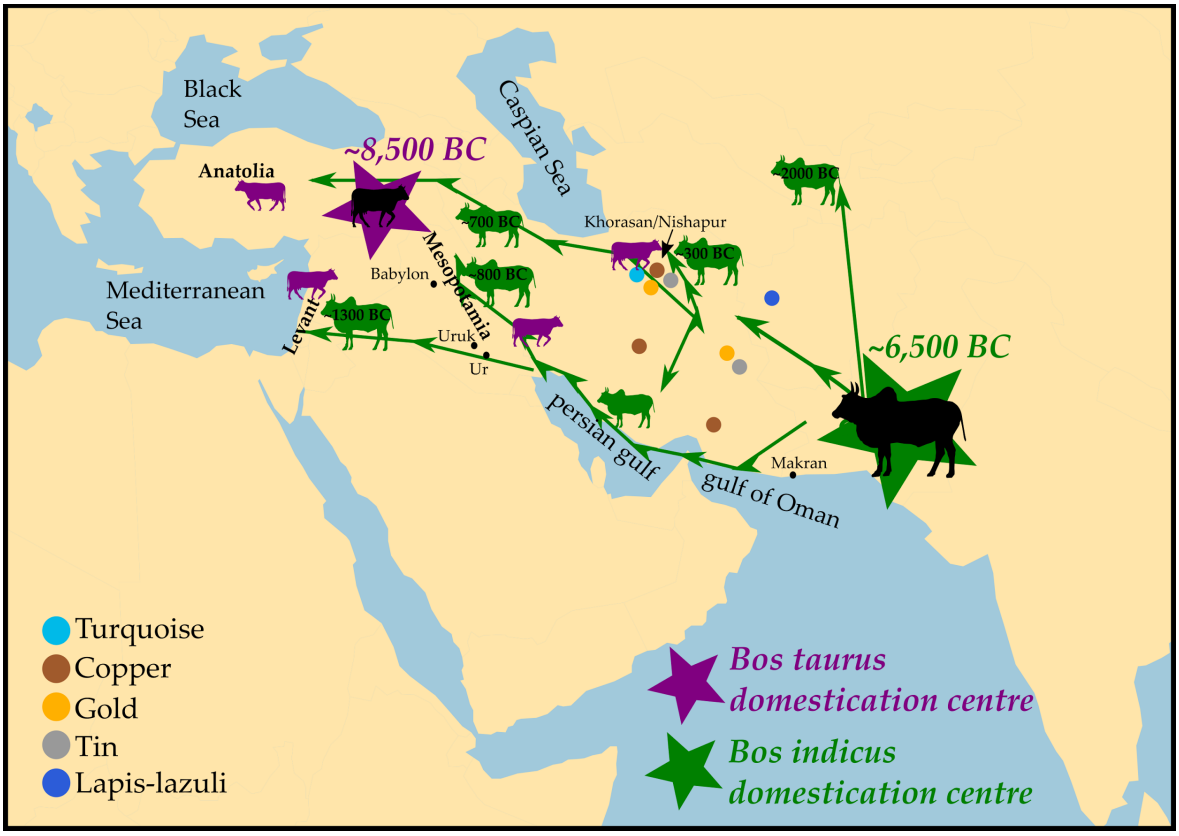


Figure 7.3 - Zebu admixture in the Near East. *Two main domestication centres for Bos taurus and Bos indicus are indicated (Loftus, MacHugh, Bradley, et al. 1994). Showing earliest dates for significant gene flow from zebu cattle observed in the ancient data in different regions of the Near East. Important Mesopotamian civilizations (Ur, Uruk and Babylon) are show with approximate locations. Important sources of metals and minerals exploited by the Harappan/Indus civilization are shown at approximate locations (Asthana 1993; Podany 2013; Cunliffe 2015). Routes shown are hypothetical and solely based on the ancient data of this thesis.*

7.2. Future directions

7.2.1. Uncovering the origins of Tango1 and Tango2

At the time of writing, is hard to exactly pinpoint an exact location for the likely origin of the Tango1 and Tango2 aurochs specimens. Genome-wide data points towards Tango1 maybe belonging to a Near Eastern population of aurochs and Tango2 possibly belongs to an Eastern European region like Moldova (Figure 7.1). Radiocarbon dating of Tango1 could be useful for decoding this aurochs origins. Also, metagenomic analysis of the soil attached to the animal remains for both aurochs of no geographical original could also bring in more clues about the origins of these individuals (Louvel *et al.* 2016).

7.2.2. Sampling from other geographical areas and other analyses

In the future, effort should be put into the sampling and sequencing of *Bos primigenius* individuals and ancient *Bos indicus*. The latter is underrepresented in ancient DNA studies and there is also no ancient genomic data for the proposed ancestor of all zebu cattle, *Bos primigenius namadicus* (Figure 7.3) (Grigson 1978; Grigson 1980; Loftus, MacHugh, Bradley, *et al.* 1994). This perhaps will be one of the most challenging to recover given the likely poor preservation of ancient remains at such latitudes. Specimens, and bone elements like the *pars petrosa*, with higher endogenous DNA percentages should always be preferred in order to minimize sequencing costs. Nevertheless, these results illustrate the power of low coverage aDNA data to infer on past population history and to fill in gaps in the genetic prehistory of wild and domestic cattle. It will also complement modern cattle studies and present new hypotheses that could not have been formulated from surveying modern variation alone. Older aurochs like Baikal1 and Gyumri1 should be sequenced to higher depth of coverage in order to infer on effective population sizes, using methods like PSMC (Li & Durbin 2011). Moreover, comparisons between these aurochs and other *Bos* species like the Yak, Banteng, Gaur and Bison could also contribute to further understanding the evolutionary history of this *genus*.

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9. Appendix

9.1. General Supplementary tables

Table 9.1.1- 700K Dataset.

Breed Code	Name	Number of Animals	Country	Genus	Species
ALE	Alentejana	9	Portugal	*Bos*	*taurus*
ANB	Anatolian Black	13	Turkey	*Bos*	*taurus*
ANG	Angus	42	Scotland	*Bos*	*taurus*
BLO	Blonde d'Aquitaine	5	France	*Bos*	*taurus*
BMA	Beef Master	23	US	*Bos*	*hybrid*
BRG	Brangus	12	US	*Bos*	*hybrid*
BRM	Brahman	46	India	*Bos*	*indicus*
BSW	Brown Swiss	22	Switzerland	*Bos*	*taurus*
BUT	Butana	7	Ethiopia	*Bos*	*indicus*
CHL	Charolais (UK)	37	France	*Bos*	*taurus*
EAR	East Anatolian Red	12	Turkey	*Bos*	*taurus*
GAL	Galloway	9	Scotland	*Bos*	*taurus*
GIR	Gir	29	India	*Bos*	*indicus*
GNS	Guernsey	21	Guernsey	*Bos*	*taurus*
GOB	Gobra	10	NA	*Bos*	*indicus*
HAR	Hariana	10	India	*Bos*	*indicus*
HFD	Hereford	35	UK	*Bos*	*taurus*
HIG	Highland	8	Scotland	*Bos*	*taurus*
HOL	Holstein (FR)	60	Netherlands	*Bos*	*taurus*
JER	Jersey (FR)	38	NA	*Bos*	*taurus*
KEN	Kenana	10	Ethiopia	*Bos*	*indicus*
KER	Kerry	9	Ireland	*Bos*	*taurus*
LAG	Lagune	5	NA	*Bos*	*taurus*
LMS	Limousin	50	France	*Bos*	*taurus*
MAR	Maremmana	4	Italy	*Bos*	*taurus*

MAU	Maure	10	Mali	*Bos*	*indicus*
MON	Montbeliarde	5	France	*Bos*	*taurus*
MUR	Murutu	11	Nigeria	*Bos*	*taurus*
NDA	N'Dama	32	Guinea	*Bos*	*taurus*
NEL	Nelore	31	India	*Bos*	*indicus*
NOR	Normande	5	France	*Bos*	*taurus*
NRC	Norwegian Red Cattle	17	Norway	*Bos*	*taurus*
OGR	Gaur	3	NA	*Bos*	*gaurus*
OYK	Yak	2	NA	*Bos*	*grunniens*
PMT	Piedmontese	21	Italy	*Bos*	*taurus*
RGU	Red Angus	10	Scotland	*Bos*	*taurus*
RMG	Romagnola	21	Italy	*Bos*	*taurus*
SAH	Sahiwal	10	Pakistan	*Bos*	*indicus*
SAR	South Anatolian Red	13	Turkey	*Bos*	*taurus*
SEN	Senepol	12	Virgin Islands	*Bos*	*taurus*
SGT	Santa Gertrudis	32	UK	*Bos*	*hybrid*
SHK	Sheko	16	Ethiopia	*Bos*	*indicus*
SIK	Sikia	5	NA	*Bos*	*taurus*
SIM	Simmental	10	Switzerland	*Bos*	*taurus*
SIS	Sistani	5	Iran	*Bos*	*indicus*
SOM	Somba	10	NA	*Bos*	*taurus*
TAL	Taleshi	5	Iran	*Bos*	*taurus*
WAG	Wagyu	13	Japan	*Bos*	*taurus*

Table 9.1.2 - Mitochondrial genomes dataset.

ID/ Haplogroup	Publication	Accession Number
V00654_T3	Anderson *et al.* 1982	V00654
DQ124372_T4a	unpublished / direct submission	DQ124372
DQ124389_P2	unpublished / direct submission	DQ124389
DQ124396_T2a	unpublished / direct submission	DQ124396
EU177841_T1e	Achilli *et al.* 2008	EU177841
EU177862_T5a	Achilli *et al.* 2008	EU177862
EU177868_I1	Achilli *et al.* 2008	EU177868
EU177870_I2	Achilli *et al.* 2008	EU177870
FJ971081_Q2	Achilli *et al.* 2009	FJ971081
FJ971084_R1a	Achilli *et al.* 2009	FJ971084
FJ971087_R2	Achilli *et al.* 2009	FJ971087
GU256940_I	unpublished / direct submission	GU256940
GU985279_P1	Edwards *et al.* 2010	GU985279
HQ184034_Q1a	Bonfiglio *et al.* 2010	HQ184034
HQ184031_Q2	Bonfiglio *et al.* 2010	HQ184031
HQ184039_Q1a	Bonfiglio *et al.* 2010	HQ184039
JQ437479_P1	Zeyland *et al.* 2012	JQ437479
KF525852_C	Zhang *et al.* 2013	KF525852
DomesticYak38	Zhang *et al.* 2016	SRR2059916
JN817315_T1a1	Bonfiglio *et al.* 2012	JN817315
JN817342_T1a2	Bonfiglio *et al.* 2012	JN817342
JN817314_T1a3	Bonfiglio *et al.* 2012	JN817314
JN817350_T1b1a	Bonfiglio *et al.* 2012	JN817350
JN817309_T1c1a1	Bonfiglio *et al.* 2012	JN817309
JN817343_T1f	Bonfiglio *et al.* 2012	JN817343

Table 9.1.3 - Whole Genome Dataset

ID	Name/Breed	Species	Origin	Sex	Coverage	Study Accession	Reference
Wag_1a	Wagyu	*Bos taurus*	Japan	Male	18	N/A	unpublished
Thar_1	Tharparkar	*Bos indicus*	India	Female	16	N/A	unpublished
Som_3437	Somba	*Bos taurus*	Africa	Female	35	N/A	unpublished
Lag_40	Lagune	*Bos taurus*	Africa	Male	24	N/A	unpublished
Har_03a	Hariana	*Bos indicus*	India	Female	35	N/A	unpublished
Aln_12	Alentejana	*Bos taurus*	Portugal	Male	31	N/A	unpublished
Hl_8059	Highland	*Bos taurus*	UK	Male	38	N/A	unpublished
Br_01	Brune d'Atlas	*Bos taurus*	France	Female	24	N/A	unpublished
Sha_3b	Sahiwal	*Bos indicus*	Pakistan	Female	21	N/A	unpublished
Sik_5	Sikias	*Bos taurus*	Greece	Female	20	N/A	unpublished
Gir22	Gir	*Bos indicus*	India	Male	37	N/A	unpublished
NDama_DB	N'Dama	*Bos taurus*	Africa	Male	32	N/A	unpublished
CPC98	Aurochs	*Bos primigenius*	UK	Male	5	PRJNA294709	Park *et al.* 2015
wyx29	Wild Yak	*Bos mutus*	Asia	Male	4	PRJNA285834	Qiu *et al.* 2015)
dys38	Domestic Yak	*Bos grunniens*	Asia	Male	8	PRJNA285834	Qiu *et al.* 2015
buffalo	Water buffalo	*Bubalus bubalis*	Asia	Female	11	PRJNA33659	Tantia *et al.* 2011
Gir03	Gir	*Bos indicus*	India	Male	10	PRJNA277147	Bickhart *et al.* 2016
Nelore03	Nelore	*Bos indicus*	India	Male	7	PRJNA277147	Bickhart *et al.* 2016
Angus_19	Angus	*Bos taurus*	Europe	Male	4	PRJNA238491	Daetwyler *et al.* 2014
Angus_28	Angus	*Bos taurus*	Europe	Male	7	PRJNA238491	Daetwyler *et al.* 2014
Angus_33	Angus	*Bos taurus*	Europe	Male	9	PRJNA238491	Daetwyler *et al.* 2014
Angus_39	Angus	*Bos taurus*	Europe	Male	7	PRJNA238491	Daetwyler *et al.* 2014
Angus_40	Angus	*Bos taurus*	Europe	Male	10	PRJNA238491	Daetwyler *et al.* 2014
Fleckvieh_39	Fleckvieh	*Bos taurus*	Europe	Male	6	PRJNA238491	Daetwyler *et al.* 2014
Fleckvieh_40	Fleckvieh	*Bos taurus*	Europe	Male	9	PRJNA238491	Daetwyler *et al.* 2014
Fleckvieh_42	Fleckvieh	*Bos taurus*	Europe	Male	7	PRJNA238491	Daetwyler *et*

							al. 2014
Fleckvieh_5	Fleckvieh	*Bos taurus*	Europe	Male	9	PRJNA238491	Daetwyler *et al.* 2014
Holstein_116	Holstein	*Bos taurus*	Europe	Male	10	PRJNA238491	Daetwyler *et al.* 2014
Holstein_71	Holstein	*Bos taurus*	Europe	Male	10	PRJNA238491	Daetwyler *et al.* 2014
Holstein_79	Holstein	*Bos taurus*	Europe	Male	8	PRJNA238491	Daetwyler *et al.* 2014
Holstein_88	Holstein	*Bos taurus*	Europe	Male	10	PRJNA238491	Daetwyler *et al.* 2014
Holstein_90	Holstein	*Bos taurus*	Europe	Male	9	PRJNA238491	Daetwyler *et al.* 2014
Jersey_12	Jersey	*Bos taurus*	Europe	Male	7	PRJNA238491	Daetwyler *et al.* 2014
Jersey_2	Jersey	*Bos taurus*	Europe	Male	8	PRJNA238491	Daetwyler *et al.* 2014
Jersey_4	Jersey	*Bos taurus*	Europe	Male	6	PRJNA238491	Daetwyler *et al.* 2014
Jersey_5	Jersey	*Bos taurus*	Europe	Male	13	PRJNA238491	Daetwyler *et al.* 2014
Jersey_7	Jersey	*Bos taurus*	Europe	Male	7	PRJNA238491	Daetwyler *et al.* 2014
Boran563006	Boran	*Bos indicus*	Africa	Female	10	PRJNA312138	Kim *et al.* 2017
Boran587	Boran	*Bos indicus*	Africa	Female	10	PRJNA312138	Kim *et al.* 2017
Kenana13	Kenana	*Bos indicus*	Africa	Female	10	PRJNA312138	Kim *et al.* 2017
Kenana4	Kenana	*Bos indicus*	Africa	Female	10	PRJNA312138	Kim *et al.* 2017
NDama166	NDama	*Bos taurus*	Africa	Female	9	PRJNA312138	Kim *et al.* 2017
NDama719	NDama	*Bos taurus*	Africa	Female	10	PRJNA312138	Kim *et al.* 2017
OgadenD6	OgadenD6	*Bos taurus*	Africa	Female?	10	PRJNA312138	Kim *et al.* 2017

Table 9.1.4 - Archaeological sites numbers

Site Number	ID	Latitude	Longitude
1	Miyanroud	30.173889	52.668056
2	Tel Masos	31.2047	34.9939
3	Nahal Tillah	31.251898	34.78608
4	Gilat	31.328497	34.649997
5	Ashkelon	31.662429	34.54638
6	Tel-Es Safi	31.699722	34.846944
7	Jerusalem	31.773611	35.235556
8	Tel-Miqne	31.77889	34.84992
9	Tel Dalit	31.9765	34.9694
10	Tel Zahara	32.5	35.5
11	Horvat Castra	32.596389	35.241944
12	Tel Yoqneam	32.6641	35.1083
13	Tel Hreiz	32.690823	34.94166
14	Tel es-Qashish	32.733333	35.05
15	Tel Dan	33.249	35.652
16	Taghit Haddouch	34.783333	-3.333333
17	Bestansur	35.376861	45.645667
18	Maral Tappeh	35.961944	50.68
19	Nishapur Qohandez	36.213333	58.795833
20	Tepe Shizar	36.266667	50
21	Tapeh-Sang-e-Caxmaq	36.266667	50
22	Monjukli Depe	36.848528	60.418056
23	Hasanlu	37.004831	45.458892
24	Suberde	37.351556	31.926972
25	Çatalhöyük	37.666667	32.828056
26	Tilla Bulak	37.7	66.8
27	Kortik Teppe	37.827695	40.966117
28	Acemhoyuk	38.4114	33.8357
29	Kul Tepe (Kültəpə)	39.1613	45.2707
30	Kok Teppe	39.893333	66.918056

31	Mentese	40.286743	29.528623
32	Gyumri	40.789444	43.8475
33	Yerqorqan	41.266667	69.216667
34	Tamara Fort	42.6575	44.645278
35	Dzulhunitsa	42.683333	23.316667
36	Plocnik	43.201944	21.355556
37	Bubanj	43.305556	21.8725
38	Blagotin	43.4353	21.0631
39	Belovode	44.378333	21.419444
40	Stubline	44.571	20.138167
41	Birnova/Byrnova Luka	48.2526	27.3136
42	Herxheim	49.145275	8.221805
43	Trier-Brüderkrankenhaus	49.75	6.633333
44	Kirschbaumhöhle	49.95	11.583333
45	Bedburg-Königshoven	51.054167	6.521667
46	Kalisz	51.766667	18.083333
47	Elst	51.915556	5.837778
48	Zijderveld	51.941944	5.139444
49	Schipluiden	51.983333	4.316667
50	Houten	52.023722	5.176972
51	Bunnik-Odjik	52.050278	5.233333
52	Belorus1	52.0976	23.7341
53	Stevenshofjespolder	52.157222	4.4925
54	Ludwinowo	52.561944	19.015833
55	Dyrotz	52.574067	12.968658
56	Kierzkowo	52.846667	17.861389
57	Carsington Pasture Cave	53.083186	-1.637178
58	Dronrijp-zuid	53.2	5.65
59	Oosterbeintum	53.233889	5.511944
60	Firdgum	53.248889	5.559722

61	Britsum	53.2531	5.7856
62	Falkenwalde	53.260309	13.977105
63	Winsum	53.333333	6.516667
64	Dublin	53.349722	-6.260278
65	Lake Baikal	53.425	108.997
66	Newgrage	53.694369	-6.475031
67	York	53.958333	-1.080278
68	Cladh Hallan	57.17116	-7.40759

Table 9.1.5 - Ancient mitochondrial haplogroups

ID	Region	Period	Haplogroup	Latitude	Longitude
Ace1	Anatolia	Bronze	T2	38.4114	33.8357
Men1	Anatolia	Neolithic	T3	40.286743	29.528623
Men2	Anatolia	Neolithic	Q	40.286743	29.528623
Sub1	Anatolia	Neolithic	T2	37.351556	31.926972
Gyumri1	Armenia	Mesolithic	R outgroup (V)	40.789444	43.8475
Gyumri2	Armenia	Neolithic	Q outgroup (G)	40.789444	43.8475
Belorus1	Belorus	Unknown	P	52.0976	23.7341
Dzh1	Bulgaria	Neolithic	T3	42.683333	23.316667
Dzh2	Bulgaria	Neolithic	T3	42.683333	23.316667
CA317	Georgia	Post Iron	T2	42.6575	44.645278
Kaz1	Georgia	Post Iron	T3	42.6575	44.645278
Kaz2	Georgia	Post Iron	T3	42.6575	44.645278
Kaz3	Georgia	Post Iron	T2	42.6575	44.645278
Kaz4	Georgia	Post Iron	T3	42.6575	44.645278
Bed3	Germany	Mesolithic	P	51.054167	6.521667
Bed4	Germany	Mesolithic	P	51.054167	6.521667
Tri1	Germany	Mesolithic	P	49.75	6.633333
Hxh1	Germany	Neolithic	T3	49.145275	8.221805
Hxh2	Germany	Neolithic	P	49.145275	8.221805
Kir4	Germany	Neolithic	R outgroup (V)	49.95	11.583333

Dyr1	Germany	Post Iron	T3	52.574067	12.968658
Fal7	Germany	Post Iron	P	53.260309	13.977105
Has1	Iran	Bronze	Q	37.004831	45.458892
Has3	Iran	Bronze	T2	37.004831	45.458892
Qaz1	Iran	Bronze	T2	36.266667	50
Azer1	Iran	Chalcolithic	Q	39.1613	45.2707
Mar1	Iran	Chalcolithic	Q	35.961944	50.68
Has4	Iran	Iron	T3	37.004831	45.458892
Far1	Iran	Neolithic	T1	30.173889	52.668056
Sac3	Iran	Neolithic	Q	36.499722	55.000556
Has5	Iran	Post Iron	T3	37.004831	45.458892
Kho1	Iran	Post Iron	I	36.213333	58.795833
Bes1	Iraq	Iron	T2	35.376861	45.645667
Bes2	Iraq	Post Iron	T3	35.376861	45.645667
New2	Ireland	Iron	T3	53.694369	-6.475031
New1	Ireland	Neolithic	T3	53.694369	-6.475031
New3	Ireland	Neolithic	T3	53.694369	-6.475031
New4	Ireland	Neolithic	T3	53.694369	-6.475031
New5	Ireland	Neolithic	T3	53.694369	-6.475031
Dub1	Ireland	Post Iron	T3	53.349722	-6.260278
Dan1	Levant	Bronze	T1?	33.249	35.652
Dav1	Levant	Bronze	T3	31.773611	35.235556
Dav2	Levant	Bronze	T1?	31.773611	35.235556
Dav4	Levant	Bronze	T1	31.773611	35.235556
Tda1	Levant	Bronze	T?	31.9765	34.9694
Tqa1	Levant	Bronze	T3	32.733333	35.05
Tqa2	Levant	Bronze	T1	32.733333	35.05
Tqa3	Levant	Bronze	T1	32.733333	35.05
Gil1	Levant	Chalcolithic	?	31.328497	34.649997
Nah1	Levant	Chalcolithic	T1	31.251898	34.78608
Ash4	Levant	Iron	T3	31.662429	34.54638
Dav3	Levant	Iron	T1	31.773611	35.235556

Mus1	Levant	Iron	T1	31.2047	34.9939
Tmq1	Levant	Iron	T2	31.77889	34.84992
Tmq2	Levant	Iron	T3	31.77889	34.84992
Tmq3	Levant	Iron	T2	31.77889	34.84992
Tmq4	Levant	Iron	T1	31.77889	34.84992
Tsa1	Levant	Iron	Q	31.699722	34.846944
Tsa2	Levant	Iron	T1?	31.699722	34.846944
Tsa3	Levant	Iron	T1	31.699722	34.846944
Tyq1	Levant	Iron	T2	32.6641	35.1083
Thr1	Levant	Neolithic	T1	32.690823	34.94166
Cas1	Levant	Post Iron	T1	32.596389	35.241944
Dav5	Levant	Post Iron	Q	31.773611	35.235556
Zah1	Levant	Post Iron	T3	32.5	35.5
Bir1	Moldova	Neolithic	T1?	48.2526	27.3136
Bir2	Moldova	Neolithic	T2	48.2526	27.3136
Bir3	Moldova	Neolithic	P	48.2526	27.3136
Th7	Morocco	Epipalaeolithic	R	34.783333	-3.333333
Viz1	Netherlands	Bronze	T3	51.941944	5.139444
Viz2	Netherlands	Bronze	T3	51.941944	5.139444
Bun1	Netherlands	Iron	T3	52.050278	5.233333
Bun2	Netherlands	Iron	T3	52.050278	5.233333
Ste1	Netherlands	Iron	T3	52.157222	4.4925
Sch1	Netherlands	Neolithic	T3	51.983333	4.316667
Dro1	Netherlands	Post Iron	T3	53.2	5.65
Els1	Netherlands	Post Iron	T3	51.915556	5.837778
Fir1	Netherlands	Post Iron	T3	53.248889	5.559722
Hou1	Netherlands	Post Iron	T3	52.023722	5.176972
Hou2	Netherlands	Post Iron	T3	52.011444	5.191139
Otb1	Netherlands	Post Iron	T3	53.233889	5.511944
Win1	Netherlands	Post Iron	T3	53.333333	6.516667
Bri1	Netherlands	Roman	T3	53.2531	5.7856
Tango1	no info	Unknown	T3	no info	no info
Tango2	no info	Unknown	T3	no info	no info
Kie1	Poland	Neolithic	T3	52.846667	17.861389

Kie2	Poland	Neolithic	T3	52.846667	17.861389
Lud1	Poland	Neolithic	T3	52.561944	19.015833
Lud2	Poland	Neolithic	T3	52.561944	19.015833
Lud3	Poland	Neolithic	T3	52.561944	19.015833
Lud4	Poland	Neolithic	T3	52.561944	19.015833
Kalisz1	Poland	Unknown	P	51.766667	18.083333
Kalisz2	Poland	Unknown	P	51.766667	18.083333
Kalisz3	Poland	Unknown	Q	51.766667	18.083333
Baikal1	Russia	Neolithic	C	53.425	108.997
Bel1	Serbia	Neolithic	Q	44.378333	21.419444
Bel2	Serbia	Neolithic	Q	44.378333	21.419444
Bla1	Serbia	Neolithic	T3	43.4353	21.0631
Bla2	Serbia	Neolithic	?	43.4353	21.0631
Bub1	Serbia	Neolithic	T3	43.305556	21.8725
Plo1	Serbia	Neolithic	Q	43.201944	21.355556
Plo2	Serbia	Neolithic	Q	43.201944	21.355556
Plo3	Serbia	Neolithic	T3	43.201944	21.355556
Plo4	Serbia	Neolithic	T2	43.201944	21.355556
Plo5	Serbia	Neolithic	T3	43.201944	21.355556
Plo6	Serbia	Neolithic	T3	43.201944	21.355556
Plo7	Serbia	Neolithic	T3	43.201944	21.355556
Plo8	Serbia	Neolithic	T2	43.201944	21.355556
Stu1	Serbia	Neolithic	T3	44.571	20.138167
Ch22	Turkey	Neolithic	T3	37.666667	32.828056
Kor1	Turkey	PPNA	T2	37.827695	40.966117
Mon1	Turkmenistan	Chalcolithic	T3	36.848528	60.418056
Cla1	UK	Bronze	T3	57.17116	-7.40759
Cla2	UK	Bronze	T3	57.17116	-7.40759
CPC98	UK	Mesolithic	P	53.083186	-1.637178
Yor1	UK	Post Iron	T3	53.958333	-1.080278
Yor2	UK	Post Iron	T3	53.958333	-1.080278
Yor3	UK	Post Iron	T3	53.958333	-1.080278

Yor4	UK	Post Iron	T3	53.958333	-1.080278
Bul1	Uzbekistan	Bronze	T2	37.7	66.8
Kok1	Uzbekistan	Iron	P?	39.893333	66.918056
Yer1	Uzbekistan	Post Iron	T3	41.266667	69.216667

Table 9.1.6 - Y chromosome coverages

ID	Y Chr Coverage	Species
Ancients		
Baikal1	0.04	*Bos primigenius*
Bes2	0.19	*Bos taurus*
Dzh1	4.06	*Bos taurus*
Gyumri1	0.02	*Bos primigenius*
Has3	0.01	*Bos taurus*
Has4	0.02	*Bos taurus*
Men1	0.03	*Bos taurus*
New1	7.6	*Bos taurus*
Plo3	0.03	*Bos taurus*
Sub1	0.14	*Bos taurus*
Tri1	1.43	*Bos primigenius*
Moderns		
dys38	3.50	*Bos grunniens*
Gir03	4.30	*Bos indicus*
Nelore03	3.20	*Bos indicus*
Gir22	14.71	*Bos indicus*
Angus19	1.75	*Bos taurus*
Angus28	2.48	*Bos taurus*
Angus33	2.68	*Bos taurus*
Angus39	3.13	*Bos taurus*
Angus40	4.29	*Bos taurus*
Fleckvieh39	1.80	*Bos taurus*
Fleckvieh5	2.81	*Bos taurus*
Holstein116	4.02	*Bos taurus*

Holstein71	4.19	*Bos taurus*
Holstein79	3.53	*Bos taurus*
Holstein88	3.09	*Bos taurus*
Holstein90	3.88	*Bos taurus*
Jersey12	2.30	*Bos taurus*
Jersey2	2.40	*Bos taurus*
Jersey4	2.30	*Bos taurus*
Jersey5	4.06	*Bos taurus*
Jersey7	2.29	*Bos taurus*
N'Dama	11.81	*Bos taurus*
Lagune	10.99	*Bos taurus*
Highland	12.69	*Bos taurus*
Alentejana	12.36	*Bos taurus*
Wagyu	7.44	*Bos taurus*

Table 9.1.7 - Drilled samples summary. Final ID for samples that were included in this thesis are shown in final column.

Lab_ID	Country	Archaeological site	Species	bone type	Archaeological Period	% DNA	Final ID
Kir4	Germany	Kirschbaumhöhle	*Bos taurus*	petrous	Late Neolithic	54.19	**Kir4**
MV001	Georgia	Dmanisi	*Ovis?*	long bone	Bronze Age	0.03	
MV002	United Kingdom	York	*Bos*	petrous	Viking	2.86	
MV003	United Kingdom	York	*Bos*	petrous	13th century	50.95	
MV004	Turkey	Mentese	*Bos*	tarsal	Neolithic	1.75	
MV005	Turkey	Mentese	*Bos*	tarsal	Neolithic	0.19	
MV006	Syria	Bouqras	*Bos*	tarsal	Neolithic	0.01	
MV007	Syria	Bouqras	*Bos*	tarsal	Neolithic	0.00	
MV008	Syria	Bouqras	*Bos*	tarsal	Neolithic	0.01	
MV009	Syria	Bouqras	*Bos*	long bone	Neolithic	0.00	
MV010	Syria	Bouqras	*Bos*	long bone	Neolithic	0.01	

MV011	Syria	Bouqras	*Ovis (sheep)*	long bone	Neolithic	0.00	
MV012	Turkey	Mentese	*Bos*	long bone	Neolithic	0.15	
MV013	Turkey	Mentese	*Bos*	astragalus	Neolithic	10.85	**Men1**
MV014	Turkey	Mentese	*Bos*	long bone	Neolithic	0.00	
MV015	Turkey	Barcin Hoyuk	*Bos taurus*	metacarpus	Neolithic	1.53	
MV016	Turkey	Barcin Hoyuk	*Bos taurus*	metatarsus	Neolithic	0.70	
MV017	Macedonia	Govrlevo	*Bos taurus*	metatarsus	Late Neolithic (Anzabegovo IV)	0.45	
MV018	Macedonia	Govrlevo	*Bos taurus*	metatarsus	Early Neolithic (Anzabegovo I)	7.94	
MV019	Macedonia	Tumba Madzari	*Bos taurus*	metacarpus	Beginnig of Middle Neolithic (Anzabegovo Vrsnik II)	1.89	
MV020	Turkey	Çukuriçi Höyük	*Bos*	petrous	Early Neolithic	1.68	
MV021	Turkey	Çukuriçi Höyük	*Bos*	petrous	Early Neolithic	2.54	
MV022	Turkey	Çukuriçi Höyük	*Bos*	petrous	Early Neolithic	0.80	
MV023	Turkey	Çukuriçi Höyük	*Bos*	petrous	Early Neolithic	1.07	
MV024	Turkey	Çukuriçi Höyük	*Bos*	petrous	Early Neolithic	1.83	
MV025	Netherlands	Winsum-Buggeburen	*Bos taurus*	petrous	Roman (possibly 2nd-3rd Century AD)	59.98	**Win1**
MV026	Switzerland	Sutz-Lattrigen VII Hafen	*Bos taurus*	petrous	3800-3850BC	1.88	
MV027	Switzerland	Sutz-Lattrigen VII Hafen	*Bos taurus*	petrous	3800-3850BC	18.81	
MV028	Switzerland	Sutz-Lattrigen VII Hafen	*Bos taurus*	petrous	3800-3850BC	0.92	
MV029	Switzerland	Sutz-Lattrigen VII Hafen	*Bos taurus*	petrous	3800-3850BC	1.59	
MV030	Switzerland	Zurich_Opera_L13	*Bos taurus*	petrous	3230BC	0.50	
MV031	Switzerland	Zurich_Opera_L13	*Bos taurus*	petrous	3230BC	1.61	
MV032	Switzerland	Zurich_Opera_L13	*Bos taurus*	petrous	3230BC	0.97	
MV033	Switzerland	Zurich_Opera_L13	*Bos taurus*	petrous	3230BC	0.94	
MV034	Turkey	Suberde	*Bos taurus*	petrous	c. 7500-7000 cal. BC	39.80	**Sub1**
MV035	Netherlands	Dronrijp-zuid	*Bos taurus*	petrous, left side Juvenile	Middle Roman (100-300AD)	35.52	**Dro1**
MV036	Netherlands	Britsum	*Bos primigenius?*	petrous, right side Juvenile	257-421 cal. AD. Direct Radiocarbon dated	56.96	**Bri1**
MV037	Netherlands	Oosterbeintum	*Bos taurus*	petrous, Left adult male	Middle Roman (100-300AD)	48.58	**Otb1**
MV038	Netherlands	Marsum	*Bos taurus*	petrous	? (coming soon!)	0.18	

MV039	Netherlands	Elst, Gelderland	*Bos taurus*	petrous	Roman (40 BC - 3rd C AD)	48.83	**Els1**
MV040	Netherlands	Jelsum, Friesland	*Bos taurus*	petrous	Roman (12BC-300AD)		
MV041	Netherlands	Firdgum, Friesland	*Bos taurus*	petrous	Early Medieval (450-1050AD)	60.45	**Fir1**
MV042	Netherlands	Tjerkwerd Arkum	*Bos taurus*	petrous	Iron Age (300BC -12 BC)	8.46	**Men2**
MV043	Turkey	Mentese	*Bos taurus*	petrous(L)	Neolithic	14.49	
MV044	Turkey	Mentese	*Bos taurus*	temporal (R)	Neolithic	0.55	
MV045	Turkey	Mentese	*Bos taurus*	petrous (L)	Neolithic	5.57	
MV046	Turkey	Mentese	*Bos taurus*	temporal (L)	Neolithic	0.15	
MV047	Iraq-Kurdistan	Bestansur	*Bos taurus*	petrous	Neolithic	37.19	**Bes1**
MV048	Iraq-Kurdistan	Bestansur	*Bos taurus*	petrous	Neolithic	36.86	**Bes2**
MV049	Turkey	Hallan Cemi	*Bos taurus*	skull + petrous	Neolithic	0.06	
MV050	Bulgaria		*Bos taurus*	long bone	Neolithic	0.04	
MV051	Turkey	Acemhoyuk	*Bos taurus*	petrous	Bronze Age	Horse (64.14%)	
MV052	Netherlands	Schipluiden	*Bos taurus*	petrous	Mid-Neolithic (3500BC)	4.07	
MV053	Netherlands	Schipluiden	*Bos taurus*	petrous	Mid-Neolithic (3500BC)	13.85	
MV054	Netherlands	Schipluiden	*Bos taurus*	petrous	Mid-Neolithic (3500BC)	46.77	**Sch1**
MV055	Netherlands	Schipluiden	*Bos taurus*	petrous	Mid-Neolithic (3500BC)	26.37	
MV056	Netherlands	Stevenshofjespolder	*Bos taurus*	petrous	Iron Age/ Roman	41.63	**Ste1**
MV057	Netherlands	Voorschoten	*Large Mammal*	petrous	Neolithic	0.04	
MV058	Netherlands	Voorschoten	*Bos taurus*	petrous	Neolithic	0.05	
MV059	Netherlands	Houten-Loerik	*Bos taurus*	petrous	Iron Age	58.93	**Hou1**
MV060	Netherlands	Vianen-Zijderveld	*Bos taurus*	petrous	Bronze Age	0.03	
MV061	Netherlands	Vianen-Zijderveld	*Bos taurus*	petrous	Bronze Age	32.75	**Viz1**
MV062	Netherlands	Vianen-Zijderveld	*Bos taurus*	petrous	Neolithic	43.20	**Viz2**
MV063	Netherlands	Houten-Hoodijk	*Bos taurus*	petrous	Neolithic	57.43	**Hou2**
MV064	Netherlands	Bunnik Odjik	*Bos taurus*	petrous	Mid-Iron Age/ Late Roman or Late Medieval	40.76	**Bun1**
MV065	Netherlands	Bunnik Odjik	*Bos taurus*	petrous	Mid-Iron Age/ Late Roman or Late Medieval		**Bun2**

MV066	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic		
MV067	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic	0.02	
MV068	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic	23.14	
MV069	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic	20.28	**Bla1**
MV070	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic		
MV071	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic	0.00	
MV072	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic	7.21	
MV073	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic	1.07	
MV074	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic	4.37	
MV075	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic	0.10	
MV076	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic	13.59	**Bla2**
MV077	Serbia	Blagotin	*Bos taurus*	petrous	Neolithic	3.45	
MV078	Serbia	Stubline-Crkvine	*Bos taurus*	petrous	Neolithic	2.06	
MV079	Serbia	Stubline-Crkvine	*Bos taurus*	petrous	Neolithic	4.60	
MV080	Serbia	Stubline-Crkvine	*Bos taurus*	petrous	Neolithic	0.02	
MV081	Serbia	Stubline-Crkvine	*Bos taurus*	petrous	Neolithic	33.22	**Stu1**
MV082	Serbia	Stubline-Crkvine	*Bos taurus*	petrous	Neolithic	0.93	
MV083	Serbia	Stubline-Crkvine	*Bos taurus*	petrous	Neolithic	13.81	
MV084	Serbia	Stubline-Crkvine	*Bos taurus*	petrous	Neolithic	18.94	
MV085	Serbia	Stubline-Crkvine	*Bos taurus*	petrous	Neolithic	15.36	
MV086	Serbia	Bubanj	*Bos taurus*	petrous	Neolithic	37.98	**Bub1**
MV087	Serbia	Bubanj	*Bos taurus*	petrous	Neolithic	10.63	
MV088	Israel	Nesher-Ramla	*Bos primigenius*	petrous	Middle Paleolithic	0.00	**Nes1**
MV089	Israel	Nesher-Ramla	*Bos primigenius*	petrous	Middle Paleolithic	0.00	
MV090	Israel	Nesher-Ramla	*Bos*	petrous	Middle Paleolithic	0.00	
MV091	Israel	Nesher-Ramla	*gazella*	petrous	Middle Paleolithic		
MV092	Israel	Nesher-Ramla	*unknown*	petrous	Middle Paleolithic		
MV093	Israel	Ashqelon	*Bos*	petrous	PPNC	0.02	
MV094	Israel	Ashqelon	*Bos*	petrous	PPNC	0.05	
MV095	Israel	Ashqelon	*Bos*	petrous	PPNC	0.07	
MV096	Israel	Ashqelon	*Bos*	petrous	PPNC	0.02	
MV097	Israel	Ashqelon	*Bos*	petrous	PPNC	0.07	
MV098	Israel	Ashqelon	*Bos*	petrous	PPNC	0.10	

MV099	Israel	Ashqelon	*Bos*	petrous	PPNC	0.13	
MV100	Israel	Ashqelon	*Bos*	petrous	PPNC	0.65	**Ash1**
MV101	Israel	Ashqelon	*Bos*	petrous	PPNC	0.04	
MV102	Israel	Ashqelon	*Bos*	petrous	PPNC	0.04	
MV103	Israel	Ashqelon	*Bos*	petrous	PPNC	2.14	**Ash2**
MV104	Israel	Ashqelon	*Bos*	petrous	PPNC	6.35	**Ash3**
MV105	Israel	Ashqelon	*Bos*	petrous	PPNC	0.02	
MV106	Israel	Altlit-Yam	*Bos*	petrous	Late PPNB/PPNC		
MV107	Israel	Altlit-Yam	*Bos*	petrous	Late PPNB/PPNC	0.01	
MV108	Israel	Tel-Es Safi	*Bos*	petrous	IRON AGE	38.62	**Tsa1**
MV109	Israel	Tel-Es Safi	*Bos*	petrous	Iron Age		
MV110	Israel	Tel-Es Safi	*Bos*	petrous	Iron Age		
MV111	Israel	Abu-Gosh	*Bos*	petrous	MPPNB	0.20	
MV112	Israel	Tel-Hreiz	*Bos*	petrous	Pottery neolithic		
MV113	Israel	Tel-Hreiz	*Bos?*	petrous	Pottery Neolithic	0.25	**Thr1**
MV114	Israel	Tel-Yarmut	*Bos?*	petrous	early bronze age		
MV115	Israel	Ashqelon	*Bos*	petrous	PPNC	0.03	
MV116	Israel	Ashqelon	*Bos*	petrous	PPNC		
MV117	Iran	Ilam	*Bos*	petrous	Chalcolithic	0.02	
MV118	Iran	Ilam	*Bos*	petrous	Chalcolithic	0.17	
MV119	Iran	Khouzestan	*Bos*	petrous	Chalcolithic	0.16	
MV120	Iran	Khouzestan	*Bos*	petrous	Chalcolithic	0.07	
MV121	Georgia	Tamara Fort	*Bos*	petrous	Medieval	57.53	**Kaz1**
MV122	Georgia	Tamara Fort	*Bos*	petrous	Medieval	56.86	**Kaz2**
MV123	Georgia	Tamara Fort	*Bos*	petrous	Medieval	61.68	**Kaz3**
MV124	Israel	Issawir	*Bos*	petrous	Pottery Neolithic	0.04	
MV125	Israel	Tel-Dalit	*Bos*	petrous	Early bronze age	0.32	**Tda1**
MV126	Israel	Tel-Miqne	*Bos*	petrous	Late Bronze Age/ Iron Age		
MV127	Israel	Tel-Miqne	*Bos*	petrous	Late bronze/Iron Age	0.07	
MV128	Israel	Tel-Miqne	*Bos*	petrous	Late Bronze/ Iron Age	0.48	**Tmq1**
MV129	Israel	Tel-Miqne	*Bos?*	petrous	Late bronze/Iron Age	0.68	**Tmq2**

MV130	Israel	Tel-Miqne	*Sus-Bos?*	petrous	Late Bronze/Iron	6.65	**Tmq3**
MV131	Israel	Tel-Miqne	*Bos*	petrous	Late Bronze/Iron	16.80	**Tmq4**
MV132	Israel	Tel-Miqne	*Sus-Bos?*	petrous	Late Bronze/Iron age	0.23	
MV133	Israel	Tel-Yoqneam	*Sus-Bos?*	petrous	Iron age or Later		
MV134	Israel	Tel-Yoqneam	*Bos?*	petrous	Iron age or Later		
MV135	Turkey	Acemhoyuk	*Sus?*	petrous	2200BC	29.69	**Ace1**
MV136	Serbia	Plocnik	*Bos*	petrous	Middle Neo (5400-5200BC)	44.34	**Plo1**
MV137	Serbia	Plocnik	*Bos taurus*	petrous	Late Neo (5200-5000BC)	36.55	**Plo2**
MV138	Serbia	Plocnik	*Bos taurus*	petrous	Late Neo (5200-5000BC)	56.71	**Plo3**
MV139	Serbia	Plocnik	*Bos taurus*	petrous	?	54.43	**Plo4**
MV140	Turkey	Kortik Teppe	*Bos taurus*	long bone	PPNA	1.75	**Kor1**
MV141	Turkey	Kortik Teppe	*Bos*	long bone	PPNA		
MV142	Turkey	Kortik Teppe	*Bos*	long bone	PPNA		
MV143	Turkey	Kortik Teppe	*Bos*	long bone	PPNA	0.26	**Kor2**
MV144	Turkey	Kortik Teppe	*Bos*	long bone	PPNA		
MV145	Turkey	Kortik Teppe	*Bos*	long bone	PPNA		
MV146	Turkey	Kortik Teppe	*Bos*	long bone	PPNA	0.45	
MV147	Israel	Tel-Es Safi	*Bos*	petrous	Iron Age II	3.79	**Tsa3**
MV148	Israel	Ashkelon Mari	*Bos*	petrous	Chalcholitic	0.11	
MV149	Israel	Gilat	*Bos?*	petrous	Chalcholitic	0.24	**Gil1**
MV150	Israel	Gilat	*Bos*	petrous	Chalcholitic	0.13	
MV151	Israel	Abu Gosh	*Bos?*	petrous	Mid-Late PPNB	0.10	
MV152	Israel	Abu Gosh	*Bos?*	petrous	Mid late PPNB		
MV153	Israel	Nahal Tillah	*Bos?*	petrous	Chalcholitic	0.26	**Nah1**
MV154	Israel	Qassis	*Bos?*	petrous	Early Bronze Age	0.58	**Tqa1**
MV155	Israel	Qassis	*Bos*	petrous	Early Bronze Age	3.84	**Tqa2**
MV156	Serbia	Plocnik	*Bos?*	petrous	Late Neo (5000-4800BC)	30.82	**Plo5**
MV157	Serbia	Plocnik	*Bos taurus*	petrous	Late Neo (5200-5000BC)	53.43	
MV158	Serbia	Plocnik	*Bos taurus*	petrous	Late Neo (5200-5000BC)	1.66	
MV159	Serbia	Plocnik	*Bos taurus*	petrous	Middle Neo (5400-5200BC)	26.15	**Plo6**
MV160	Serbia	Plocnik	*Bos taurus*	petrous	Late Neo (5200-5000BC)	32.59	**Plo7**

MV161	Serbia	Plocnik	*Bos taurus*	petrous	Late Neo (5200-5000BC)	48.19	
MV162	Serbia	Plocnik	*Bos taurus*	petrous	Late Neo (5200-5000BC)	29.02	**Plo8**
MV163	Serbia	Plocnik	*Bos taurus*	petrous	?	36.81	
MV164	Serbia	Belovode-Veliko	*?*	petrous	?	21.23	**Bel1**
MV165	Serbia	Belovode-Veliko	*?*	petrous	?	27.89	**Bel2**
MV166	Georgia	Kazbegi	*Bos*	petrous	Medieval	53.78	**Kaz4**
MV167	Iran	Hasanlu	*Bos*	petrous	Middle Bronze	21.95	**Has1**
MV168	Iran	Hasanlu	*Bos*	petrous	Iron III	0.37	**Has2**
MV169	Iran	Hasanlu	*Bos*	petrous	Early Bronze	43.13	**Has3**
MV170	Iran	Hasanlu	*Bos*	petrous	Iron II	23.97	**Has4**
MV171	Iran	Hasanlu	*Bos*	petrous	Achaemenid/Persian Empire	12.83	**Has5**
MV172	Iran	Qazvin	*Bos*	petrous	Neolithic/Chalcolithic	48.42	**Qaz1**
MV173	Iran	Khorasan Central	*Bos*	petrous	Parthian Empire	50.96	**Kho1**
MV174	Iran	Zagros Central	*Bos*	petrous	Iron Age	0.04	
MV175	Iran	Luristan	*Large Mammal*	petrous	Chalcolithic,Iron	0.38	
MV176	Iran	Fars	*Bos*	petrous	Chalcolithic,Bronze	7.45	**Far1**
MV177	Iran	Azerbaijan	*Bos*	petrous	Bronze	0.36	
MV178	Iran		*Horse cf. by D*	petrous	Paleolithic	0.36	
MV179	Poland	Ludwinowo	*Bos*	petrous	Early Neo	0.17	
MV180	Poland	Ludwinowo	*Bos*	petrous	Early Neo	34.68	**Lud1**
MV181	Poland	Ludwinowo	*Bos*	petrous	Early Neo	49.33	**Lud2**
MV182	Poland	Ludwinowo	*Bos*	petrous	Early Neo	53.34	**Lud3**
MV183	Poland	Ludwinowo	*Bos*	petrous	Early Neo	35.41	**Lud4**
MV184	Poland	Rzucewo	*Bos*	petrous	Late Neo	2.88	
MV185	Poland	Rzucewo	*Bos*	petrous	Late Neo	8.00	
MV186	Poland	Kierzkowo	*Bos*	petrous	Late Neo	13.99	**Kie1**
MV187	Poland	Kierzkowo	*Bos*	petrous	Late Neo	46.35	**Kie2**
MV188	Poland	Kierzkowo	*Bos*	petrous	Late Neo	1.06	**Baikal1**
MV189	Russia	Barguzin river, Baikal	*Bos primigenius*	petrous	?	58.61	**BRus1**
MV190	Russia	Volgograd	*Bison priscus*	petrous	?	21.90	**BRus2**

MV191	Yakutia	North Yakutia	*Bison priscus*	petrous	?	59.26	**BRus3**
MV192	Russia	Astrackhan	*Bison priscus*	petrous	?	0.06	**Kalisz1**
MV193	Poland	Kalisz, Pros River	*Bos primigenius*	petrous	?	0.00	**Tula1**
MV194	Russia	Tula Region	*Bos primigenius*	petrous	?	0.03	**Kalisz2**
MV195	Poland	Kalisz, Pros River	*Bos primigenius*	petrous	?	0.35	**Kalisz3**
MV196	Poland	Kalisz, Pros River	*Bos primigenius*	petrous	?	0.06	**Belorus1**
MV197	Belorus	Brest district	*Bos primigenius*	petrous	?	0.22	**Gyumri1**
MV198	Armenia	Gyumri district	*Bos primigenius*	petrous	?	0.53	**Tango1**
MV199	no info	no info	*Bos primigenius*	petrous	?	0.45	**Tango2**
MV200	no info	no info	*Bos primigenius*	petrous	?	0.49	**Gyumri2**
MV201	Armenia	Gyumri district	*Bos primigenius*	petrous	?	0.25	**Bir1**
MV202	Moldova	Birnova Luka	*Bos taurus*	tooth	Cucuteni-Trypillian Culture (early)	0.00	**Bir2**
MV203	Moldova	Birnova Luka	*Bos taurus*	tooth	Cucuteni-Trypillian Culture (early)	0.00	**Bir3**
MV204	Moldova	Birnova Luka	*Bos taurus*	tooth	Cucuteni-Trypillian Culture (early)	0.01	**Bir4**
MV205	Moldova	Birnova Luka	*Bos taurus*	tooth	Cucuteni-Trypillian Culture (early)	0.00	
MV206	Israel	Tel-Es Safi	*Bos*	petrous	Cf. Early Bronze Age	0.62	
MV207	Israel	Tel-Es Safi	*Bos*	petrous	Cf. Early Bronze Age		
MV208	Israel	Tel-Es Safi	*Horse cf. by D*	petrous	Cf. Early Bronze Age	0.91	
MV209	Israel	Tel-Es Safi	*Bos*	petrous	Cf. Early Bronze Age	4.43	
MV210	Israel	Tel-Aphek	*Bos*	petrous	Middle Bronze- Iron Age	66.41	
MV211	Israel	Tel-Michal	*Bos*	petrous	Middle Bronze- Iron Age		
MV212	Israel	Bi res-Safadi	*Bos*	petrous	Chalcolithic		
MV213	Israel	Jerusalem	*Bos*	petrous	Persian-Roman (to check!!)		
MV214	Israel	Jerusalem	*Bos*	petrous	Persian-Roman (to check!!)		
MV215	Israel	Jerusalem	*Bos*	petrous	Persian-Roman (to check!!)		**Dav3**
MV216	Israel	Tel- Yoqneam	*Bos*	petrous	Bronze age -Cruzader (to check)	9.85	
MV217	Israel	Tel- Yoqneam	*Bos*	petrous	Bronze age -Cruzader (to check)		

MV218	Israel	Tel- Yoqneam	*Bos*	petrous	Bronze age -Cruzader (to check)		
MV219	Israel	Tel- Yoqneam	*Bos*	petrous	Bronze age -Cruzader (to check)		
MV220	South Kenya	Ngamuriak, Mara	*Bos*	petrous		0.00	
MV221	South Kenya	Ngamuriak, Mara	*Bos*	petrous		0.00	
MV222	Iran	Hasanlu		petrous			
MV223	Iran	Hasanlu		petrous			
MV224	Iran	Chalou	*Bos*	petrous			
MV225	Tanzania	Luxmanda	*Bos taurus*	petrous		0.00	
MV226	Tanzania	Luxmanda	*Bos taurus*	petrous		0.00	
MV227	Tanzania	Luxmanda	*Bos*	petrous		0.00	
MV228	Tanzania	Luxmanda	*Bos taurus*	petrous		~5% human	
MV229	Tanzania	Luxmanda	*Bos taurus*	petrous		0.00	
MV230	Tanzania	Luxmanda	*Cf. Bos*	petrous		0.00	
MV231	Tanzania	Luxmanda	*Bos taurus*	petrous		0.00	
MV232	Tanzania	Luxmanda	*Bos taurus*	petrous		0.00	
MV233	Tanzania	Luxmanda	*Bos taurus*	petrous		0.00	
MV234	Turkmenistan	Monjukli Depe	*Bos taurus*	petrous	Chalcolithic	7.78	**Mon1**
MV235	Turkmenistan	Monjukli Depe	*Bos taurus*	petrous		3.24	
MV236	Turkmenistan	Monjukli Depe	*Bos taurus*	petrous		1.93	
MV237	Uzbekistan	Tilla Bulak	*Bos taurus*	petrous		24.41	**Bul1**
MV238	Iran	Darre-ye Bolaghi	*Bos taurus*	petrous		0.77	
MV239	Uzbekistan	Kok Tepe	*Bos*	petrous	Iron Age	5.91	**Kok1**
MV240	Uzbekistan	Yerqorqan	*Bos*	petrous	Achaemenid (Late 1st Cen BC)	45.91	**Yer1**
MZ1	India	?	*Bos indicus*	petrous	90's?	13.41	
MZ2	India	?	*Bos indicus*	petrous	90's?	38.93	
SAC2	Iran	Tapeh-Sang-e-Caxmaq	*Bos*	long bone	Neolithic	0.28	
SAC3	Iran	Tapeh-Sang-e-Caxmaq	*Bos*	long bone	Neolithic	4.39	**Sac3**
SAC4	Iran	Tapeh-Sang-e-Caxmaq	*Bos*	long bone	Neolithic	0.24	
SAC5	Iran	Tapeh-Sang-e-Caxmaq	*Bos*	long bone	Neolithic	0.20	
SAC6	Iran	Tapeh-Sang-e-Caxmaq	*Bos*	long bone	Neolithic	0.08	

SAC7	Iran	Tapeh-Sang-e-Caxmaq	*Bos*	long bone	Neolithic	0.58	
TAS1	Iran	Tapeh-Sang-e-Caxmaq	*Bos*	long bone	Neolithic	0.32	

9.2. Chapter 4 Supplementary tables

Table 9.2.1- Ancient DNA preservation.

ID	% DNA	Latitude
Ace1	29	38.4114
Ash4	2.3	31.662429
Azer1	0.29	39.1613
Baikal1	70	53.425
Bed3	30	51.054167
Bed4	17	51.054167
Bel1	21	44.378333
Bel2	28	44.378333
Belorus1	22	51.054167
Bes1	35	35.376861
Bes2	39	35.376861
Bir1	0.27	48.2526
Bir2	0.05	48.2526
Bir3	1.45	48.2526
Bla1	14	43.4353
Bla2	17	43.4353
Bri1	56	53.2531
Bub1	38	43.305556
Bul1	24	37.7
Bun1	41	52.050278
Bun2	50	52.050278
CA317	9	42.6575
Cas1	38.14	32.596389
Ch22	3	37.666667
Cla1	59	57.17116
Cla2	51	57.17116
Cpc98	21	53.083186
Dan1	0.1	33.249

Dav1	16	31.773611
Dav2	0.22	31.773611
Dav3	7	31.773611
Dav4	6	31.773611
Dav5	0.22	31.773611
Dro1	53	53.2
Dub1	32	53.349722
Dyr1	68	52.574067
Dzh1	58	42.683333
Dzh2	26	42.683333
Els1	55	51.915556
Fal7	30	53.260309
Far1	7.5	30.173889
Fir1	60	53.248889
Gil1	0.24	31.328497
Gyumri1	53	40.789444
Gyumri2	25	40.789444
Has1	22	37.004831
Has3	43	37.004831
Has4	24	37.004831
Has5	13	37.004831
Hou1	59	52.023722
Hou2	57	52.011444
Hxh1	33	49.145275
Hxh2	53	49.145275
Kalisz1	0.2	51.766667
Kalisz2	35	51.766667
Kalisz3	6	51.766667
Kaz1	58	42.6575
Kaz2	57	42.6575
Kaz3	62	42.6575
Kaz4	54	42.6575
Kho1	51	36.213333
Kie1	14	52.846667

Kie2	46	52.846667
Kir4	54	49.95
Kok1	6	39.893333
Kor1	1	37.827695
Lud1	34	52.561944
Lud2	49	52.561944
Lud3	53	52.561944
Lud4	35	52.561944
Mar1	3.2	35.961944
Men1	13	40.286743
Men2	20	40.286743
Mon1	8	36.848528
Mus1	2	31.2047
Nah1	0.26	31.251898
New1	55	53.694369
New2	36	53.694369
New3	49	53.694369
New4	43	53.694369
New5	51	53.694369
Otb1	57	53.233889
Plo1	44	43.201944
Plo2	36	43.201944
Plo3	57	43.201944
Plo4	54	43.201944
Plo5	31	43.201944
Plo6	26	43.201944
Plo7	32	43.201944
Plo8	29	43.201944
Qaz1	48	36.266667
Sac3	4.4	36.499722
Sch1	47	51.983333
Ste1	42	52.157222

Stu1	33	44.57
Sub1	40	37.351556
Tango1	45	N/A
Tango2	49	N/A
Tda1	0.32	31.9765
Th7	0.81	34.783333
Thr1	0.25	32.690823
Tmq1	0.48	31.77889
Tmq2	0.68	31.77889
Tmq3	6.65	31.77889
Tmq4	17	31.77889
Tqa1	0.58	32.733333
Tqa2	3.84	32.733333
Tqa3	3.5	32.733333
Tri1	24	49.75
Tsa1	38	31.699722
Tsa2	0.3	31.699722
Tsa3	3.7	31.699722
Tula1	3	54.2
Tyq1	29	32.6641
Viz1	33	51.941944
Viz2	43	51.941944
Win1	63	53.333333
Yer1	46	41.266667
Yor1	58	53.958333
Yor2	41	53.958333
Yor3	48	53.958333
Yor4	46	53.958333
Zah1	20.35	32.5

Table 9.2.2 - Procrustes projection PCA analyses.

ID	Number of Loci Covered	Average Coverage	Procrustes Similarity	PC1	PC2
Ace1	76097	0.122	0.999	-211.174	109.968
Azer1	879	0.001	0.975	-201.431	63.4152
Bed3	663544	20.545	1.000	-128.768	-17.6548
Bed4	567098	2.314	1.000	-135.288	-19.8156
Bel1	55822	0.088	0.999	-259.622	-18.4413
Bel2	85405	0.138	0.999	-254.661	-1.42557
Belorus1	549568	2.083	1.000	-148.324	-14.7443
Bir1	1076	0.002	0.979	-229.072	57.9252
Bir2	895	0.001	0.977	-220.27	1.43727
Bir3	2028	0.003	0.989	-117.19	30.405
Bla1	13382	0.020	0.998	-252.98	8.61233
Bla2	2213	0.003	0.989	-322.412	-29.3853
Bri1	627810	3.583	1.000	-247.046	-31.6743
Bub1	192590	0.353	0.999	-281.895	-20.0858
Bun1	547592	1.867	1.000	-261.743	-41.9868
Bun2	600879	2.527	1.000	-261.375	-42.0358
Ch22	187790	0.340	0.999	-200.66	80.7494
Cla1	664556	16.316	1.000	-261.183	-77.4191
Cla2	568105	2.032	1.000	-272.819	-77.6521
CPC98	627616	3.880	1.000	-142.204	-23.2448
Dan1	122	0.000	0.846	-119.889	54.9559
Dav1	649876	5.762	1.000	-171.375	251.046
Dav2	2751	0.004	0.992	-185.873	230.635
Dav3	10987	0.017	0.997	-171.043	229.5
Dav4	8337	0.013	0.997	-151.714	255.456
Dav5	2867	0.004	0.992	246.51	59.5337
Dro1	625265	3.138	1.000	-259.256	-50.7622
Dub1	578501	2.206	1.000	-284.664	-93.8003
Dyr1	603951	2.526	1.000	-246.22	-25.7777
Dzh1	663445	10.871	1.000	-236.893	12.83

Dzh2	643211	4.416	1.000	-224.036	33.8791
Els1	613008	2.788	1.000	-252.051	-45.9447
Fal7	577412	2.121	1.000	-160.57	-19.5265
Far1	21923	0.034	0.998	-201.233	114.271
Fir1	631432	3.433	1.000	-253.41	-40.3105
Gil1	438	0.001	0.952	-146.656	178.473
Gyumri2	532718	1.988	1.000	-139.424	111.84
Has1	23888	0.037	0.998	-195.848	63.0903
Has3	444575	1.345	1.000	-209.148	81.3783
Has4	479711	1.523	1.000	-170.698	76.4532
Has5	24947	0.038	0.999	-180.59	81.3245
Hou1	615910	2.781	1.000	-251.909	-35.1898
Hou2	615539	2.779	1.000	-254.4	-35.1413
Hxh1	662528	9.255	1.000	-249.967	-18.3478
Hxh2	664400	24.538	1.000	-128.674	-17.6825
Kalisz2	612338	3.018	1.000	-143.774	-8.43008
Kalisz3	9494	0.014	0.997	-148.863	-11.4735
Kie1	31383	0.048	0.999	-265.549	-31.6311
Kie2	140981	0.241	0.999	-227.885	-25.1924
Kir4	664523	15.848	1.000	-208.005	30.5606
Lud1	101418	0.167	0.999	-266.263	-12.4019
Lud2	211390	0.391	0.999	-258.554	-14.7554
Lud3	180672	0.322	0.999	-256.608	-8.94503
Lud4	124001	0.208	0.999	-265.011	-13.6132
Mar1	26281	0.040	0.999	-200.443	102.301
Men1	615175	3.078	1.000	-210.434	74.1733
Men2	529234	1.927	1.000	-216.551	67.6786
Nah1	214	0.000	0.907	-125.972	256.222
New1	664562	18.148	1.000	-270.048	-68.3066
New2	645417	4.112	1.000	-281.685	-99.1547
New3	659490	5.589	1.000	-272.673	-69.3121
New4	649642	4.406	1.000	-276.603	-71.0394
New5	655520	5.051	1.000	-275.363	-71.2043
Otb1	617479	2.842	1.000	-247.552	-43.7375

Plo1	82122	0.133	0.999	-243.277	-4.68486
Plo2	198138	0.363	0.999	-259.859	-8.31835
Plo3	615527	2.880	1.000	-244.447	-1.09255
Plo4	619260	2.944	1.000	-240.952	5.71727
Plo5	56778	0.089	0.999	-261.376	-7.20628
Plo6	72971	0.117	0.999	-271.302	-15.7414
Plo7	73781	0.118	0.999	-254.467	-1.87316
Plo8	118796	0.203	0.999	-251.425	-9.41854
Sac3	13595	0.021	0.998	-206.251	108.452
Sch1	537882	1.774	1.000	-266.594	-49.3612
Ste1	404407	1.011	1.000	-272.166	-53.2435
Stu1	99731	0.164	0.999	-252.479	-1.68256
Sub1	663789	14.534	1.000	-207.345	66.6524
Tda1	732	0.001	0.970	-190.899	249.155
Th7	47374	0.081	0.999	-101.301	191.97
Thr1	833	0.001	0.973	-208.227	293.725
Tri1	581650	2.384	1.000	-143.864	-22.0482
Tula1	766	0.001	0.972	68.1943	63.4446
Viz1	343255	0.775	1.000	-264.707	-41.9419
Viz2	590189	2.284	1.000	-255.399	-39.7261
Win1	664651	19.830	1.000	-252.693	-48.6656
Yor1	663318	8.515	1.000	-270.768	-81.9001
Yor2	651257	4.259	1.000	-270.439	-78.6532
Yor3	612451	2.738	1.000	-272.341	-74.6357
Yor4	633815	3.326	1.000	-271.235	-79.8264

Table 9.2.3 -ADMIXTURE Figures 4.5 A and B. Ancient specimens only. Values are rounded to 2 decimal places for this table.

ID	Indicine	European taurine	African taurine	Latitude	Longitude	Time
Bed3	0.11	0.74	0.14	51.054167	6.521667	Mesolithic
Bed4	0.12	0.75	0.13	51.054167	6.521667	Mesolithic
Bel1	0.01	0.84	0.16	44.378333	21.419444	Neolithic
Bel2	0.00	0.83	0.17	44.378333	21.419444	Neolithic
Bla1	0.00	0.83	0.17	43.4353	21.0631	Neolithic
Bla2	0.00	0.79	0.21	43.4353	21.0631	Neolithic
Bir1	0.00	0.73	0.27	48.2526	27.3136	Neolithic
Bir2	0.00	0.90	0.10	48.2526	27.3136	Neolithic
Bir3	0.14	0.73	0.13	48.2526	27.3136	Neolithic
Bri1	0.00	0.90	0.10	53.2531	5.7856	Roman
Bub1	0.00	0.86	0.14	43.305556	21.8725	Neolithic
Bun1	0.00	0.90	0.10	52.050278	5.233333	Iron
Bun2	0.00	0.91	0.09	52.050278	5.233333	Iron
Ch22	0.01	0.69	0.31	37.666667	32.828056	Neolithic
Cla1	0.00	0.97	0.03	57.17116	-7.40759	Bronze
Cla2	0.00	0.96	0.04	57.17116	-7.40759	Bronze
CPC98	0.11	0.76	0.14	53.079803	1.640942	Mesolithic
Dan1	0.00	0.89	0.11	33.249	35.652	Bronze
Dav1	0.00	0.40	0.60	31.773611	35.235556	Bronze
Dav2	0.00	0.46	0.54	31.773611	35.235556	Bronze
Dav3	0.02	0.35	0.63	31.773611	35.235556	Bronze
Dav4	0.06	0.25	0.69	31.773611	35.235556	Bronze
Dro1	0.00	0.92	0.08	53.2	5.65	Post Iron
Dub1	0.00	0.99	0.01	53.349722	-6.260278	Post Iron
Dyr1	0.01	0.89	0.10	52.574067	12.968658	Post Iron
Dzh1	0.00	0.83	0.17	42.683333	23.316667	Neolithic
Dzh2	0.00	0.79	0.21	42.683333	23.316667	Neolithic
Els1	0.00	0.92	0.08	51.915556	5.837778	Post Iron
Fal7	0.08	0.78	0.14	53.260309	13.977105	Post Iron
Far1	0.00	0.58	0.42	30.173889	52.668056	Neolithic

Fir1	0.00	0.92	0.08	53.248889	5.559722	Post Iron
Gil1	0.08	0.21	0.70	31.328497	34.649997	Chalcolithic
Gyumri2	0.07	0.57	0.36	40.789444	43.8475	Neolithic
Hou1	0.00	0.91	0.09	52.023722	5.176972	Post Iron
Hou2	0.00	0.90	0.10	52.011444	5.191139	Post Iron
Hxh1	0.00	0.88	0.12	49.145275	8.221805	Neolithic
Hxh2	0.11	0.75	0.14	49.145275	8.221805	Neolithic
Kalisz1	0.00	1.00	0.00	51.766667	18.083333	Unknown
Kalisz2	0.10	0.75	0.15	51.766667	18.083333	Unknown
Kalisz3	0.07	0.78	0.15	51.766667	18.083333	Unknown
Kie1	0.01	0.91	0.08	52.846667	17.861389	Neolithic
Kie2	0.02	0.84	0.14	52.846667	17.861389	Neolithic
Kir4	0.00	0.79	0.21	49.95	11.583333	Neolithic
Lud1	0.00	0.88	0.12	52.561944	19.015833	Neolithic
Lud2	0.00	0.87	0.13	52.561944	19.015833	Neolithic
Lud3	0.00	0.87	0.13	52.561944	19.015833	Neolithic
Lud4	0.00	0.86	0.14	52.561944	19.015833	Neolithic
Mar1	0.01	0.63	0.36	35.961944	50.68	Neolithic
Men1	0.00	0.72	0.28	40.286743	29.528623	Neolithic
Men2	0.00	0.71	0.29	40.286743	29.528623	Neolithic
Nah1	0.25	0.00	0.75	31.251898	34.78608	Bronze
New1	0.00	0.95	0.05	53.694369	-6.475031	Neolithic
New2	0.00	0.99	0.01	53.694369	-6.475031	Post Iron
New3	0.00	0.95	0.05	53.694369	-6.475031	Neolithic
New4	0.00	0.95	0.05	53.694369	-6.475031	Neolithic
New5	0.00	0.96	0.04	53.694369	-6.475031	Neolithic
Otb1	0.00	0.91	0.09	53.233889	5.511944	Post Iron
Plo1	0.00	0.84	0.16	43.201944	21.355556	Neolithic
Plo2	0.00	0.85	0.15	43.201944	21.355556	Neolithic
Plo3	0.00	0.85	0.15	43.201944	21.355556	Neolithic
Plo4	0.00	0.83	0.17	43.201944	21.355556	Neolithic
Plo5	0.00	0.85	0.15	43.201944	21.355556	Neolithic

Plo6	0.00	0.87	0.13	43.201944	21.355556	Neolithic
Plo7	0.00	0.84	0.16	43.201944	21.355556	Neolithic
Plo8	0.00	0.85	0.15	43.201944	21.355556	Neolithic
Sac3	0.00	0.62	0.38	36.266667	50	Neolithic
Sch1	0.00	0.92	0.08	51.983333	4.316667	Neolithic
Ste1	0.00	0.93	0.07	52.157222	4.4925	Iron
Stu1	0.00	0.84	0.16	44.57	20.14	Neolithic
Sub1	0.00	0.73	0.27	37.351556	31.926972	Neolithic
Tda1	0.03	0.57	0.40	31.9765	34.9694	Bronze
Thr1	0.00001	0.07	0.93	32.690823	34.94166	Neolithic
Tri1	0.11	0.76	0.13	49.75	6.633333	Mesolithic
Viz1	0.00	0.90	0.10	51.941944	5.139444	Bronze
Viz2	0.00	0.91	0.09	51.941944	5.139444	Bronze
Win1	0.00	0.92	0.08	53.333333	6.516667	Post Iron
Yor1	0.00	0.98	0.02	53.958333	-1.080278	Post Iron
Yor2	0.00	0.96	0.04	53.958333	-1.080278	Post Iron
Yor3	0.00	0.96	0.04	53.958333	-1.080278	Post Iron
Yor4	0.00	0.96	0.04	53.958333	-1.080278	Post Iron

Table 9.2.4 - ADMIXTURE Figure 4.6. Modern 700K populations only. ADMIXTURE proportions correspond to the median value for each breed. Values are rounded to 2 decimal places for this table.

Breed Code	Name	No of individuals	Country	Indicine	European taurine	African taurine	Latitude	Longitude
ALE	Alentejana	9	Portugal	0.00	0.81	0.19	38.95	-7.666667
ANB	Anatolian Black	13	Turkey	0.33	0.46	0.22	38.847305	35.326303
ANG	Angus	42	Scotland	0.00	1.00	0.00	55.953056	-3.188889
BLO	Blonde d'Aquitaine	5	France	0.00	0.88	0.12	48.85	2.35
BRM	Brahman	46	India	0.95	0.05	0.01	23.116108	79.437682
BSW	Brown Swiss	22	Switzerland	0.00	0.90	0.10	46.875323	8.092078

BUT	Butana	7	Ethiopia	0.72	0.00	0.28	9.03	38.74
CHL	Charolais (UK)	37	France	0.01	0.91	0.07	48.85	2.35
EAR	East Anatolian Red	12	Turkey	0.35	0.44	0.21	38.847305	35.326303
GAL	Galloway	9	Scotland	0.00	0.97	0.03	55.953056	-3.188889
GIR	Gir	29	India	1.00	0.00	0.00	23.116108	79.437682
GNS	Guernsey	21	Guernsey	0.00	0.93	0.07	49.45	-2.6
GOB	Gobra	10	Senegal	0.54	0.00	0.45	14.348622	-14.562787
HAR	Hariana	10	India	1.00	0.00	0.00	23.116108	79.437682
HIG	Highland	8	Scotland	0.00	0.97	0.03	55.953056	-3.188889
HOL	Holstein (FR)	60	Netherlands ?	0.00	0.98	0.02	52.366667	4.883333
JER	Jersey (FR)	38	Jersey	0.00	0.97	0.03	49.212714	2.132474
KEN	Kenana	10	Ethiopia	0.72	0.00	0.27	9.03	38.74
KER	Kerry	9	Ireland	0.00	0.99	0.01	52.060038	-9.505326
LAG	Lagune	5	Ghana	0.00	0.00	1.00	8.018138	-1.109819
LMS	Limousin	50	France	0.00	0.90	0.10	48.85	2.35
MAR	Maremmana	4	Italy	0.09	0.74	0.17	42.9983	12.447301
MAU	Maure	10	Mali	0.55	0.00	0.45	17.649168	-1.294065
MON	Montbeliarde	5	France	0.00	0.89	0.11	48.85	2.35
MUR	Murutu	11	Nigeria	0.00	0.00	1.00	9.70394	8.048066
NDA	N'Dama	32	Guinea	0.00	0.00	1.00	10.383333	-12.083333
NEL	Nelore	31	India	1.00	0.00	0.00	23.116108	79.437682
NOR	Normande	5	France	0.00	0.92	0.08	48.85	2.35
NRC	Norwegian Red Cattle	17	Norway	0.00	0.96	0.04	61.863647	10.086065
OGR	Gaur	3	South Asia/ South East Asia	0.95	0.03	0.02	25.149424	90.257418
OYK	Yak	2	Central Asia/Tibete /Mongolia/ Russia	0.93	0.04	0.02	33	88
PMT	Piedmontese	21	Italy	0.00	0.87	0.12	42.9983	12.447301

RGU	Red Angus	10	Scotland	0.00	1.00	0.00	55.953056	-3.188889
RMG	Romagnola	21	Italy	0.08	0.75	0.17	42.9983	12.447301
SAH	Sahiwal	10	Pakistan	1.00	0.00	0.00	29.935612	69.194106
SAR	South Anatolian Red	13	Turkey	0.32	0.34	0.34	38.847305	35.326303
SHK	Sheko	16	Ethiopia	0.56	0.02	0.42	9.03	38.74
SIK	Sikia	5	Greece	0.12	0.72	0.16	39.511042	22.337491
SIM	Simmental	10	Switzerland	0.00	0.92	0.08	46.875323	8.092078
SIS	Sistani	5	Iran	0.94	0.03	0.03	31.974037	53.968441
SOM	Somba	10	Benin/Togo	0.02	0.00	0.98	9.000939	1.626503
TAL	Taleshi	5	Iran	0.49	0.34	0.18	31.974037	53.968441
WAG	Wagyu	13	Japan	0.02	0.76	0.22	36.508534	138.573993

Table 9.2.5 - ADMIXTURE Chapter 4 Figure 4.7. Modern 700K populations only. ADMIXTURE proportions showed for each modern individual, for each population. Values are rounded to 2 decimal places for this table.

Breed Code	Individual	Indicine	European taurine	African taurine
ALE	AL10	0.00	0.81	0.19
ALE	AL12	0.00	0.80	0.20
ALE	AL13	0.00	0.81	0.19
ALE	AL17	0.01	0.81	0.18
ALE	AL18	0.00	0.80	0.20
ALE	AL19	0.00	0.80	0.20
ALE	AL23	0.00	0.81	0.19
ALE	AL25	0.00	0.83	0.17
ALE	AL26	0.00	0.82	0.18
ANB	AB01	0.33	0.47	0.21
ANB	AB08	0.33	0.45	0.22
ANB	AB10	0.33	0.46	0.22
ANB	AB14	0.34	0.45	0.21
ANB	AB17	0.15	0.71	0.14

ANB	AB21	0.23	0.58	0.18
ANB	AB28	0.33	0.45	0.21
ANB	AB29	0.31	0.47	0.22
ANB	AB32	0.31	0.47	0.22
ANB	AB36	0.33	0.43	0.23
ANB	AB38	0.33	0.46	0.21
ANB	AB40	0.32	0.46	0.22
ANB	AB41	0.33	0.44	0.23
ANG	ANG_000017	0.00	1.00	0.00
ANG	ANG_000022	0.00	1.00	0.00
ANG	ANG_001	0.00	1.00	0.00
ANG	ANG_002	0.00	1.00	0.00
ANG	ANG_003	0.00	1.00	0.00
ANG	ANG_004	0.00	1.00	0.00
ANG	ANG_005	0.00	1.00	0.00
ANG	ANG_006	0.00	1.00	0.00
ANG	ANG_007	0.00	1.00	0.00
ANG	ANG_008	0.00	1.00	0.00
ANG	ANG_009	0.00	1.00	0.00
ANG	ANG_001400	0.00	1.00	0.00
ANG	ANG_001778	0.00	1.00	0.00
ANG	ANG_001781	0.00	1.00	0.00
ANG	ANG_010	0.00	1.00	0.00
ANG	ANG_011	0.00	1.00	0.00
ANG	ANG_012	0.00	1.00	0.00
ANG	ANG_013	0.00	1.00	0.00
ANG	ANG_014	0.00	1.00	0.00
ANG	ANG_015	0.00	1.00	0.00
ANG	ANG_016	0.00	1.00	0.00
ANG	ANG_017	0.00	1.00	0.00
ANG	ANG_018	0.00	1.00	0.00
ANG	ANG_019	0.00	1.00	0.00

ANG	ANG_020	0.00	1.00	0.00
ANG	ANG_021	0.00	1.00	0.00
ANG	ANG_022	0.00	1.00	0.00
ANG	ANG_023	0.00	1.00	0.00
ANG	ANG_024	0.00	1.00	0.00
ANG	ANG_026	0.00	1.00	0.00
ANG	ANG_027	0.00	1.00	0.00
ANG	ANG_028	0.00	1.00	0.00
ANG	ANG_029	0.00	1.00	0.00
ANG	ANG_031	0.00	1.00	0.00
ANG	ANG_032	0.00	1.00	0.00
ANG	ANG_033	0.00	1.00	0.00
ANG	ANG_034	0.00	1.00	0.00
ANG	ANG_035	0.00	1.00	0.00
ANG	ANG_036	0.00	1.00	0.00
ANG	ANG_038	0.00	1.00	0.00
ANG	ANG_039	0.00	1.00	0.00
ANG	ANG_041	0.00	1.00	0.00
BLO	BLO_001	0.00	0.88	0.12
BLO	BLO_002	0.00	0.90	0.10
BLO	BLO_003	0.00	0.88	0.12
BLO	BLO_004	0.00	0.87	0.13
BLO	BLO_005	0.00	0.89	0.11
BRM	BRM_000014	0.96	0.03	0.01
BRM	BRM_001	0.98	0.02	0.00
BRM	BRM_002	0.97	0.03	0.01
BRM	BRM_003	0.95	0.04	0.01
BRM	BRM_004	0.85	0.13	0.02
BRM	BRM_005	0.94	0.05	0.00
BRM	BRM_006	0.93	0.06	0.01
BRM	BRM_007	0.98	0.02	0.00
BRM	BRM_008	0.95	0.05	0.00
BRM	BRM_009	0.94	0.06	0.00
BRM	BRM_010	0.93	0.07	0.00

BRM	BRM_011	0.96	0.04	0.00
BRM	BRM_012	0.96	0.04	0.00
BRM	BRM_013	0.88	0.11	0.01
BRM	BRM_014	0.95	0.04	0.01
BRM	BRM_015	0.89	0.11	0.00
BRM	BRM_016	0.87	0.13	0.00
BRM	BRM_017	0.86	0.13	0.00
BRM	BRM_018	0.89	0.11	0.00
BRM	BRM_019	0.95	0.04	0.01
BRM	BRM_021	0.96	0.03	0.01
BRM	BRM_022	0.96	0.03	0.02
BRM	BRM_023	0.95	0.04	0.01
BRM	BRM_024	0.94	0.05	0.01
BRM	BRM_025	0.97	0.03	0.00
BRM	BRM_026	0.92	0.07	0.00
BRM	BRM_027	0.94	0.05	0.01
BRM	BRM_028	0.92	0.07	0.01
BRM	BRM_029	0.92	0.07	0.01
BRM	BRM_030	0.92	0.06	0.01
BRM	BRM_031	0.95	0.04	0.01
BRM	BRM_032	0.93	0.06	0.01
BRM	BRM_033	0.96	0.03	0.01
BRM	BRM_034	0.94	0.05	0.01
BRM	BRM_035	0.91	0.08	0.01
BRM	BRM_036	0.97	0.03	0.01
BRM	BRM_037	0.95	0.04	0.00
BRM	BRM_038	0.95	0.04	0.01
BRM	BRM_039	0.97	0.02	0.01
BRM	BRM_040	0.95	0.04	0.01
BRM	BRM_041	0.98	0.02	0.00
BRM	BRM_042	0.94	0.06	0.00
BRM	BRM_043	0.94	0.05	0.01

BRM	BRM_044	0.95	0.04	0.01
BRM	BRM_045	0.98	0.01	0.01
BRM	BRM_046	0.92	0.07	0.01
BSW	BSW_000024	0.00	0.91	0.09
BSW	BSW_001	0.00	0.91	0.09
BSW	BSW_002	0.00	0.91	0.09
BSW	BSW_003	0.00	0.91	0.09
BSW	BSW_004	0.00	0.89	0.11
BSW	BSW_005	0.00	0.90	0.10
BSW	BSW_006	0.00	0.92	0.08
BSW	BSW_007	0.00	0.90	0.10
BSW	BSW_008	0.00	0.90	0.10
BSW	BSW_009	0.00	0.91	0.09
BSW	BSW_010	0.00	0.91	0.09
BSW	BSW_011	0.00	0.89	0.11
BSW	BSW_012	0.00	0.89	0.11
BSW	BSW_013	0.00	0.90	0.10
BSW	BSW_014	0.00	0.89	0.11
BSW	BSW_015	0.00	0.91	0.09
BSW	BSW_016	0.00	0.90	0.10
BSW	BSW_017	0.00	0.90	0.10
BSW	BSW_018	0.00	0.90	0.10
BSW	BSW_019	0.00	0.90	0.10
BSW	BSW_020	0.00	0.92	0.08
BSW	BSW_022	0.00	0.90	0.10
BUT	BUT12	0.73	0.01	0.27
BUT	BUT13	0.72	0.00	0.28
BUT	BUT15	0.73	0.00	0.27
BUT	BUT16	0.72	0.01	0.28
BUT	BUT17	0.72	0.00	0.28
BUT	BUT18	0.72	0.00	0.28
BUT	BUT21	0.72	0.00	0.28
CHL	CHL_000019	0.02	0.90	0.08
CHL	CHL_001	0.00	0.91	0.09

CHL	CHL_002	0.00	0.93	0.07
CHL	CHL_003	0.00	0.92	0.08
CHL	CHL_004	0.00	0.91	0.09
CHL	CHL_005	0.03	0.91	0.06
CHL	CHL_006	0.01	0.92	0.07
CHL	CHL_007	0.01	0.91	0.08
CHL	CHL_008	0.01	0.93	0.06
CHL	CHL_009	0.02	0.92	0.06
CHL	CHL_010	0.01	0.91	0.09
CHL	CHL_011	0.03	0.91	0.06
CHL	CHL_012	0.01	0.91	0.07
CHL	CHL_013	0.00	0.92	0.08
CHL	CHL_014	0.04	0.90	0.07
CHL	CHL_015	0.01	0.91	0.08
CHL	CHL_016	0.03	0.90	0.07
CHL	CHL_017	0.03	0.90	0.07
CHL	CHL_018	0.01	0.92	0.07
CHL	CHL_019	0.03	0.90	0.07
CHL	CHL_020	0.02	0.91	0.07
CHL	CHL_021	0.02	0.90	0.08
CHL	CHL_022	0.04	0.90	0.06
CHL	CHL_023	0.01	0.91	0.08
CHL	CHL_024	0.05	0.89	0.06
CHL	CHL_025	0.04	0.90	0.07
CHL	CHL_026	0.04	0.90	0.06
CHL	CHL_027	0.01	0.91	0.08
CHL	CHL_028	0.04	0.88	0.09
CHL	CHL_030	0.04	0.88	0.08
CHL	CHL_031	0.04	0.88	0.08
CHL	CHL_032	0.03	0.91	0.06
CHL	CHL_033	0.00	0.92	0.08
CHL	CHL_034	0.00	0.92	0.08

CHL	CHL_035	0.00	0.92	0.08
CHL	CHL_036	0.00	0.91	0.09
CHL	CHL_037	0.00	0.93	0.07
EAR	EA23	0.36	0.37	0.28
EAR	EA24	0.35	0.44	0.21
EAR	EA25	0.36	0.43	0.21
EAR	EA26	0.37	0.43	0.21
EAR	EA27	0.34	0.45	0.21
EAR	EAR9	0.33	0.46	0.21
EAR	EAR11	0.34	0.44	0.22
EAR	EAR13	0.28	0.53	0.19
EAR	EAR14	0.32	0.45	0.23
EAR	EAR17	0.34	0.45	0.21
EAR	EAR30	0.36	0.44	0.21
EAR	EAR31	0.36	0.39	0.25
GAL	GALL8022	0.00	0.97	0.03
GAL	GALL8025	0.00	0.97	0.03
GAL	GALL8034	0.00	0.97	0.03
GAL	GALL8039	0.00	0.98	0.02
GAL	GALL8042	0.00	0.98	0.02
GAL	GALL8043X	0.00	0.98	0.02
GAL	GALL8044	0.00	0.97	0.03
GAL	GALL8046	0.00	0.97	0.03
GAL	GALL8057	0.00	0.97	0.03
GIR	GIR20	1.00	0.00	0.00
GIR	GIR22	1.00	0.00	0.00
GIR	GIR_000016	1.00	0.00	0.00
GIR	GIR_001	1.00	0.00	0.00
GIR	GIR_002	1.00	0.00	0.00
GIR	GIR_003	1.00	0.00	0.00
GIR	GIR_004	1.00	0.00	0.00
GIR	GIR_005	1.00	0.00	0.00
GIR	GIR_006	1.00	0.00	0.00
GIR	GIR_007	1.00	0.00	0.00

GIR	GIR_008	1.00	0.00	0.00
GIR	GIR_009	1.00	0.00	0.00
GIR	GIR_010	1.00	0.00	0.00
GIR	GIR_011	1.00	0.00	0.00
GIR	GIR_012	1.00	0.00	0.00
GIR	GIR_014	1.00	0.00	0.00
GIR	GIR_015	1.00	0.00	0.00
GIR	GIR_016	1.00	0.00	0.00
GIR	GIR_017	1.00	0.00	0.00
GIR	GIR_018	1.00	0.00	0.00
GIR	GIR_019	1.00	0.00	0.00
GIR	GIR_020	1.00	0.00	0.00
GIR	GIR_021	1.00	0.00	0.00
GIR	GIR_022	1.00	0.00	0.00
GIR	GIR_023	1.00	0.00	0.00
GIR	GIR_024	1.00	0.00	0.00
GIR	GIR_025	1.00	0.00	0.00
GIR	GIR_026	1.00	0.00	0.00
GIR	GIR_027	1.00	0.00	0.00
GNS	GNS_000011	0.00	0.92	0.08
GNS	GNS_000012	0.00	0.93	0.07
GNS	GNS_000015	0.00	0.93	0.07
GNS	GNS_000021	0.00	0.93	0.07
GNS	GNS_001	0.00	0.93	0.07
GNS	GNS_002	0.00	0.94	0.06
GNS	GNS_003	0.00	0.93	0.07
GNS	GNS_004	0.00	0.92	0.08
GNS	GNS_005	0.00	0.94	0.06
GNS	GNS_006	0.00	0.93	0.07
GNS	GNS_007	0.00	0.93	0.07
GNS	GNS_008	0.00	0.93	0.07
GNS	GNS_009	0.00	0.92	0.08

GNS	GNS_010	0.00	0.93	0.07
GNS	GNS_013	0.00	0.92	0.08
GNS	GNS_014	0.00	0.92	0.08
GNS	GNS_016	0.00	0.93	0.07
GNS	GNS_017	0.00	0.93	0.07
GNS	GNS_018	0.00	0.93	0.07
GNS	GNS_019	0.00	0.92	0.08
GNS	GNS_020	0.00	0.93	0.07
GOB	G0-Z48	0.52	0.00	0.48
GOB	G0-Z54	0.54	0.00	0.46
GOB	GO-Z49	0.62	0.02	0.36
GOB	GO-Z50	0.54	0.01	0.45
GOB	GO-Z51	0.55	0.00	0.45
GOB	GO-Z52	0.54	0.00	0.46
GOB	GO-Z53	0.56	0.00	0.44
GOB	GO-Z55	0.55	0.00	0.45
GOB	GO-Z56	0.54	0.00	0.46
GOB	GO-Z58	0.54	0.00	0.46
HAR	HAR1	1.00	0.00	0.00
HAR	HAR2	1.00	0.00	0.00
HAR	HAR3	1.00	0.00	0.00
HAR	HAR4	1.00	0.00	0.00
HAR	HAR5	1.00	0.00	0.00
HAR	HAR6	1.00	0.00	0.00
HAR	HAR7	1.00	0.00	0.00
HAR	HAR8	1.00	0.00	0.00
HAR	HAR9	1.00	0.00	0.00
HAR	HAR10	1.00	0.00	0.00
HIG	H8012	0.00	0.98	0.02
HIG	H8052	0.00	0.98	0.02
HIG	H8053	0.00	0.97	0.03
HIG	H8055	0.00	0.97	0.03
HIG	H8059	0.00	0.98	0.02
HIG	HI10	0.00	0.97	0.03

HIG	HI13	0.00	0.97	0.03
HIG	HI14	0.00	0.96	0.04
HOL	HOL_000006	0.00	0.97	0.03
HOL	HOL_000007	0.00	0.96	0.04
HOL	HOL_000008	0.00	0.98	0.02
HOL	HOL_000013	0.00	0.97	0.03
HOL	HOL_000015	0.00	0.97	0.03
HOL	HOL_000016	0.00	0.96	0.04
HOL	HOL_000017	0.00	0.97	0.03
HOL	HOL_000019	0.00	0.98	0.02
HOL	HOL_000020	0.00	0.98	0.02
HOL	HOL_000021	0.00	0.98	0.02
HOL	HOL_000023	0.00	0.97	0.03
HOL	HOL_000027	0.00	0.97	0.03
HOL	HOL_000038	0.00	0.98	0.02
HOL	HOL_000041	0.00	0.97	0.03
HOL	HOL_000042	0.00	0.99	0.01
HOL	HOL_000043	0.00	0.97	0.03
HOL	HOL_001	0.00	0.97	0.03
HOL	HOL_002	0.00	0.98	0.02
HOL	HOL_003	0.00	0.98	0.02
HOL	HOL_004	0.00	0.98	0.02
HOL	HOL_005	0.00	0.98	0.02
HOL	HOL_006	0.00	0.96	0.04
HOL	HOL_007	0.00	0.98	0.02
HOL	HOL_008	0.00	0.98	0.02
HOL	HOL_009	0.00	0.98	0.02
HOL	HOL_010	0.00	0.96	0.04
HOL	HOL_011	0.00	0.98	0.02
HOL	HOL_012	0.00	0.99	0.01
HOL	HOL_013	0.00	0.97	0.03
HOL	HOL_017	0.00	0.97	0.03

HOL	HOL_018	0.00	0.98	0.02
HOL	HOL_019	0.00	0.97	0.03
HOL	HOL_021	0.00	0.98	0.02
HOL	HOL_025	0.00	0.97	0.03
HOL	HOL_029	0.00	0.98	0.02
HOL	HOL_031	0.00	0.97	0.03
HOL	HOL_032	0.00	0.98	0.02
HOL	HOL_034	0.00	0.99	0.01
HOL	HOL_035	0.00	0.94	0.06
HOL	HOL_036	0.00	0.96	0.04
HOL	HOL_037	0.00	0.95	0.05
HOL	HOL_038	0.00	0.97	0.03
HOL	HOL_039	0.00	0.96	0.04
HOL	HOL_040	0.00	0.98	0.02
HOL	HOL_042	0.00	0.97	0.03
HOL	HOL_043	0.00	0.98	0.02
HOL	HOL_047	0.00	0.98	0.02
HOL	HOL_048	0.00	0.98	0.02
HOL	HOL_049	0.00	0.97	0.03
HOL	HOL_050	0.00	0.99	0.01
HOL	HOL_051	0.00	0.97	0.03
HOL	HOL_052	0.00	0.99	0.01
HOL	HOL_053	0.00	0.98	0.02
HOL	HOL_054	0.00	0.98	0.02
HOL	HOL_055	0.00	0.98	0.02
HOL	HOL_056	0.00	0.98	0.02
HOL	HOL_057	0.00	0.96	0.04
HOL	HOL_058	0.00	0.97	0.03
HOL	HOL_059	0.00	0.97	0.03
HOL	HOL_060	0.00	0.96	0.04
JER	JER_000003	0.00	0.96	0.04
JER	JER_000020	0.00	0.96	0.04
JER	JER_000027	0.00	0.96	0.04
JER	JER_001	0.00	0.97	0.03

JER	JER_002	0.00	0.96	0.04
JER	JER_003	0.00	0.96	0.04
JER	JER_004	0.00	0.97	0.03
JER	JER_005	0.00	0.98	0.02
JER	JER_006	0.00	0.96	0.04
JER	JER_007	0.00	0.98	0.02
JER	JER_008	0.00	0.97	0.03
JER	JER_009	0.00	0.97	0.03
JER	JER_010	0.00	0.97	0.03
JER	JER_011	0.00	0.97	0.03
JER	JER_012	0.00	0.98	0.02
JER	JER_014	0.00	0.96	0.04
JER	JER_015	0.00	0.97	0.03
JER	JER_016	0.00	0.97	0.03
JER	JER_017	0.00	0.98	0.02
JER	JER_018	0.00	0.97	0.03
JER	JER_019	0.00	0.96	0.04
JER	JER_020	0.00	0.96	0.04
JER	JER_021	0.00	0.96	0.04
JER	JER_022	0.00	0.96	0.04
JER	JER_023	0.00	0.98	0.02
JER	JER_024	0.00	0.98	0.02
JER	JER_026	0.00	0.97	0.03
JER	JER_027	0.00	0.98	0.02
JER	JER_028	0.00	0.98	0.02
JER	JER_029	0.00	0.97	0.03
JER	JER_030	0.00	0.97	0.03
JER	JER_031	0.00	0.95	0.05
JER	JER_033	0.00	0.94	0.06
JER	JER_034	0.00	0.95	0.05
JER	JER_035	0.00	0.97	0.03
JER	JER_036	0.00	0.98	0.02

JER	JER_037	0.00	0.95	0.05
JER	JER_038	0.00	0.98	0.02
KEN	K19B	0.73	0.00	0.27
KEN	K20	0.71	0.00	0.28
KEN	K21	0.74	0.00	0.26
KEN	K22B	0.72	0.00	0.28
KEN	K23	0.73	0.00	0.27
KEN	K24A	0.71	0.00	0.29
KEN	K25	0.73	0.00	0.27
KEN	K32	0.72	0.01	0.27
KEN	K33	0.72	0.01	0.27
KEN	K34	0.73	0.01	0.26
KER	KER16	0.00	0.98	0.02
KER	KER17	0.00	0.98	0.02
KER	KER18	0.00	0.99	0.01
KER	KER19	0.00	1.00	0.00
KER	KER20	0.00	0.98	0.02
KER	KER21	0.00	0.99	0.01
KER	KER22	0.00	0.99	0.01
KER	KER23	0.00	0.99	0.01
KER	KER24	0.00	0.99	0.01
LAG	LAG_9410	0.00	0.00	1.00
LAG	LAG_9416	0.00	0.00	1.00
LAG	LAG_9428	0.00	0.00	1.00
LAG	LAG_9433	0.00	0.00	1.00
LAG	LAG_9445	0.00	0.00	1.00
LMS	LMS_000002	0.00	0.90	0.10
LMS	LMS_000015	0.00	0.90	0.10
LMS	LMS_000017	0.00	0.92	0.08
LMS	LMS_000025	0.00	0.88	0.12
LMS	LMS_000027	0.00	0.89	0.11
LMS	LMS_000028	0.00	0.90	0.10
LMS	LMS_000031	0.00	0.88	0.12
LMS	LMS_001	0.00	0.89	0.11

LMS	LMS_003	0.00	0.91	0.09
LMS	LMS_004	0.00	0.92	0.08
LMS	LMS_005	0.00	0.89	0.11
LMS	LMS_006	0.00	0.91	0.09
LMS	LMS_007	0.00	0.91	0.09
LMS	LMS_008	0.00	0.92	0.08
LMS	LMS_009	0.00	0.89	0.11
LMS	LMS_010	0.00	0.93	0.07
LMS	LMS_011	0.00	0.91	0.09
LMS	LMS_012	0.00	0.92	0.08
LMS	LMS_013	0.00	0.93	0.07
LMS	LMS_014	0.00	0.93	0.07
LMS	LMS_015	0.00	0.90	0.10
LMS	LMS_017	0.00	0.90	0.10
LMS	LMS_019	0.00	0.93	0.07
LMS	LMS_020	0.00	0.91	0.09
LMS	LMS_021	0.00	0.92	0.08
LMS	LMS_022	0.00	0.94	0.06
LMS	LMS_023	0.00	0.91	0.09
LMS	LMS_024	0.00	0.89	0.11
LMS	LMS_025	0.00	0.88	0.12
LMS	LMS_027	0.00	0.90	0.10
LMS	LMS_030	0.00	0.89	0.11
LMS	LMS_031	0.00	0.90	0.10
LMS	LMS_033	0.00	0.90	0.10
LMS	LMS_034	0.00	0.88	0.12
LMS	LMS_035	0.00	0.90	0.10
LMS	LMS_036	0.00	0.88	0.12
LMS	LMS_037	0.00	0.89	0.11
LMS	LMS_038	0.00	0.89	0.11
LMS	LMS_039	0.00	0.90	0.10
LMS	LMS_040	0.00	0.90	0.10

LMS	LMS_041	0.00	0.90	0.10
LMS	LMS_042	0.00	0.90	0.10
LMS	LMS_043	0.00	0.90	0.10
LMS	LMS_044	0.00	0.90	0.10
LMS	LMS_045	0.00	0.91	0.09
LMS	LMS_046	0.00	0.94	0.06
LMS	LMS_047	0.00	0.90	0.10
LMS	LMS_048	0.00	0.90	0.10
LMS	LMS_049	0.00	0.93	0.07
LMS	LMS_050	0.00	0.88	0.12
MAR	39	0.09	0.74	0.17
MAR	40	0.09	0.73	0.18
MAR	42	0.09	0.72	0.19
MAR	43	0.08	0.74	0.17
MAU	MAU-Z36	0.54	0.00	0.46
MAU	MAU-Z38	0.55	0.00	0.45
MAU	MAU-Z39	0.56	0.00	0.44
MAU	MAU-Z40	0.55	0.00	0.45
MAU	MAU-Z44	0.55	0.00	0.45
MAU	MAU-Z45	0.56	0.00	0.44
MAU	MAU-Z48	0.56	0.02	0.43
MAU	MAU-Z57	0.54	0.01	0.45
MAU	MAU-Z59	0.58	0.00	0.41
MAU	MAU-Z60	0.56	0.01	0.43
MON	MON_001	0.00	0.89	0.11
MON	MON_002	0.00	0.89	0.11
MON	MON_003	0.00	0.88	0.12
MON	MON_004	0.00	0.89	0.11
MON	MON_005	0.00	0.90	0.10
MUR	MT1	0.02	0.00	0.98
MUR	MT2	0.00	0.00	1.00
MUR	MT3	0.41	0.02	0.58
MUR	MT4	0.40	0.00	0.60
MUR	MT5	0.31	0.00	0.69

MUR	MT6	0.00	0.00	1.00
MUR	MT7	0.00	0.00	1.00
MUR	MT25	0.00	0.00	1.00
MUR	MT26	0.00	0.00	1.00
MUR	MT27	0.00	0.00	1.00
MUR	MT28	0.00	0.00	1.00
NDA	NDA_001	0.00	0.00	1.00
NDA	NDA_002	0.00	0.00	1.00
NDA	NDA_003	0.00	0.00	1.00
NDA	NDA_004	0.00	0.00	1.00
NDA	NDA_005	0.00	0.00	1.00
NDA	NDA_006	0.00	0.00	1.00
NDA	NDA_007	0.00	0.00	1.00
NDA	NDA_008	0.00	0.00	1.00
NDA	NDA_009	0.00	0.00	1.00
NDA	NDA_010	0.00	0.00	1.00
NDA	NDA_011	0.00	0.00	1.00
NDA	NDA_012	0.00	0.00	1.00
NDA	NDA_013	0.00	0.00	1.00
NDA	NDA_014	0.00	0.00	1.00
NDA	NDA_015	0.00	0.00	1.00
NDA	NDA_016	0.00	0.00	1.00
NDA	NDA_017	0.00	0.00	1.00
NDA	NDA_018	0.00	0.00	1.00
NDA	NDA_019	0.00	0.00	1.00
NDA	NDA_020	0.00	0.00	1.00
NDA	NDA_021	0.00	0.00	1.00
NDA	NDA_022	0.00	0.00	1.00
NDA	NDA_023	0.00	0.00	1.00
NDA	NDG54	0.00	0.00	1.00
NDA	NDG55	0.00	0.00	1.00
NDA	NDG56	0.00	0.00	1.00

NDA	NDG57	0.00	0.00	1.00
NDA	NDG58	0.00	0.00	1.00
NDA	NDG59	0.00	0.00	1.00
NDA	NDG60	0.00	0.00	1.00
NDA	NDG62	0.00	0.00	1.00
NDA	NDG63	0.00	0.00	1.00
NEL	NEL_001	1.00	0.00	0.00
NEL	NEL_002	1.00	0.00	0.00
NEL	NEL_003	1.00	0.00	0.00
NEL	NEL_004	1.00	0.00	0.00
NEL	NEL_005	1.00	0.00	0.00
NEL	NEL_006	1.00	0.00	0.00
NEL	NEL_007	1.00	0.00	0.00
NEL	NEL_008	1.00	0.00	0.00
NEL	NEL_009	1.00	0.00	0.00
NEL	NEL_010	1.00	0.00	0.00
NEL	NEL_011	1.00	0.00	0.00
NEL	NEL_012	1.00	0.00	0.00
NEL	NEL_013	1.00	0.00	0.00
NEL	NEL_014	0.99	0.01	0.00
NEL	NEL_015	1.00	0.00	0.00
NEL	NEL_016	1.00	0.00	0.00
NEL	NEL_017	0.99	0.01	0.00
NEL	NEL_018	1.00	0.00	0.00
NEL	NEL_019	1.00	0.00	0.00
NEL	NEL_020	1.00	0.00	0.00
NEL	NEL_021	1.00	0.00	0.00
NEL	NEL_022	1.00	0.00	0.00
NEL	NEL_023	1.00	0.00	0.00
NEL	NEL_024	1.00	0.00	0.00
NEL	NEL_025	1.00	0.00	0.00
NEL	NEL_026	1.00	0.00	0.00
NEL	NEL_027	1.00	0.00	0.00
NEL	NEL_028	1.00	0.00	0.00

NEL	NEL_029	1.00	0.00	0.00
NEL	NEL_030	1.00	0.00	0.00
NEL	NEL_031	1.00	0.00	0.00
NOR	NOR_001	0.00	0.92	0.08
NOR	NOR_002	0.00	0.92	0.08
NOR	NOR_003	0.00	0.94	0.06
NOR	NOR_004	0.00	0.93	0.07
NOR	NOR_005	0.00	0.91	0.09
NRC	NRC_001	0.00	0.96	0.04
NRC	NRC_002	0.00	0.96	0.04
NRC	NRC_003	0.00	0.98	0.02
NRC	NRC_004	0.00	0.95	0.05
NRC	NRC_005	0.00	0.96	0.04
NRC	NRC_006	0.00	0.96	0.04
NRC	NRC_007	0.00	0.97	0.03
NRC	NRC_008	0.00	0.96	0.04
NRC	NRC_009	0.00	0.96	0.04
NRC	NRC_010	0.00	0.96	0.04
NRC	NRC_011	0.00	0.97	0.03
NRC	NRC_012	0.00	0.95	0.05
NRC	NRC_013	0.00	0.97	0.03
NRC	NRC_014	0.00	0.96	0.04
NRC	NRC_015	0.00	0.95	0.05
NRC	NRC_016	0.00	0.96	0.04
NRC	NRC_017	0.00	0.98	0.02
OGR	Gaur2	0.95	0.03	0.02
OGR	OGR_001	0.95	0.03	0.02
OGR	OGR_002	0.94	0.04	0.02
OYK	OYK_001	0.93	0.04	0.02
OYK	OYK_002	0.93	0.04	0.02
PMT	PMT_001	0.01	0.86	0.13
PMT	PMT_002	0.01	0.87	0.13

PMT	PMT_003	0.00	0.88	0.12
PMT	PMT_004	0.00	0.86	0.14
PMT	PMT_005	0.00	0.86	0.14
PMT	PMT_006	0.00	0.88	0.12
PMT	PMT_007	0.00	0.88	0.11
PMT	PMT_008	0.00	0.87	0.13
PMT	PMT_009	0.00	0.87	0.13
PMT	PMT_010	0.00	0.88	0.12
PMT	PMT_011	0.00	0.87	0.13
PMT	PMT_012	0.00	0.88	0.12
PMT	PMT_013	0.00	0.87	0.12
PMT	PMT_014	0.00	0.87	0.12
PMT	PMT_015	0.00	0.87	0.12
PMT	PMT_016	0.00	0.88	0.12
PMT	PMT_017	0.00	0.88	0.12
PMT	PMT_018	0.00	0.87	0.13
PMT	PMT_019	0.00	0.88	0.11
PMT	PMT_020	0.00	0.86	0.13
PMT	PMT_021	0.00	0.86	0.13
RGU	RGU_000012	0.00	1.00	0.00
RGU	RGU_001	0.00	1.00	0.00
RGU	RGU_002	0.00	1.00	0.00
RGU	RGU_003	0.00	1.00	0.00
RGU	RGU_004	0.00	1.00	0.00
RGU	RGU_005	0.00	1.00	0.00
RGU	RGU_006	0.00	1.00	0.00
RGU	RGU_007	0.00	1.00	0.00
RGU	RGU_008	0.00	1.00	0.00
RGU	RGU_010	0.00	1.00	0.00
RMG	RMG_000002	0.08	0.76	0.16
RMG	RMG_000008	0.08	0.75	0.17
RMG	RMG_000017	0.08	0.75	0.17
RMG	RMG_002	0.08	0.76	0.16
RMG	RMG_003	0.08	0.75	0.17

RMG	RMG_004	0.08	0.76	0.16
RMG	RMG_005	0.09	0.74	0.17
RMG	RMG_007	0.08	0.75	0.17
RMG	RMG_008	0.08	0.75	0.17
RMG	RMG_009	0.08	0.75	0.17
RMG	RMG_010	0.07	0.76	0.17
RMG	RMG_011	0.08	0.76	0.17
RMG	RMG_012	0.09	0.74	0.17
RMG	RMG_013	0.08	0.74	0.17
RMG	RMG_015	0.08	0.75	0.17
RMG	RMG_016	0.09	0.75	0.16
RMG	RMG_017	0.09	0.74	0.17
RMG	RMG_018	0.08	0.77	0.15
RMG	RMG_019	0.08	0.76	0.17
RMG	RMG_020	0.08	0.75	0.17
RMG	RMG_021	0.08	0.75	0.17
SAH	SAH1A	1.00	0.00	0.00
SAH	SAH2A	1.00	0.00	0.00
SAH	SAH3B	1.00	0.00	0.00
SAH	SAH4B	1.00	0.00	0.00
SAH	SAH5A	1.00	0.00	0.00
SAH	SAH6B	1.00	0.00	0.00
SAH	SAH7A	1.00	0.00	0.00
SAH	SAH8B	1.00	0.00	0.00
SAH	SAH9A	1.00	0.00	0.00
SAH	SAH10A	1.00	0.00	0.00
SAR	SAR1	0.32	0.30	0.38
SAR	SAR2	0.27	0.39	0.34
SAR	SAR4	0.32	0.30	0.38
SAR	SAR5	0.33	0.31	0.36
SAR	SAR11	0.30	0.35	0.36
SAR	SAR12	0.34	0.33	0.33

SAR	SAR13	0.34	0.31	0.35
SAR	SAR14	0.32	0.36	0.32
SAR	SAR15	0.35	0.34	0.31
SAR	SAR21	0.27	0.40	0.33
SAR	SAR33	0.28	0.38	0.35
SAR	SAR37	0.33	0.33	0.34
SAR	SAR39	0.38	0.37	0.25
SHK	SHK_001	0.57	0.02	0.41
SHK	SHK_002	0.56	0.02	0.42
SHK	SHK_003	0.55	0.01	0.43
SHK	SHK_004	0.56	0.03	0.41
SHK	SHK_005	0.52	0.03	0.44
SHK	SHK_006	0.54	0.04	0.42
SHK	SHK_007	0.57	0.02	0.41
SHK	SHK_008	0.57	0.03	0.40
SHK	SHK_009	0.52	0.03	0.44
SHK	SHK_010	0.53	0.02	0.44
SHK	SHK_011	0.54	0.03	0.43
SHK	SHK_012	0.57	0.04	0.40
SHK	SHK_013	0.57	0.02	0.40
SHK	SHK_014	0.55	0.02	0.43
SHK	SHK_015	0.55	0.02	0.43
SHK	SHK_016	0.56	0.02	0.42
SIK	SK1	0.14	0.69	0.17
SIK	SK2	0.04	0.84	0.12
SIK	SK3	0.14	0.70	0.16
SIK	SK4	0.12	0.73	0.15
SIK	SK5	0.11	0.72	0.17
SIM	SIM_001	0.00	0.87	0.13
SIM	SIM_002	0.01	0.91	0.08
SIM	SIM_003	0.00	0.96	0.04
SIM	SIM_004	0.00	0.90	0.10
SIM	SIM_005	0.00	0.92	0.08
SIM	SIM_006	0.00	0.91	0.09

SIM	SIM_007	0.00	0.91	0.09
SIM	SIM_008	0.00	0.92	0.08
SIM	SIM_009	0.00	0.92	0.08
SIM	SIM_010	0.00	0.97	0.03
SIS	S20	0.94	0.03	0.03
SIS	S22	0.94	0.03	0.03
SIS	S23	0.93	0.04	0.03
SIS	S32	0.94	0.03	0.03
SIS	S46	0.66	0.28	0.06
SOM	3201	0.03	0.00	0.97
SOM	3224	0.02	0.00	0.98
SOM	3232	0.03	0.00	0.97
SOM	3248	0.00	0.00	1.00
SOM	3421	0.01	0.00	0.99
SOM	3437	0.04	0.00	0.96
SOM	3441	0.04	0.00	0.96
SOM	3454	0.03	0.00	0.97
SOM	3482	0.02	0.00	0.98
SOM	3496	0.02	0.00	0.98
TAL	T5	0.49	0.35	0.16
TAL	T20	0.49	0.33	0.18
TAL	T21	0.48	0.34	0.18
TAL	T22	0.49	0.34	0.18
TAL	T28	0.50	0.33	0.17
WAG	WAG_001	0.02	0.74	0.23
WAG	WAG_002	0.02	0.74	0.23
WAG	WAG_003	0.02	0.78	0.20
WAG	WAG_004	0.02	0.79	0.19
WAG	WAG_005	0.03	0.74	0.23
WAG	WAG_006	0.02	0.81	0.18
WAG	WAG_007	0.02	0.76	0.22
WAG	WAG_008	0.03	0.75	0.23

WAG	WAG_009	0.01	0.80	0.18
WAG	WAG_010	0.02	0.80	0.19
WAG	WAG_011	0.03	0.74	0.23
WAG	WAG_012	0.02	0.80	0.19
WAG	WAG_013	0.03	0.75	0.23

Table 9.2.6-D(((Test,Sub1),Bed3),Yak) vs Years BP. Values are rounded to two decimal places for this table.

Test	Dstat	Z	BABA	ABBA	SE	Number of SNPs present in all Populations	Years BP	Region	Wild/Domestic
Bed4	0.19	17.60	7760	5276	0.01	89933	11708	Central Europe	wild
Bel1	-0.03	-1.20	598	640	0.03	9518	6925	Balkans	domestic
Bel2	0.03	1.14	924	874	0.02	14733	6925	Balkans	domestic
Bla1	-0.08	-1.25	108	127	0.06	2242	8100	Balkans	domestic
Bri1	0.04	3.91	6722	6218	0.01	98363	2300	Northern Europe	domestic
Bub1	0.06	3.84	2330	2060	0.02	35899	7600	Balkans	domestic
Bun1	0.04	3.65	6114	5657	0.01	88104	2300	Northern Europe	domestic
Bun2	0.04	3.70	6557	6056	0.01	95555	2300	Northern Europe	domestic
Ch22	-0.01	-0.35	1872	1894	0.02	30821	8000	Anatolia	domestic
Cla1	0.05	5.33	7310	6560	0.01	103986	2789	British and Irish Isles	domestic
Cla2	0.06	6.17	6366	5609	0.01	90613	2789	British and Irish Isles	domestic
CPC98	0.18	18.19	8600	5974	0.01	99518	6738	British and Irish Isles	wild
Dav1	-0.02	-1.87	6400	6644	0.01	102265	3500	Levant	domestic
Dro1	0.05	4.64	6890	6263	0.01	98406	200	Northern Europe	domestic
Dub1	0.04	4.07	6519	6002	0.01	92508	950	British and Irish Isles	domestic
Dyr1	0.04	3.84	6666	6165	0.01	95738	1000	Central Europe	domestic
Dzh1	0.00	0.33	6419	6372	0.01	103919	7800	Central Europe	domestic
Dzh2	0.01	0.59	6186	6105	0.01	101322	7600	Central Europe	domestic
Els1	0.04	3.69	6650	6184	0.01	96612	1950	Northern Europe	domestic
Fal7	0.15	15.18	7608	5624	0.01	92172	800	Central Europe	wild

Far1	0.05	1.03	231	208	0.05	3534	7700	Iran	domestic
Fir1	0.05	5.21	6951	6242	0.01	98891	1200	Northern Europe	domestic
Gyumri2	-0.01	-0.79	5672	5765	0.01	83681	7260	Southern Caucasus	wild
Hou1	0.03	2.77	6662	6290	0.01	97671	1000	Northern Europe	domestic
Hou2	0.05	4.51	6820	6218	0.01	97703	850	Northern Europe	domestic
Hxh1	0.02	2.24	6634	6332	0.01	103823	7000	Central Europe	domestic
Hxh2	0.18	17.85	8838	6200	0.01	103965	7001	Central Europe	wild
Kalisz2	0.15	15.36	8009	5896	0.01	96637	0	Eastern Europe	wild
Kie1	0.07	1.74	350	306	0.04	5168	5000	Eastern Europe	domestic
Kie2	0.08	4.19	1670	1415	0.02	23098	5001	Eastern Europe	domestic
Kir4	0.01	0.54	6782	6707	0.01	103979	4195	Central Europe	domestic
Lud1	0.01	0.63	1086	1056	0.02	16881	7500	Eastern Europe	domestic
Lud2	0.01	0.36	2088	2062	0.02	33755	7500	Eastern Europe	domestic
Lud3	0.00	0.25	1799	1782	0.02	28935	7500	Eastern Europe	domestic
Lud4	-0.02	-0.81	1254	1296	0.02	20155	7500	Eastern Europe	domestic
Mar1	-0.05	-1.19	262	290	0.04	4245	7000	Iran	domestic
Men1	-0.01	-1.12	5835	5975	0.01	97735	7000	Anatolia	domestic
Men2	-0.03	-2.32	4974	5238	0.01	86113	7092	Anatolia	domestic
New1	0.05	4.84	7161	6500	0.01	103983	1674	British and Irish Isles	domestic
New2	0.05	5.33	7224	6490	0.01	101828	4200	British and Irish Isles	domestic
New3	0.03	3.16	7043	6618	0.01	103424	4200	British and Irish Isles	domestic
New4	0.04	3.92	7034	6512	0.01	102402	4337	British and Irish Isles	domestic
New5	0.04	4.56	7117	6514	0.01	103094	1800	British and Irish Isles	domestic
Otb1	0.03	2.65	6570	6210	0.01	97029	1800	Northern Europe	domestic
Plo1	0.07	2.59	928	814	0.03	14036	7125	Balkans	domestic
Plo2	0.02	1.40	2134	2036	0.02	33232	6950	Balkans	domestic
Plo3	0.01	1.24	6120	5964	0.01	97801	7000	Balkans	domestic
Plo4	0.01	1.30	6188	6014	0.01	98407	7000	Balkans	domestic
Plo5	-0.04	-1.30	553	599	0.03	9658	6650	Balkans	domestic

Plo6	0.03	0.97	816	776	0.03	12950	7126	Balkans	domestic
Plo7	0.01	0.54	778	758	0.02	12345	7000	Balkans	domestic
Plo8	-0.02	-0.87	1230	1276	0.02	20241	7001	Balkans	domestic
Sac3	0.03	0.45	141	133	0.06	2215	7673	Iran	domestic
Sch1	0.03	3.30	5960	5558	0.01	87079	5000	Northern Europe	domestic
Ste1	0.05	4.31	4589	4148	0.01	65567	1400	Northern Europe	domestic
Stu1	0.03	1.57	1066	998	0.02	16564	6600	Balkans	domestic
Tri1	0.19	18.07	8108	5572	0.01	93563	8116	Central Europe	wild
Viz1	0.04	3.25	3840	3517	0.01	56547	3400	Northern Europe	domestic
Viz2	0.03	3.15	6404	6014	0.01	93868	3401	Northern Europe	domestic
Win1	0.05	5.31	7261	6558	0.01	103988	1800	Northern Europe	domestic
Yor1	0.06	5.96	7319	6472	0.01	103872	1929	British and Irish Isles	domestic
Yor2	0.05	5.06	7246	6572	0.01	102283	1100	British and Irish Isles	domestic
Yor3	0.05	4.80	6886	6246	0.01	97050	650	British and Irish Isles	domestic
Yor4	0.05	4.77	7001	6362	0.01	99820	1050	British and Irish Isles	domestic

Table 9.2.7-D(((Moderns,Sub1),Bed3),Yak). Values are rounded to two decimal places for this table.

Test	Dstat	Z	SE	BABA	ABBA	Number of SNPs present in all Populations
Galloway	0.04	4.83	0.01	7307	6753	104000
Highland	0.04	4.08	0.01	7297	6801	104005
Kerry	0.03	4.32	0.01	7265	6800	103999
Jersey	0.03	3.64	0.01	7272	6863	104006
Guernsey	0.03	3.61	0.01	7147	6757	104006
Norwegian Red Cattle	0.03	3.33	0.01	7219	6851	104006
Normande	0.02	2.54	0.01	7123	6825	104006
Simmental	0.02	2.53	0.01	7136	6854	104006

Alentejana	0.02	2.17	0.01	7105	6865	104003
Holstein	0.01	1.77	0.01	7182	6985	104006
Montbeliarde	0.01	1.43	0.01	7054	6886	104006
Red Angus	0.01	1.38	0.01	7135	6975	104006
Piedmontese	0.01	1.46	0.01	7004	6852	104006
Blonde d'Aquitaine	0.01	1.30	0.01	7026	6885	104006
Limousin	0.01	1.34	0.01	7037	6901	104006
Brown Swiss	0.01	1.13	0.01	7011	6886	104006
Angus	0.01	1.11	0.01	7140	7015	104006
Charolais	0.00	0.05	0.01	7077	7072	104006
Wagyu	-0.02	-2.15	0.01	6752	6991	104006
N'Dama	-0.07	-8.01	0.01	6394	7330	104006
Lagune	-0.07	-7.68	0.01	6404	7352	104004
Romagnola	-0.07	-8.53	0.01	6630	7622	104006
Maremmana	-0.07	-8.39	0.01	6622	7675	103977
Sikia	-0.09	-10.73	0.01	6666	7937	103998
Somba	-0.09	-10.26	0.01	6329	7569	104002
Muturu	-0.15	-17.97	0.01	6133	8290	104003
Anatolian Black	-0.25	-32.38	0.01	5896	9760	103992
South Anatolian Red	-0.27	-34.71	0.01	5806	10020	104006
East Anatolian Red	-0.27	-35.53	0.01	5799	10154	104006
Taleshi	-0.37	-43.66	0.01	5365	11604	103998
Sheko	-0.42	-53.33	0.01	5161	12632	104006
Gobra	-0.42	-53.91	0.01	5148	12717	104005
Maure	-0.42	-52.67	0.01	5145	12720	104001
Butana	-0.50	-60.03	0.01	4821	14304	104001
Kenana	-0.50	-64.08	0.01	4788	14297	104005
Sistani	-0.56	-77.92	0.01	4430	15928	104001
Brahman	-0.58	-84.97	0.01	4379	16355	104006
Nelore	-0.60	-89.32	0.01	4223	17146	104006

Gir	-0.61	-89.49	0.01	4173	17056	104006
Sahiwal	-0.61	-89.27	0.01	4127	17111	104001
Hariana	-0.61	-91.09	0.01	4142	17181	103999
Gaur	-0.88	-100.00	0.01	1384	22121	103028

Table 9.2.8-D(((Test,Sub1),Somba),Yak) vs. Years BP

Test	Dstat	Z	SE	BABA	ABBA	Number of SNPs present in all Populations	Years BP	Region	Wild/Domestic
Bed3	-0.18	-21.17	0.01	6329	9122	104002	11558	Central Europe	wild
Bed4	-0.19	-22.67	0.01	5366	7945	89977	11708	Central Europe	wild
Bel1	-0.05	-2.22	0.02	616	687	9528	6925	Balkans	domestic
Bel2	-0.01	-0.52	0.02	917	936	14741	6925	Balkans	domestic
Bla1	-0.06	-1.29	0.05	126	143	2242	8100	Balkans	domestic
Bri1	-0.02	-2.74	0.01	6614	6952	98456	2300	Northern Europe	domestic
Bub1	0.01	0.51	0.01	2359	2328	35939	7600	Balkans	domestic
Bun1	-0.03	-3.29	0.01	6015	6398	88179	2300	Northern Europe	domestic
Bun2	-0.02	-2.01	0.01	6437	6688	95652	2300	Northern Europe	domestic
Ch22	-0.01	-0.65	0.01	1976	2012	30841	8000	Anatolia	domestic
Cla1	-0.05	-5.87	0.01	6857	7640	104103	2789	British and Irish Isles	domestic
Cla2	-0.04	-4.42	0.01	6044	6567	90705	2789	British and Irish Isles	domestic
CPC98	-0.18	-21.42	0.01	6141	8860	99603	6738	British and Irish Isles	wild
Dav1	0.10	11.14	0.01	7671	6269	102360	3500	Levant	domestic
Dro1	-0.03	-2.89	0.01	6675	7043	98504	200	Northern Europe	domestic
Dub1	-0.04	-3.80	0.01	6227	6690	92593	950	British and Irish Isles	domestic
Dyr1	-0.03	-2.98	0.01	6533	6907	95828	1000	Central Europe	domestic
Dzh1	0.00	-0.07	0.01	6725	6734	104033	7800	Central Europe	domestic
Dzh2	0.01	0.63	0.01	6526	6450	101417	7600	Central Europe	domestic
Els1	-0.04	-4.56	0.01	6393	6947	96718	1950	Northern Europe	domestic
Fal7	-0.15	-17.59	0.01	5773	7832	92267	800	Central Europe	wild
Far1	0.03	0.86	0.04	244	228	3536	7700	Iran	domestic
Fir1	-0.01	-1.15	0.01	6815	6964	98981	1200	Northern Europe	domestic

Gyumri2	-0.08	-8.59	0.01	5422	6366	83734	7260	Southern Caucasus	wild
Hou1	-0.03	-3.15	0.01	6586	6975	97761	1000	Northern Europe	domestic
Hou2	-0.02	-2.20	0.01	6600	6879	97805	850	Northern Europe	domestic
Hxh1	-0.01	-0.83	0.01	6735	6845	103933	7000	Central Europe	domestic
Hxh2	-0.17	-20.45	0.01	6377	9070	104079	7001	Central Europe	wild
Kalisz2	-0.16	-18.21	0.01	6044	8396	96706	0	Eastern Europe	wild
Kie1	-0.03	-1.09	0.03	339	364	5171	5000	Eastern Europe	domestic
Kie2	-0.04	-2.59	0.02	1547	1682	23119	5001	Eastern Europe	domestic
Kir4	-0.03	-3.98	0.01	6834	7319	104099	4195	Central Europe	domestic
Lud1	-0.01	-0.79	0.02	1104	1136	16890	7500	Eastern Europe	domestic
Lud2	-0.02	-1.73	0.01	2154	2260	33768	7500	Eastern Europe	domestic
Lud3	-0.01	-0.48	0.02	1893	1921	28944	7500	Eastern Europe	domestic
Lud4	0.00	-0.12	0.02	1310	1315	20171	7500	Eastern Europe	domestic
Mar1	-0.02	-0.63	0.04	274	287	4251	7000	Iran	domestic
Men1	0.00	-0.28	0.01	6199	6232	97827	7000	Anatolia	domestic
Men2	0.00	-0.38	0.01	5450	5491	86191	7092	Anatolia	domestic
New1	-0.02	-2.22	0.01	6974	7260	104103	1674	British and Irish Isles	domestic
New2	-0.04	-4.75	0.01	6811	7446	101928	4200	British and Irish Isles	domestic
New3	-0.03	-3.52	0.01	6888	7343	103531	4200	British and Irish Isles	domestic
New4	-0.03	-2.89	0.01	6857	7237	102501	4337	British and Irish Isles	domestic
New5	-0.04	-4.05	0.01	6837	7360	103207	1800	British and Irish Isles	domestic
Otb1	-0.04	-4.43	0.01	6447	6998	97124	1800	Northern Europe	domestic
Plo1	-0.02	-0.90	0.02	918	952	14042	7125	Balkans	domestic
Plo2	-0.02	-1.54	0.01	2131	2224	33256	6950	Balkans	domestic
Plo3	-0.01	-1.38	0.01	6303	6470	97891	7000	Balkans	domestic
Plo4	-0.01	-0.90	0.01	6400	6508	98497	7000	Balkans	domestic
Plo5	-0.04	-1.45	0.02	595	639	9667	6650	Balkans	domestic
Plo6	0.00	0.07	0.02	842	839	12959	7126	Balkans	domestic
Plo7	-0.02	-1.06	0.02	794	829	12354	7000	Balkans	domestic
Plo8	-0.03	-1.53	0.02	1303	1372	20261	7001	Balkans	domestic

Sac3	0.03	0.72	0.05	156	146	2218	7673	Iran	domestic
Sch1	-0.03	-3.84	0.01	5778	6189	87163	5000	Northern Europe	domestic
Ste1	-0.03	-2.89	0.01	4410	4675	65616	1400	Northern Europe	domestic
Stu1	0.01	0.82	0.02	1114	1082	16573	6600	Balkans	domestic
Tri1	-0.19	-21.82	0.01	5667	8260	93627	8116	Central Europe	wild
Viz1	-0.03	-3.03	0.01	3753	4011	56584	3400	Northern Europe	domestic
Viz2	-0.03	-3.18	0.01	6346	6751	93963	3401	Northern Europe	domestic
Win1	-0.03	-3.29	0.01	7012	7427	104107	1800	Northern Europe	domestic
Yor1	-0.03	-3.99	0.01	6957	7461	103987	1929	British and Irish Isles	domestic
Yor2	-0.03	-3.78	0.01	6962	7449	102389	1100	British and Irish Isles	domestic
Yor3	-0.04	-4.81	0.01	6532	7121	97152	650	British and Irish Isles	domestic
Yor4	-0.04	-3.92	0.01	6714	7224	99920	1050	British and Irish Isles	domestic

Table 9.2.9-(((Test,Sub1),Gyumri2),Yak) vs. Years BP

Test	Dstat	Z	SE	BABA	ABBA	Number of SNPs present in all Populations	Years BP	Region	Wild/Domestic
Bed3	-0.09	-8.52	0.01	5672	6814	83681	11558	Central Europe	wild
Bed4	-0.11	-10.14	0.01	4888	6114	74060	11708	Central Europe	wild
Bel1	-0.05	-1.53	0.03	490	542	7689	6925	Balkans	domestic
Bel2	-0.02	-0.85	0.03	746	778	11858	6925	Balkans	domestic
Bri1	-0.01	-0.85	0.01	5426	5536	80032	2300	Northern Europe	domestic
Bub1	0.03	1.79	0.02	1876	1760	28565	7600	Balkans	domestic
Bun1	-0.02	-1.61	0.01	4806	4996	71317	2300	Northern Europe	domestic
Bun2	-0.03	-2.77	0.01	5068	5403	76978	2300	Northern Europe	domestic
Ch22	0.01	0.72	0.02	1631	1587	25174	8000	Anatolia	domestic
Cla1	-0.02	-2.05	0.01	5604	5868	83724	2789	British and Irish Isles	domestic
Cla2	-0.03	-2.44	0.01	4826	5122	73225	2789	British and Irish Isles	domestic
CPC98	-0.10	-9.62	0.01	5394	6613	80037	6738	British and Irish Isles	wild

Dav1	-0.01	-0.71	0.01	5438	5526	82667	3500	Levant	domestic
Dro1	-0.02	-2.03	0.01	5403	5642	79584	200	Northern Europe	domestic
Dub1	-0.04	-3.02	0.01	5013	5382	74747	950	British and Irish Isles	domestic
Dyr1	-0.02	-2.08	0.01	5205	5459	77435	1000	Central Europe	domestic
Dzh1	0.00	-0.22	0.01	5359	5387	83695	7800	Central Europe	domestic
Dzh2	0.02	1.35	0.01	5244	5078	81822	7600	Central Europe	domestic
Els1	-0.03	-3.05	0.01	5173	5539	78419	1950	Northern Europe	domestic
Fal7	-0.08	-7.59	0.01	5028	5951	74476	800	Central Europe	wild
Far1	0.09	1.66	0.05	218	183	2995	7700	Iran	domestic
Fir1	-0.02	-1.88	0.01	5371	5602	80234	1200	Northern Europe	domestic
Hou1	-0.03	-2.19	0.01	5228	5504	78813	1000	Northern Europe	domestic
Hou2	-0.03	-2.31	0.01	5185	5470	78651	850	Northern Europe	domestic
Hxh1	0.01	0.71	0.01	5504	5412	83644	7000	Central Europe	domestic
Hxh2	-0.11	-9.86	0.01	5526	6834	83715	7001	Central Europe	wild
Kalisz2	-0.09	-7.67	0.01	5348	6367	78722	0	Eastern Europe	wild
Kie1	0.02	0.53	0.04	290	277	4299	5000	Eastern Europe	domestic
Kie2	-0.02	-1.19	0.02	1300	1364	19463	5001	Eastern Europe	domestic
Kir4	-0.01	-1.11	0.01	5587	5720	83723	4195	Central Europe	domestic
Lud1	-0.04	-1.53	0.02	870	938	14107	7500	Eastern Europe	domestic
Lud2	0.00	-0.19	0.02	1844	1856	28342	7500	Eastern Europe	domestic
Lud3	-0.01	-0.62	0.02	1594	1634	24302	7500	Eastern Europe	domestic
Lud4	0.01	0.65	0.02	1090	1058	16866	7500	Eastern Europe	domestic
Mar1	-0.04	-0.76	0.05	224	241	3510	7000	Iran	domestic
Men1	0.00	-0.13	0.01	4922	4936	78827	7000	Anatolia	domestic
Men2	0.01	1.09	0.01	4407	4290	69850	7092	Anatolia	domestic

New1	-0.01	-0.86	0.01	5599	5707	83725	1674	British and Irish Isles	domestic
New2	-0.03	-3.13	0.01	5514	5914	81956	4200	British and Irish Isles	domestic
New3	-0.01	-1.10	0.01	5598	5738	83309	4200	British and Irish Isles	domestic
New4	-0.03	-2.29	0.01	5474	5771	82476	4337	British and Irish Isles	domestic
New5	-0.01	-0.76	0.01	5652	5746	83040	1800	British and Irish Isles	domestic
Otb1	-0.03	-2.42	0.01	5198	5486	78600	1800	Northern Europe	domestic
Plo1	0.02	0.71	0.03	744	716	11398	7125	Balkans	domestic
Plo2	-0.01	-0.40	0.02	1709	1734	27245	6950	Balkans	domestic
Plo3	-0.01	-0.82	0.01	5000	5094	79036	7000	Balkans	domestic
Plo4	-0.01	-0.77	0.01	5106	5192	79511	7000	Balkans	domestic
Plo5	-0.03	-0.79	0.03	486	512	7830	6650	Balkans	domestic
Plo6	0.03	1.03	0.03	684	644	10293	7126	Balkans	domestic
Plo7	0.03	0.97	0.03	696	660	10156	7000	Balkans	domestic
Plo8	0.00	-0.12	0.02	1057	1062	16349	7001	Balkans	domestic
Sch1	-0.02	-1.81	0.01	4690	4895	70391	5000	Northern Europe	domestic
Ste1	-0.01	-1.12	0.01	3611	3718	53501	1400	Northern Europe	domestic
Stu1	0.03	1.49	0.02	898	838	13847	6600	Balkans	domestic
Tri1	-0.11	-9.15	0.01	5007	6195	75518	8116	Central Europe	wild
Viz1	-0.02	-1.25	0.01	3096	3204	46752	3400	Northern Europe	domestic
Viz2	-0.02	-2.15	0.01	5089	5349	75975	3401	Northern Europe	domestic
Win1	-0.02	-1.85	0.01	5604	5833	83729	1800	Northern Europe	domestic
Yor1	-0.02	-1.49	0.01	5725	5916	83651	1929	British and Irish Isles	domestic
Yor2	-0.04	-3.17	0.01	5520	5934	82442	1100	British and Irish Isles	domestic
Yor3	-0.02	-1.80	0.01	5354	5576	78470	650	British and Irish Isles	domestic
Yor4	-0.03	-2.59	0.01	5435	5761	80535	1050	British and Irish Isles	domestic

Table 9.2.10-D(((Modern,Sub1),Gyumri2),Yak)

Test	Dstat	Z	SE	BABA	ABBA	Number of SNPs present in all Populations
Alentejana	-0.04	-3.97	0.01	5571	5977	83735
Anatolian Black	-0.26	-31.19	0.01	4865	8232	83728
Angus	-0.05	-5.71	0.01	5581	6196	83738
Blonde d'Aquitaine	-0.03	-3.71	0.01	5574	5969	83738
Brahman	-0.60	-85.38	0.01	3448	13951	83738
Brown Swiss	-0.04	-3.84	0.01	5593	6011	83738
Butana	-0.51	-58.11	0.01	3970	12123	83734
Charolais	-0.05	-6.17	0.01	5567	6194	83738
East Anatolian Red	-0.28	-32.92	0.01	4833	8552	83738
Galloway	-0.02	-2.72	0.01	5719	6003	83734
Gir	-0.63	-90.70	0.01	3296	14538	83738
Gobra	-0.03	-3.66	0.01	5569	5954	83738
Guernsey	-0.43	-49.77	0.01	4295	10741	83737
Hariana	-0.64	-92.19	0.01	3256	14629	83731
Highland	-0.03	-3.43	0.01	5688	6072	83737
Holstein	-0.05	-5.54	0.01	5609	6172	83738
Jersey	-0.04	-3.83	0.01	5637	6050	83738
Kenana	-0.51	-62.70	0.01	3935	12076	83737
Kerry	-0.03	-3.56	0.01	5641	6022	83734
Lagune	-0.04	-4.42	0.01	5491	5985	83736
Limousin	-0.04	-4.42	0.01	5565	6009	83738
Maremmana	-0.10	-10.03	0.01	5320	6494	83713
Maure	-0.43	-50.11	0.01	4282	10791	83733
Montbeliarde	-0.03	-3.44	0.01	5612	5997	83738
Muturu	-0.13	-13.78	0.01	5289	6828	83736

N'Dama	-0.05	-4.94	0.01	5472	5998	83738
Nelore	-0.63	-92.17	0.01	3306	14608	83738
Normande	-0.04	-3.78	0.01	5555	5958	83738
Norwegian Red Cattle	-0.04	-4.02	0.01	5594	6007	83738
Gaur	-0.90	-100.00	0.01	1020	18978	82957
Piedmontese	-0.04	-4.13	0.01	5553	5959	83738
Red Angus	-0.04	-4.84	0.01	5611	6129	83738
Romagnola	-0.09	-10.34	0.01	5385	6485	83738
Sahiwal	-0.63	-91.48	0.01	3269	14547	83733
South Anatolian Red	-0.27	-31.65	0.01	4877	8428	83738
Sheko	-0.42	-49.10	0.01	4323	10659	83738
Sikia	-0.12	-12.57	0.01	5372	6803	83733
Simmental	-0.04	-3.93	0.01	5594	6006	83738
Sistani	-0.59	-80.23	0.01	3517	13560	83734
Somba	-0.07	-7.14	0.01	5422	6180	83734
Taleshi	-0.38	-41.91	0.01	4439	9787	83731
Wagyu	-0.04	-4.49	0.01	5469	5948	83738

9.3. Chapter 5 Supplementary tables

Table 9.3.1 - Mitochondrial variants in relation to T3 Reference (V00654). Mutations that ambiguous and could be resulting of ancient DNA damage are shown in red.

Mitochondrial Variants			
Baikal1	**Gyumri1**	**Kir4**	**Gyumri2**
143C	106C	106C	169G
144T	166C	166G	583+C
173G	169G	169G	2558A
249T	249C	215+C	3559A
296C	296C	249C	3560C
300A	300A	296C	4000A
926T	565A	300A	4497C
2044C	583+C	565A	4537A
2335C	1552A	583+C	5501T
2558A	2146T	1552A	5718A
2979G	2434A	1662C	5754G
3139T	2558A	1954 deletion	5853T
3302A	2627C	2146T	7994A
3379C	2979G	2434A	8370C
3421A	3379C	2536A	10717A
3439G	3439G	2558A	11000T
3481T	3550A	2627C	11233A
3550A	3559A	2979G	11245A
3559A	3560C	3379C	11803C
3560C	3640C	3439G	12158T
3600T	3844C	3550A	12433C
3841T	4031G	3600T	12468C
3895A	4292C	3640C	12675T
4497C	4497C	3844C	12750C
4537A	4537A	4031G	13005G
4589G	4953C	4292C	14036A

4740A	5501T	4953C	15134T
4989A	5670A	5501T	15510C
5066T	5718A	5670A	15556C
5501T	5743C	5743C	15627G
5718A	5754G	5890T	15818G
5743C	5853T	6436A	15953G
5754G	5890T	6772T	16042T
5773G	6436A	7330C	16093G
5853T	6772T	7356G	16247T
5890T	7330C	7514A	16255C
6049A	7356G	7931A	16264A
6193T	7514A	8188C	
6370C	7931A	8195G	
6436A	7994A	8326A	
6526T	8188C	8370C	
6772T	8195G	8494G	
6994A	8326A	9005T	
7072G	8370C	9682C	
7330C	8494G	9729A	
7356G	9005T	9864T	
7514A	9729A	9978C	
7881T	9864T	10331G	
7925C	9978C	10364C	
7994A	10331G	10445C	
8045A	10364C	10691G	
8188C	10445C	10708T	
8370C	10691G	10822A	
8494G	10708T	10882C	
9005T	10822A	11000T	
9284T	10882C	11002G	
9644C	11000T	11089C	
9864T	11002G	11134C	
9978C	11089C	11419C	
10331G	11134C	11654G	

10691G	11233A	11663T	
10730C	11419C	11824A	
10741A	11654G	11842G	
10808T	11663T	12234T	
10825A	11842G	12433C	
10867A	12158T	12468C	
11000T	12234T	12469T	
11134C	12433C	12622G	
11233A	12468C	12651C	
11419C	12469T	12669G	
11842G	12622G	12675T	
12123T	12651C	12679G	
12145A	12669G	12684C	
12158T	12675T	12750C	
12234T	12679G	12801A	
12240T	12684C	12834T	
12433C	12750C	12867A	
12468C	12801A	12900C	
12469T	12834T	12903T	
12622G	12867A	13005G	
12675T	12900C	13056A	
12684C	12903T	13310C	
12750C	13005G	13458A	
12801A	13056A	13524C	
12825T	13128T	13554A	
12900C	13458A	13683A	
13005G	13524C	14036A	
13056A	13554A	14120C	
13071G	13683A	14138T	
13300A	14036A	14144T	
13521C	14138T	14624A	
13620T	14144T	14825T	

13758T	14624A	15134T	
14036A	14825T	15371T	
14825T	15134T	15396A	
15082C	15371T	15617A	
15134T	15396A	15627G	
15157C	15510C	15740A	
15326A	15617A	15818G	
15371T	15627G	15902T	
15510C	15951C	15951C	
15563T	15953G	15953G	
15617A	15994G	15994G	
15627G	16042T	16050T	
15741T	*16050T*	16057A	
15750T	*16057A*	16068C	
15818G	*16085C (N)*	16079G	
15951C	*16093G*	16085C	
15953G	*16095G*	16095G	
16042T	*16133C*	16121A	
16068T	*16135C*	16122C	
16083G	*16138C*	16125G	
16084T	16200+A	16133C	
16085C	16250G	16135C	
16093G	16255C	16138C	
16095G	16260T	16200+A	
16119C	16264A	16250G	
16125T		16225C	
16154G		16260T	
16200+A		16264A	
16231T			
16250G			
16260T			
16264A			
16301T			

Table 9.3.2- D(((Baikal1, Gyumri1),X),Yak). A negative value means that H1 is closer to H3 than H2 is. A positive value means that H2 is closer to H3 than H1 is.

Test(((H1,H2),H3)Yak)	nABBA	nBABA	Dstat	jackEst	SE	Z
((Baikal1,Gyumri1),Tango1)	118096	116644	0.01	0.01	0.01	1.17
((Baikal1,Gyumri1),Th7)	10759	10682	0.00	0.00	0.01	0.42
((Baikal1,Gyumri1),Tango2)	117832	113345	0.02	0.02	0.01	3.56
((Baikal1,Gyumri1),Kalisz2)	124802	121241	0.01	0.01	0.01	2.78
((Baikal1,Gyumri1),Belorus1)	110817	108394	0.01	0.01	0.01	1.99
((Baikal1,Gyumri1),Bed3)	137034	132367	0.02	0.02	0.01	3.32
((Baikal1,Gyumri1),Bed4)	114482	110736	0.02	0.02	0.01	3.19
((Baikal1,Gyumri1),Tri1)	117721	113826	0.02	0.02	0.01	3.07
((Baikal1,Gyumri1),Hxh2)	136720	132568	0.02	0.02	0.01	2.78
((Baikal1,Gyumri1),Fal7)	116717	113159	0.02	0.02	0.01	2.79
((Baikal1,Gyumri1),Ch22)	37757	37002	0.01	0.01	0.01	1.61
((Baikal1,Gyumri1),Sub1)	136200	131210	0.02	0.02	0.01	3.41
((Baikal1,Gyumri1),Gyumri2)	108759	104311	0.02	0.02	0.01	3.77

Table 9.3.3- D(((Baikal1 or Gyumri1,Tango1), X),Yak) and D(((Baikal1 or Gyumri1,Th7), X),Yak). A negative value means that H1 is closer to H3 than H2 is. A positive value means that H2 is closer to H3 than H1 is.

Test(((H1,H2),H3),Yak)	nABBA	nBABA	Dstat	jackEst	SE	Z
((Baikal1,Th7),Kalisz2)	22558	15119	0.20	0.20	0.01	27.01
((Baikal1,Th7),Belorus1)	20070	13358	0.20	0.20	0.01	26.47
((Baikal1,Th7),Gyumri2)	19712	12765	0.21	0.21	0.01	27.70
((Baikal1,Th7),Tango2)	20745	14555	0.18	0.18	0.01	22.30
((Baikal1,Th7),Bed3)	24582	16102	0.21	0.21	0.01	30.23
((Baikal1,Th7),Bed4)	21237	14071	0.20	0.20	0.01	26.80
((Baikal1,Th7),Tri1)	22436	14719	0.21	0.21	0.01	30.11
((Baikal1,Th7),Hxh2)	24228	16485	0.19	0.19	0.01	26.49
((Baikal1,Th7),Fal7)	21240	13968	0.21	0.21	0.01	28.35
((Baikal1,Th7),Ch22)	7903	4893	0.24	0.24	0.01	24.57
((Baikal1,Th7),Sub1)	25265	15516	0.24	0.24	0.01	33.98

((Gyumri1,Th7),Kalisz2)	20552	13904	0.19	0.19	0.01	26.30
((Gyumri1,Th7),Belorus)	18508	12307	0.20	0.20	0.01	26.82
((Gyumri1,Th7),Gyumri2)	18140	11774	0.21	0.21	0.01	26.07
((Gyumri1,Th7),Tango2)	18986	13513	0.17	0.17	0.01	21.78
((Gyumri1,Th7),Bed3)	22275	14826	0.20	0.20	0.01	28.30
((Gyumri1,Th7),Bed4)	19481	12983	0.20	0.20	0.01	26.51
((Gyumri1,Th7),Tri1)	20282	13398	0.20	0.20	0.01	28.67
((Gyumri1,Th7),Hxh2)	21987	14958	0.19	0.19	0.01	26.22
((Gyumri1,Th7),Fal7)	19242	12787	0.20	0.20	0.01	27.06
((Gyumri1,Th7),Ch22)	7305	4537	0.23	0.23	0.01	23.97
((Gyumri1,Th7),Sub1)	22936	14189	0.24	0.24	0.01	33.20
((Baikal1,Tango1),Kalisz2)	223769	128341	0.27	0.27	0.01	48.29
((Baikal1,Tango1),Belorus1)	200047	115828	0.27	0.27	0.01	46.56
((Baikal1,Tango1),Gyumri2)	190128	114502	0.25	0.25	0.01	48.52
((Baikal1,Tango1),Tango2)	205418	125296	0.24	0.24	0.01	43.57
((Baikal1,Tango1),Bed3)	241023	140252	0.26	0.26	0.01	46.51
((Baikal1,Tango1),Bed4)	205832	118420	0.27	0.27	0.01	47.35
((Baikal1,Tango1),Tri1)	209108	120779	0.27	0.27	0.01	48.47
((Baikal1,Tango1),Hxh2)	241957	140487	0.27	0.27	0.01	45.85
((Baikal1,Tango1),Fal7)	208304	119245	0.27	0.27	0.01	46.94
((Baikal1,Tango1),Ch22)	66519	39534	0.25	0.25	0.01	44.43
((Baikal1,Tango1),Sub1)	236050	140287	0.25	0.25	0.01	48.76
((Gyumri1,Tango1),Kalisz2)	205757	119987	0.26	0.26	0.01	45.29
((Gyumri1,Tango1),Belorus1)	184676	107747	0.26	0.26	0.01	46.92
((Gyumri1,Tango1),Gyumri2)	175614	108749	0.24	0.24	0.01	43.42
((Gyumri1,Tango1),Tango2)	189737	118108	0.23	0.23	0.01	40.57
((Gyumri1,Tango1),Bed3)	220425	130525	0.26	0.26	0.01	44.11
((Gyumri1,Tango1),Bed4)	190033	111463	0.26	0.26	0.01	45.03
((Gyumri1,Tango1),Tri1)	191402	112596	0.26	0.26	0.01	45.82
((Gyumri1,Tango1),Hxh2)	220737	130064	0.26	0.26	0.01	44.64
((Gyumri1,Tango1),Fal7)	190911	111356	0.26	0.26	0.01	45.19
((Gyumri1,Tango1),Ch22)	61464	36832	0.25	0.25	0.01	42.69
((Gyumri1,Tango1),Sub1)	214813	130592	0.24	0.24	0.01	45.09

Table 9.3.4- D(((Tango1,Th7),X),Yak).A negative value means that H1 is closer to H3 than H2 is. A positive value means that H2 is closer to H3 than H1 is.

Test((H1,H2),H3),Yak)	nABBA	nBABA	Dstat	jackEst	SE	Z
((Tango1,Th7),Ch22)	5135	4877	0.03	0.03	0.01	2.28
((Tango1,Th7),Sub1)	16069	15344	0.02	0.02	0.01	2.96
((Tango1,Th7),Gyumri2)	12807	12795	0.00	0.00	0.01	0.06
((Tango1,Th7),Bed3)	15351	16262	-0.03	-0.03	0.01	-3.58
((Tango1,Th7),Tri1)	14078	14929	-0.03	-0.03	0.01	-3.55
((Tango1,Th7),Fal7)	13228	14124	-0.03	-0.03	0.01	-3.85
((Tango1,Th7),Tango2)	13291	14303	-0.04	-0.04	0.01	-4.52
((Tango1,Th7),Belorus1)	12703	13700	-0.04	-0.04	0.01	-4.57
((Tango1,Th7),Bed4)	13414	14531	-0.04	-0.04	0.01	-4.58
((Tango1,Th7),Hxh2)	15095	16501	-0.04	-0.04	0.01	-5.34
((Tango1,Th7),Kalisz2)	14078	15489	-0.05	-0.05	0.01	-5.70
((Tango1,Th7),Gyumri1)	11431	15811	-0.16	-0.16	0.01	-18.77
((Tango1,Th7),Baikal1)	12292	17182	-0.17	-0.17	0.01	-19.12

Table 9.3.5- D(((aurochs,aurochs),Th7),Yak). A negative value means that H1 is closer to H3 than H2 is. A positive value means that H2 is closer to H3 than H1 is.

H1	H2	H3	nABBA	nBABA	Dstat	jackEst	SE	Z
Baikal1	**Gyumri2**	**Th7**	19712	12564	0.22	0.22	0.01	30.95
Gyumri1	**Gyumri2**	**Th7**	18140	11632	0.22	0.22	0.01	30.27
Gyumri1	**Tango2**	**Th7**	18986	12359	0.21	0.21	0.01	29.29
Baikal1	**Tango2**	**Th7**	20745	13554	0.21	0.21	0.01	28.74
Baikal1	**Sub1**	**Th7**	25265	16576	0.21	0.21	0.01	28.08
Gyumri1	**Sub1**	**Th7**	22936	15090	0.21	0.21	0.01	27.97
Gyumri1	**Ch22**	**Th7**	7305	4819	0.21	0.21	0.01	19.71
Baikal1	**Ch22**	**Th7**	7903	5236	0.20	0.20	0.01	19.82
Baikal1	**Tri1**	**Th7**	22436	15026	0.20	0.20	0.01	28.29
Gyumri1	**Tri1**	**Th7**	20282	13630	0.20	0.20	0.01	27.51
Baikal1	**Kalisz2**	**Th7**	22558	15206	0.19	0.19	0.01	27.04
Baikal1	**Belorus1**	**Th7**	20070	13545	0.19	0.19	0.01	26.78

Gyumri1	**Bed4**	**Th7**	19481	13208	0.19	0.19	0.01	27.03
Baikal1	**Bed4**	**Th7**	21237	14442	0.19	0.19	0.01	26.87
Gyumri1	**Bed3**	**Th7**	22275	15164	0.19	0.19	0.01	28.70
Baikal1	**Bed3**	**Th7**	24582	16825	0.19	0.19	0.01	28.08
Gyumri1	**Hxh2**	**Th7**	21987	15558	0.17	0.17	0.01	24.83
Baikal1	**Hxh2**	**Th7**	24228	17182	0.17	0.17	0.01	24.77
Gyumri1	**Fal7**	**Th7**	19242	13649	0.17	0.17	0.01	22.98
Baikal1	**Fal7**	**Th7**	21240	15110	0.17	0.17	0.01	22.91
Baikal1	**Tango1**	**Th7**	17110	12292	0.16	0.16	0.01	22.58
Gyumri1	**Tango1**	**Th7**	15886	11431	0.16	0.16	0.01	21.57
Tango1	**Sub1**	**Th7**	16069	13691	0.08	0.08	0.01	10.22
Tango1	**Ch22**	**Th7**	5135	4387	0.08	0.08	0.01	6.61
Fal7	**Ch22**	**Th7**	5206	4557	0.07	0.07	0.01	6.00
Tango1	**Tango2**	**Th7**	13291	11642	0.07	0.07	0.01	8.53
Tango1	**Tri1**	**Th7**	14078	12405	0.06	0.06	0.01	8.15
Fal7	**Sub1**	**Th7**	16287	14554	0.06	0.06	0.01	6.95
Tango1	**Bed3**	**Th7**	15351	13773	0.05	0.05	0.01	7.15
Tango1	**Bed4**	**Th7**	13414	12049	0.05	0.05	0.01	6.91
Hxh2	**Ch22**	**Th7**	5786	5248	0.05	0.05	0.01	4.53
Hxh2	**Sub1**	**Th7**	19016	17286	0.05	0.05	0.01	6.38
Belorus1	**Gyumri2**	**Th7**	11891	11009	0.04	0.04	0.01	4.86
Tango1	**Hxh2**	**Th7**	15095	14014	0.04	0.04	0.01	5.13
Tango1	**Fal7**	**Th7**	13228	12384	0.03	0.03	0.01	4.03
Kalisz2	**Gyumri2**	**Th7**	12957	12186	0.03	0.03	0.01	4.05
Belorus1	**Sub1**	**Th7**	14495	13662	0.03	0.03	0.01	3.87
Bed4	**Sub1**	**Th7**	15446	14606	0.03	0.03	0.01	3.69
Bed3	**Sub1**	**Th7**	18420	17464	0.03	0.03	0.01	3.54
Bed3	**Tri1**	**Th7**	13312	12969	0.01	0.01	0.01	1.68
Tango2	**Sub1**	**Th7**	14900	14532	0.01	0.01	0.01	1.61
Bed4	**Tri1**	**Th7**	11510	11234	0.01	0.01	0.01	1.41
Belorus1	**Tri1**	**Th7**	11179	10990	0.01	0.01	0.01	1.11
Ch22	**Sub1**	**Th7**	4857	4799	0.01	0.01	0.01	0.53
Kalisz2	**Tri1**	**Th7**	12504	12356	0.01	0.01	0.01	0.75
Tango2	**Ch22**	**Th7**	4681	4647	0.00	0.00	0.01	0.33

Baikal1	**Gyumri1**	**Th7**	10759	10682	0.00	0.00	0.01	0.42
Belorus1	**Bed3**	**Th7**	12223	12224	0.00	0.00	0.01	-0.01
Belorus1	**Bed4**	**Th7**	10684	10699	0.00	0.00	0.01	-0.09
Bed3	**Bed4**	**Th7**	12311	12429	0.00	0.00	0.01	-0.61
Tango2	**Tri1**	**Th7**	12274	12415	-0.01	-0.01	0.01	-0.73
Kalisz2	**Bed3**	**Th7**	13690	13873	-0.01	-0.01	0.01	-0.87
Kalisz2	**Bed4**	**Th7**	11800	11998	-0.01	-0.01	0.01	-1.02
Gyumri2	**Sub1**	**Th7**	12967	13229	-0.01	-0.01	0.01	-1.27
Kalisz2	**Belorus1**	**Th7**	11217	11446	-0.01	-0.01	0.01	-1.28
Gyumri2	**Ch22**	**Th7**	4175	4275	-0.01	-0.01	0.01	-1.01
Tango2	**Bed3**	**Th7**	13544	13888	-0.01	-0.01	0.01	-1.74
Hxh2	**Fal7**	**Th7**	13163	13543	-0.01	-0.01	0.01	-1.77
Tango2	**Bed4**	**Th7**	11680	12083	-0.02	-0.02	0.01	-2.10
Bed4	**Hxh2**	**Th7**	12464	12925	-0.02	-0.02	0.01	-2.34
Belorus1	**Hxh2**	**Th7**	12032	12599	-0.02	-0.02	0.01	-3.05
Gyumri2	**Tango2**	**Th7**	11443	11987	-0.02	-0.02	0.01	-3.11
Bed3	**Hxh2**	**Th7**	14674	15414	-0.02	-0.02	0.01	-3.60
Gyumri2	**Tri1**	**Th7**	12090	12818	-0.03	-0.03	0.01	-3.76
Kalisz2	**Hxh2**	**Th7**	13426	14235	-0.03	-0.03	0.01	-3.97
Belorus1	**Fal7**	**Th7**	10566	11306	-0.03	-0.03	0.01	-4.12
Bed3	**Fal7**	**Th7**	13034	14001	-0.04	-0.04	0.01	-4.37
Tango2	**Hxh2**	**Th7**	13161	14146	-0.04	-0.04	0.01	-4.75
Tri1	**Hxh2**	**Th7**	12864	13843	-0.04	-0.04	0.01	-4.75
Gyumri2	**Bed3**	**Th7**	13323	14365	-0.04	-0.04	0.01	-5.08
Bed4	**Fal7**	**Th7**	11050	11917	-0.04	-0.04	0.01	-4.41
Gyumri2	**Bed4**	**Th7**	11596	12518	-0.04	-0.04	0.01	-4.83
Kalisz2	**Fal7**	**Th7**	11755	12750	-0.04	-0.04	0.01	-5.00
Tri1	**Fal7**	**Th7**	11568	12591	-0.04	-0.04	0.01	-5.03
Tango2	**Fal7**	**Th7**	11632	12700	-0.04	-0.04	0.01	-5.21
Gyumri2	**Hxh2**	**Th7**	13120	14695	-0.06	-0.06	0.01	-7.64
Kalisz2	**Tango1**	**Th7**	12462	14078	-0.06	-0.06	0.01	-8.03
Belorus1	**Tango1**	**Th7**	11217	12703	-0.06	-0.06	0.01	-8.14

Gyumri2	**Fal7**	**Th7**	11347	12955	-0.07	-0.07	0.01	-8.42
Gyumri2	**Tango1**	**Th7**	10697	12807	-0.09	-0.09	0.01	-11.63
Belorus1	**Gyumri1**	**Th7**	12466	18508	-0.20	-0.20	0.01	-27.52
Kalisz2	**Gyumri1**	**Th7**	13806	20552	-0.20	-0.20	0.01	-27.51

Table 9.3.6- D(((EU_aurochs,EU_aurochs), Gyumri1/Baikal1),Yak). A negative value means that H1 is closer to H3 than H2 is. A positive value means that H2 is closer to H3 than H1 is.

Test(((H1,H2),H3),Yak)	**nABBA**	**nBABA**	**Dstat**	**jackEst**	**SE**	**Z**
((Bed3,Bed4),Baikal1)	135885	134788	0.00	0.00	0.00	0.88
((Bed3,Bed4),Gyumri1)	124957	124313	0.00	0.00	0.00	0.56
((Bed3,Fal7),Baikal1)	149907	158069	-0.03	-0.03	0.01	-5.12
((Bed3,Fal7),Gyumri1)	136494	144248	-0.03	-0.03	0.01	-5.15
((Bed3,Hxh2),Baikal1)	172202	174745	-0.01	-0.01	0.00	-1.52
((Bed3,Hxh2),Gyumri1)	155716	158560	-0.01	-0.01	0.00	-1.85
((Bed3,Tri1),Baikal1)	142646	139968	0.01	0.01	0.00	2.05
((Bed3,Tri1),Gyumri1)	129704	127690	0.01	0.01	0.00	1.65
((Bed4,Hxh2),Baikal1)	138229	140775	-0.01	-0.01	0.00	-1.89
((Bed4,Hxh2),Gyumri1)	127561	129945	-0.01	-0.01	0.00	-1.93
((Bed4,Tri1),Baikal1)	119508	118270	0.01	0.01	0.00	1.13
((Bed4,Tri1),Gyumri1)	110544	109317	0.01	0.01	0.00	1.17
((Hxh2,Fal7),Baikal1)	151395	157903	-0.02	-0.02	0.01	-3.99
((Hxh2,Fal7),Gyumri1)	137966	143623	-0.02	-0.02	0.01	-3.89
((Tri1,Fal7),Baikal1)	125443	132724	-0.03	-0.03	0.01	-5.56
((Tri1,Fal7),Gyumri1)	114780	121277	-0.03	-0.03	0.01	-5.29
((Tri1,Hxh2),Baikal1)	142570	145887	-0.01	-0.01	0.01	-2.25
((Tri1,Hxh2),Gyumri1)	129601	132834	-0.01	-0.01	0.01	-2.40

Table 9.3.7- D(((Ch22,Sub1),X),Yak). A negative value means that H1 is closer to H3 than H2 is. A positive value means that H2 is closer to H3 than H1 is.

Test (((Ch22,Sub1),X),Yak)	nABBA	nBABA	Dstat	jackEst	SE	Z
((Ch22,Sub1),Baikal1)	47420	47875	0.00	0.00	0.01	-0.83
((Ch22,Sub1),Kalisz2)	51077	52710	-0.02	-0.02	0.01	-2.59
((Ch22,Sub1),Belorus1)	45551	46576	-0.01	-0.01	0.01	-1.72
((Ch22,Sub1),Gyumri1)	43825	43779	0.00	0.00	0.01	0.09
((Ch22,Sub1),Gyumri2)	45238	45762	-0.01	-0.01	0.01	-0.94
((Ch22,Sub1),Tango1)	44141	44278	0.00	0.00	0.01	-0.25
((Ch22,Sub1),Tango2)	47710	48443	-0.01	-0.01	0.01	-1.19
((Ch22,Sub1),Bed3)	55704	57479	-0.02	-0.02	0.01	-2.51
((Ch22,Sub1),Bed4)	46787	48567	-0.02	-0.02	0.01	-2.98
((Ch22,Sub1),Tri1)	48928	50267	-0.01	-0.01	0.01	-2.22
((Ch22,Sub1),Hxh2)	56353	57871	-0.01	-0.01	0.01	-2.17
((Ch22,Sub1),Fal7)	48286	49993	-0.02	-0.02	0.01	-2.72
((Ch22,Sub1),Th7)	4857	4799	0.01	0.01	0.01	0.53

Table 9.3.8- D(((X, Y),Gyumri2),Yak). A negative value means that H1 is closer to H3 than H2 is. A positive value means that H2 is closer to H3 than H1 is.

Test(((H1,H2),H3),Yak)	nABBA	nBABA	Dstat	jackEst	SE	Z
((Baikal1,Gyumri1),Gyumri2)	108759	104311	0.02	0.02	0.01	3.77
((Bed3,Hxh2),Gyumri2)	154586	157847	-0.01	-0.01	0.00	-2.10
((Bed3,Tri1),Gyumri2)	129950	128101	0.01	0.01	0.01	1.38
((Bed3,Kalisz2),Gyumri2)	146303	138651	0.03	0.03	0.01	5.18
((Bed3,Fal7),Gyumri2)	137051	142525	-0.02	-0.02	0.01	-3.73
((Bed3,Belorus1),Gyumri2)	131258	126074	0.02	0.02	0.01	3.90
((Bed3,Tango2),Gyumri2)	146787	138672	0.03	0.03	0.01	5.57
((Belorus1,Tango2),Gyumri2)	120281	118319	0.01	0.01	0.01	1.51
((Belorus1,Tri1),Gyumri2)	109831	112900	-0.01	-0.01	0.01	-2.63
((Belorus1,Kalisz2),Gyumri2)	119373	118018	0.01	0.01	0.01	1.08
((Belorus1,Fal7),Gyumri2)	109901	118053	-0.04	-0.04	0.01	-6.52

((Belorus1,Hxh2),Gyumri2)	125949	133299	-0.03	-0.03	0.01	-5.53
((Belorus1,Bed3),Gyumri2)	126074	131258	-0.02	-0.02	0.01	-3.90
((Belorus1,Bed4),Gyumri2)	109830	113321	-0.02	-0.02	0.01	-3.08
((Hxh2,Fal7),Gyumri2)	137798	140782	-0.01	-0.01	0.01	-1.99
((Hxh2,Bed4),Gyumri2)	131716	128701	0.01	0.01	0.00	2.34
((Hxh2,Tri1),Gyumri2)	133180	129403	0.01	0.01	0.01	2.79
((Hxh2,Tango2),Gyumri2)	149301	138736	0.04	0.04	0.01	6.87
((Kalisz2,Tango2),Gyumri2)	131199	130425	0.00	0.00	0.01	0.56
((Gyumri1,Tango1),Gyumri2)	175614	108749	0.24	0.24	0.01	43.42
((Gyumri1,Tango2),Gyumri2)	209223	120880	0.27	0.27	0.01	53.29
((Tango1,Th7),Gyumri2)	12807	12795	0.00	0.00	0.01	0.06
((Ch22,Sub1),Gyumri2)	45238	45762	-0.01	-0.01	0.01	-0.94

Table 9.3.9- D(((Tango2, European aurochs), Eurasian aurochs,Yak). A negative value means that H1 is closer to H3 than H2 is. A positive value means that H2 is closer to H3 than H1 is.

H1	H2	H3	nABBA	nBABA	Dstat	jackEst	SE	Z
Tango2	Bed3	Baikal1	145971	163925	-0.06	-0.06	0.01	-11.00
Tango2	Bed4	Baikal1	123933	137751	-0.05	-0.05	0.01	-9.50
Tango2	Tri1	Baikal1	126404	139468	-0.05	-0.05	0.01	-9.56
Tango2	Hxh2	Baikal1	147316	166853	-0.06	-0.06	0.01	-11.19
Tango2	Fal7	Baikal1	125784	146823	-0.08	-0.08	0.01	-14.06
Tango2	Bed3	Gyumri1	134625	151806	-0.06	-0.06	0.01	-11.34
Tango2	Bed4	Gyumri1	115108	128857	-0.06	-0.06	0.01	-10.16
Tango2	Tri1	Gyumri1	116409	129365	-0.05	-0.05	0.01	-10.01
Tango2	Hxh2	Gyumri1	134774	154017	-0.07	-0.07	0.01	-12.09
Tango2	Fal7	Gyumri1	116184	136012	-0.08	-0.08	0.01	-14.25
Tango2	Bed3	Gyumri2	138672	146787	-0.03	-0.03	0.01	-5.57
Tango2	Bed4	Gyumri2	120636	126474	-0.02	-0.02	0.01	-4.50
Tango2	Tri1	Gyumri2	120881	126025	-0.02	-0.02	0.01	-3.91
Tango2	Hxh2	Gyumri2	138736	149301	-0.04	-0.04	0.01	-6.87
Tango2	Fal7	Gyumri2	120479	130848	-0.04	-0.04	0.01	-7.49

Tango2	Bed3	Tango1	140754	148239	-0.03	-0.03	0.00	-5.34
Tango2	Bed4	Tango1	122095	127389	-0.02	-0.02	0.01	-4.08
Tango2	Tri1	Tango1	123457	127489	-0.02	-0.02	0.01	-3.18
Tango2	Hxh2	Tango1	141903	150182	-0.03	-0.03	0.01	-5.30
Tango2	Fal7	Tango1	122272	132301	-0.04	-0.04	0.01	-7.04
Tango2	Bed3	Fal7	178567	153329	0.08	0.08	0.01	14.00
Tango2	Bed4	Fal7	151146	128937	0.08	0.08	0.01	13.59
Tango2	Tri1	Fal7	155536	130563	0.09	0.09	0.01	15.15
Tango2	Hxh2	Fal7	181920	154417	0.08	0.08	0.01	13.22
Tango2	Bed3	Hxh2	223328	177240	0.12	0.12	0.01	19.44
Tango2	Bed4	Hxh2	184219	147132	0.11	0.11	0.01	19.11
Tango2	Tri1	Hxh2	191445	148653	0.13	0.13	0.01	21.41
Tango2	Fal7	Hxh2	181920	163208	0.05	0.05	0.01	8.53
Tango2	Bed3	Tri1	193587	150118	0.13	0.13	0.01	21.75
Tango2	Bed4	Tri1	161606	128871	0.11	0.11	0.01	19.45
Tango2	Hxh2	Tri1	191445	153171	0.11	0.11	0.01	18.18
Tango2	Fal7	Tri1	155536	141018	0.05	0.05	0.01	8.01
Tango2	Bed3	Bed4	188620	143851	0.13	0.13	0.01	23.46
Tango2	Tri1	Bed4	161606	126034	0.12	0.12	0.01	20.85
Tango2	Hxh2	Bed4	184219	148875	0.11	0.11	0.01	17.51
Tango2	Fal7	Bed4	151146	136999	0.05	0.05	0.01	7.96
Tango2	Bed4	Bed3	188620	144671	0.13	0.13	0.01	21.45
Tango2	Tri1	Bed3	193587	147816	0.13	0.13	0.01	21.94
Tango2	Hxh2	Bed3	223328	181642	0.10	0.10	0.01	16.04
Tango2	Fal7	Bed3	178567	165209	0.04	0.04	0.01	6.12
Tango2	Bed3	Belorus1	170854	147259	0.07	0.07	0.01	13.33
Tango2	Bed4	Belorus1	146483	127051	0.07	0.07	0.01	12.33
Tango2	Tri1	Belorus1	147723	126558	0.08	0.08	0.01	13.36
Tango2	Hxh2	Belorus1	171056	149509	0.07	0.07	0.01	11.78
Tango2	Fal7	Belorus1	145006	133744	0.04	0.04	0.01	6.64
Tango2	Bed3	Kalisz2	193002	166256	0.07	0.07	0.01	12.19
Tango2	Bed4	Kalisz2	163637	141763	0.07	0.07	0.01	11.67

Tango2	Tri1	Kalisz2	167670	143176	0.08	0.08	0.01	13.02
Tango2	Hxh2	Kalisz2	192594	170118	0.06	0.06	0.01	9.88
Tango2	Fal7	Kalisz2	161481	152639	0.03	0.03	0.01	4.46

Table 9.3.10- D(((Sub1,Test),Bed3),Yak). Values are rounded to two decimal places for this table.

Test	nABBA	nBABA	Dstat	jackEst	SE	Z	Years BP	Region	Wild/Domestic
Ace1	23623	22742	0.02	0.02	0.01	2.84	4200	Anatolia	domestic
Ash4	1936	5537	-0.48	-0.48	0.01	-37.29	3100	Levant	domestic
Baikal1	193385	375905	-0.32	-0.32	0.00	-73.04	12095	Southern Siberia	wild
Bed4	254848	166828	0.21	0.21	0.01	39.97	11708	Central Europe	wild
Bel1	19226	17383	0.05	0.05	0.01	7.26	6925	Balkans	domestic
Bel2	28189	25831	0.04	0.04	0.01	6.69	6925	Balkans	domestic
Belorus1	232155	165736	0.17	0.17	0.01	31.34	0	Eastern Europe	wild
Bes1	166283	408461	-0.42	-0.42	0.01	-50.47	2800	Mesopotamia	domestic
Bes2	179413	770719	-0.62	-0.62	0.01	-112.72	629	Mesopotamia	domestic
Bir3	982	1029	-0.02	-0.02	0.02	-1.01	6000	Eastern Europe	domestic
Bla1	3998	3827	0.02	0.02	0.01	1.79	8100	Balkans	domestic
Bri1	210232	203342	0.02	0.02	0.01	3.11	2300	Northern Europe	domestic
Bub1	69733	65918	0.03	0.03	0.01	5.08	7600	Balkans	domestic
Bul1	9817	24330	-0.43	-0.43	0.01	-41.76	3700	Central Asia	domestic
Bun1	189146	168240	0.06	0.06	0.01	11.55	2300	Northern Europe	domestic
Bun2	206501	185682	0.05	0.05	0.01	10.42	2300	Northern Europe	domestic
CA317	4634	10033	-0.37	-0.37	0.01	-34.93	1300	Southern Caucasus	domestic
Cas1	12721	36976	-0.49	-0.49	0.01	-61.89	1400	Levant	domestic
Ch22	56709	55723	0.01	0.01	0.01	1.56	8000	Anatolia	domestic
Cla1	242090	217953	0.05	0.05	0.01	10.09	2789	British&Irish Isles	domestic
Cla2	197627	172195	0.07	0.07	0.01	13.25	2789	British&Irish Isles	domestic
CPC98	279047	183963	0.21	0.21	0.01	40.01	6738	British&Irish Isles	wild
Dav1	204633	216219	-0.03	-0.03	0.01	-5.42	3500	Levant	domestic
Dav3	3387	3546	-0.02	-0.02	0.01	-1.76	4110	Levant	domestic
Dav4	2504	2755	-0.05	-0.05	0.02	-2.87	4000	Levant	domestic
Dav5	852	2582	-0.50	-0.50	0.02	-31.54	2300	Levant	domestic
Dro1	215431	197214	0.04	0.04	0.01	8.33	1800	Northern Europe	domestic

Dub1	199010	176034	0.06	0.06	0.01	11.91	1100	British&Irish Isles	domestic
Dyr1	200993	189357	0.03	0.03	0.01	5.60	1000	Central Europe	domestic
Dzh1	207496	207248	0.00	0.00	0.01	0.11	7800	Balkans	domestic
Dzh2	200178	195953	0.01	0.01	0.01	2.08	7600	Balkans	domestic
Els1	210525	191711	0.05	0.05	0.01	9.27	1950	Northern Europe	domestic
Fal7	247976	196311	0.12	0.12	0.01	21.41	800	Central Europe	wild
Far1	6394	6212	0.01	0.01	0.01	1.41	7500	Iran	domestic
Fir1	213880	203568	0.02	0.02	0.01	4.84	1200	Northern Europe	domestic
Gyumri1	176639	334535	-0.31	-0.31	0.00	-66.94	13780	Southern Caucasus	wild
Gyumri2	171865	172716	0.00	0.00	0.00	-0.51	7260	Southern Caucasus	wild
Has1	7454	8385	-0.06	-0.06	0.01	-5.51	3700	Iran	domestic
Has3	134540	132399	0.01	0.01	0.01	1.53	4470	Iran	domestic
Has4	144503	169433	-0.08	-0.08	0.01	-9.95	2900	Iran	domestic
Has5	7867	8681	-0.05	-0.05	0.01	-5.04	2300	Iran	domestic
Hou1	208924	196488	0.03	0.03	0.01	6.02	1000	Northern Europe	domestic
Hou2	210986	194293	0.04	0.04	0.01	8.17	850	Northern Europe	domestic
Hxh1	216163	207336	0.02	0.02	0.01	3.99	7000	Central Europe	domestic
Hxh2	317586	223658	0.17	0.17	0.01	34.12	7001	Central Europe	wild
Kalisz2	266464	189713	0.17	0.17	0.01	32.07	0	Eastern Europe	wild
Kalisz3	3966	2979	0.14	0.14	0.01	11.18	0	Eastern Europe	wild
Kaz1	195846	293257	-0.20	-0.20	0.01	-25.76	1000	Southern Caucasus	domestic
Kaz2	52413	93193	-0.28	-0.28	0.01	-33.63	1050	Southern Caucasus	domestic
Kaz3	77791	115799	-0.20	-0.20	0.01	-23.97	1050	Southern Caucasus	domestic
Kaz4	77590	127651	-0.24	-0.24	0.01	-29.60	1040	Southern Caucasus	domestic
Kho1	32620	136443	-0.61	-0.61	0.01	-113.18	950	Iran	domestic
Kie1	10037	8960	0.06	0.06	0.01	6.76	5000	Eastern Europe	domestic
Kie2	48823	39931	0.10	0.10	0.01	17.00	5001	Eastern Europe	domestic
Kir4	227132	225454	0.00	0.00	0.00	0.77	4195	Central Europe	domestic
Kok1	2008	7245	-0.57	-0.57	0.01	-51.22	4000	Central Asia	domestic
Lud1	31292	29299	0.03	0.03	0.01	5.05	7500	Eastern Europe	domestic
Lud2	63719	59699	0.03	0.03	0.01	5.61	7500	Eastern Europe	domestic
Lud3	52982	50681	0.02	0.02	0.01	3.68	7500	Eastern Europe	domestic

Lud4	37249	34750	0.03	0.03	0.01	6.11	7500	Eastern Europe	domestic
Mar1	8405	8689	-0.02	-0.02	0.01	-1.94	7000	Iran	domestic
Men1	184652	189888	-0.01	-0.01	0.00	-2.84	7900	Anatolia	domestic
Men2	158133	155446	0.01	0.01	0.00	1.82	7900	Anatolia	domestic
New1	228881	215968	0.03	0.03	0.01	5.46	4600	British&Irish Isles	domestic
New2	223819	196693	0.06	0.06	0.01	12.64	1550	British&Irish Isles	domestic
New3	224661	210634	0.03	0.03	0.01	6.04	4200	British&Irish Isles	domestic
New4	221332	197815	0.06	0.06	0.00	11.42	4200	British&Irish Isles	domestic
New5	223522	202354	0.05	0.05	0.01	9.74	4337	British&Irish Isles	domestic
Otb1	210624	197493	0.03	0.03	0.01	6.08	1800	Northern Europe	domestic
Plo1	28200	25540	0.05	0.05	0.01	7.61	7125	Balkans	domestic
Plo2	62708	58143	0.04	0.04	0.01	6.74	6950	Balkans	domestic
Plo3	190761	181392	0.03	0.03	0.01	4.90	7000	Balkans	domestic
Plo4	193377	181983	0.03	0.03	0.01	5.86	7000	Balkans	domestic
Plo5	18776	16966	0.05	0.05	0.01	7.50	6650	Balkans	domestic
Plo6	25339	24108	0.02	0.02	0.01	3.83	7126	Balkans	domestic
Plo7	23686	21783	0.04	0.04	0.01	6.31	7000	Balkans	domestic
Plo8	39116	37426	0.02	0.02	0.01	3.54	7001	Balkans	domestic
Qaz1	151149	152671	-0.01	-0.01	0.01	-0.96	4800	Iran	domestic
Sac3	4258	4428	-0.02	-0.02	0.01	-1.59	7373	Iran	domestic
Sch1	179930	160360	0.06	0.06	0.01	11.01	5000	Northern Europe	domestic
Ste1	139137	122744	0.06	0.06	0.01	12.25	1400	Northern Europe	domestic
Stu1	31422	28612	0.05	0.05	0.01	7.23	6600	Balkans	domestic
Tango1	183921	209268	-0.06	-0.06	0.01	-10.57	0	Unknown	wild
Tango2	220208	180429	0.10	0.10	0.01	17.84	4425	Unknown	wild
Th7	16811	20610	-0.10	-0.10	0.01	-15.63	8800	North Africa	wild
Tmq2	798	2054	-0.44	-0.44	0.02	-23.46	3150	Levant	domestic
Tmq3	3770	10592	-0.48	-0.48	0.01	-45.81	2925	Levant	domestic
Tmq4	4645	11349	-0.42	-0.42	0.01	-38.49	3300	Levant	domestic
Tqa2	1219	1171	0.02	0.02	0.02	0.96	4800	Levant	domestic
Tri1	267444	174480	0.21	0.21	0.01	40.64	8116	Central Europe	wild
Tsa1	112297	258621	-0.39	-0.39	0.01	-46.29	2920	Levant	domestic
Tsa3	3645	4528	-0.11	-0.11	0.01	-8.46	2900	Levant	domestic
Tyq1	10436	30158	-0.49	-0.49	0.01	-59.91	2200	Levant	domestic

Viz1	114365	100738	0.06	0.06	0.01	12.24	3400	Northern Europe	domestic
Viz2	200822	187429	0.03	0.03	0.00	6.98	3401	Northern Europe	domestic
Win1	234013	223275	0.02	0.02	0.01	4.52	1800	Northern Europe	domestic
Yer1	11115	41234	-0.58	-0.58	0.01	-80.44	2050	Central Asia	domestic
Yor1	238166	214067	0.05	0.05	0.01	10.51	1929	British&Irish Isles	domestic
Yor2	226472	207029	0.04	0.04	0.01	8.72	1100	British&Irish Isles	domestic
Yor3	212369	189197	0.06	0.06	0.01	10.92	650	British&Irish Isles	domestic
Yor4	219981	201245	0.04	0.04	0.01	8.82	1050	British&Irish Isles	domestic
Zah1	5749	16598	-0.49	-0.49	0.01	-54.81	1700	Levant	domestic

Table 9.3.11- D(((Sub1,Test),Kalisz2),Yak). Values are rounded to two decimal places for this table.

Test	nABBA	nBABA	Dstat	jackEst	SE	Z	Years BP	Region	Wild/Domestic
Ace1	21809	21148	0.02	0.02	0.01	2.38	4200	Anatolia	domestic
Ash4	1749	5175	-0.49	-0.49	0.01	-37.03	3100	Levant	domestic
Baikal1	173319	340262	-0.33	-0.33	0.00	-74.05	12095	Southern Siberia	domestic
Bed3	266464	196532	0.15	0.15	0.01	28.80	11558	Central Europe	domestic
Bed4	218849	160767	0.15	0.15	0.01	30.59	11708	Central Europe	domestic
Bel1	17596	15739	0.06	0.06	0.01	7.51	6925	Balkans	domestic
Bel2	25966	23448	0.05	0.05	0.01	8.10	6925	Balkans	domestic
Belorus1	209427	152046	0.16	0.16	0.01	30.20	0	Eastern Europe	domestic
Bes1	149964	370487	-0.42	-0.42	0.01	-51.36	2800	Mesopotamia	domestic
Bes2	157046	690626	-0.63	-0.63	0.01	-114.57	629	Mesopotamia	domestic
Bla1	3664	3573	0.01	0.01	0.01	0.99	8100	Balkans	domestic
Bri1	189609	180555	0.02	0.02	0.01	4.73	2300	Northern Europe	domestic
Bub1	63292	58647	0.04	0.04	0.01	6.61	7600	Balkans	wild
Bul1	8955	22639	-0.43	-0.43	0.01	-41.79	3700	Central Asia	domestic
Bun1	171586	150545	0.07	0.07	0.00	13.49	2300	Northern Europe	domestic
Bun2	185462	165284	0.06	0.06	0.01	11.01	2300	Northern Europe	domestic
CA317	4271	9091	-0.36	-0.36	0.01	-32.95	1300	Southern Caucasus	domestic
Cas1	11946	34755	-0.49	-0.49	0.01	-61.76	1400	Levant	domestic

Ch22	52029	51011	0.01	0.01	0.01	1.80	8000	Anatolia	domestic
Cla1	211739	190799	0.05	0.05	0.00	10.43	2789	British&Irish Isles	domestic
Cla2	177316	154133	0.07	0.07	0.01	13.87	2789	British&Irish Isles	domestic
CPC98	238209	174670	0.15	0.15	0.00	31.10	6738	British&Irish Isles	domestic
Dav1	183027	193668	-0.03	-0.03	0.00	-5.84	3500	Levant	domestic
Dav3	3235	3422	-0.03	-0.03	0.01	-2.17	4110	Levant	domestic
Dav4	2344	2608	-0.05	-0.05	0.02	-3.23	4000	Levant	domestic
Dav5	785	2372	-0.50	-0.50	0.02	-28.50	2300	Levant	domestic
Dro1	193120	175648	0.05	0.05	0.00	9.74	1800	Northern Europe	wild
Dub1	178123	157699	0.06	0.06	0.00	12.41	1100	British&Irish Isles	domestic
Dyr1	180981	170217	0.03	0.03	0.01	5.63	1000	Central Europe	domestic
Dzh1	185651	180988	0.01	0.01	0.01	2.48	7800	Balkans	domestic
Dzh2	180037	174181	0.02	0.02	0.00	3.38	7600	Balkans	domestic
Els1	189308	170684	0.05	0.05	0.00	10.42	1950	Northern Europe	domestic
Fal7	218842	174307	0.11	0.11	0.01	20.94	800	Central Europe	domestic
Far1	6062	5725	0.03	0.03	0.01	2.80	7500	Iran	domestic
Fir1	193701	179647	0.04	0.04	0.01	7.23	1200	Northern Europe	domestic
Gyumri1	159474	305533	-0.31	-0.31	0.00	-68.77	13780	Southern Caucasus	domestic
Gyumri2	158019	157381	0.00	0.00	0.00	0.42	7260	Southern Caucasus	domestic
Has1	7185	7664	-0.03	-0.03	0.01	-2.93	3700	Iran	domestic
Has3	124947	120505	0.02	0.02	0.00	3.68	4470	Iran	domestic
Has4	134576	153966	-0.07	-0.07	0.01	-8.30	2900	Iran	domestic
Has5	7352	7975	-0.04	-0.04	0.01	-3.95	2300	Iran	domestic
Hou1	187931	174548	0.04	0.04	0.01	7.17	1000	Northern Europe	domestic
Hou2	188142	173551	0.04	0.04	0.01	7.97	850	Northern Europe	domestic
Hxh1	191619	181637	0.03	0.03	0.01	5.20	7000	Central Europe	domestic
Hxh2	266007	202084	0.14	0.14	0.01	26.39	7001	Central Europe	domestic
Kalisz3	3682	2801	0.14	0.14	0.01	10.18	0	Eastern Europe	domestic
Kaz1	176620	260841	-0.19	-0.19	0.01	-23.90	1000	Southern Caucasus	domestic
Kaz2	47536	84392	-0.28	-0.28	0.01	-32.77	1050	Southern Caucasus	domestic
Kaz3	70905	104595	-0.19	-0.19	0.01	-23.20	1050	Southern Caucasus	domestic
Kaz4	71631	116819	-0.24	-0.24	0.01	-28.58	1040	Southern Caucasus	domestic

Kho1	29987	127191	-0.62	-0.62	0.01	-116.80	950	Iran	domestic
Kie1	9269	8338	0.05	0.05	0.01	5.98	5000	Eastern Europe	domestic
Kie2	45766	36813	0.11	0.11	0.01	18.36	5001	Eastern Europe	domestic
Kir4	202221	194984	0.02	0.02	0.00	3.68	4195	Central Europe	domestic
Kok1	1941	6793	-0.56	-0.56	0.01	-48.94	4000	Central Asia	domestic
Lud1	29141	26865	0.04	0.04	0.01	6.35	7500	Eastern Europe	domestic
Lud2	59647	54681	0.04	0.04	0.01	7.70	7500	Eastern Europe	domestic
Lud3	49585	46520	0.03	0.03	0.01	5.10	7500	Eastern Europe	wild
Lud4	34860	32183	0.04	0.04	0.01	6.72	7500	Eastern Europe	wild
Mar1	7756	7886	-0.01	-0.01	0.01	-0.90	7000	Iran	domestic
Men1	167118	166850	0.00	0.00	0.00	0.17	7900	Anatolia	domestic
Men2	143739	140104	0.01	0.01	0.00	2.65	7900	Anatolia	wild
Mus1	613	1642	-0.46	-0.46	0.02	-23.07	3100	Levant	domestic
New1	202668	187345	0.04	0.04	0.01	7.56	4600	British&Irish Isles	wild
New2	199931	175510	0.07	0.07	0.00	13.06	1550	British&Irish Isles	domestic
New3	200385	184528	0.04	0.04	0.00	8.24	4200	British&Irish Isles	domestic
New4	197511	175550	0.06	0.06	0.00	11.80	4200	British&Irish Isles	domestic
New5	198479	179269	0.05	0.05	0.01	10.02	4337	British&Irish Isles	domestic
Otb1	188960	175575	0.04	0.04	0.01	6.80	1800	Northern Europe	domestic
Plo1	25845	23139	0.06	0.06	0.01	8.90	7125	Balkans	domestic
Plo2	58251	52743	0.05	0.05	0.01	9.01	6950	Balkans	domestic
Plo3	173865	162025	0.04	0.04	0.00	7.12	7000	Balkans	domestic
Plo4	175746	161850	0.04	0.04	0.01	7.96	7000	Balkans	domestic
Plo5	17329	15565	0.05	0.05	0.01	7.37	6650	Balkans	domestic
Plo6	23271	21542	0.04	0.04	0.01	5.42	7126	Balkans	domestic
Plo7	22021	19849	0.05	0.05	0.01	7.81	7000	Balkans	domestic
Plo8	36436	33555	0.04	0.04	0.01	6.77	7001	Balkans	domestic
Qaz1	140271	138765	0.01	0.01	0.00	1.11	4800	Iran	domestic
Sac3	3866	3962	-0.01	-0.01	0.01	-0.91	7373	Iran	domestic
Sch1	163729	144171	0.06	0.06	0.00	13.46	5000	Northern Europe	domestic
Ste1	126322	110874	0.07	0.07	0.01	12.92	1400	Northern Europe	domestic
Stu1	29348	26292	0.05	0.05	0.01	9.08	6600	Balkans	domestic

Tango1	168638	191935	-0.06	-0.06	0.01	-10.49	0	Unknown	domestic
Tango2	201427	165137	0.10	0.10	0.01	18.88	4425	Unknown	domestic
Th7	15093	19262	-0.12	-0.12	0.01	-17.15	8800	North Africa	domestic
Tmq1	610	1789	-0.49	-0.49	0.02	-23.71	3150	Levant	domestic
Tmq2	750	1866	-0.43	-0.43	0.02	-21.82	3150	Levant	domestic
Tmq3	3393	9655	-0.48	-0.48	0.01	-44.37	2925	Levant	domestic
Tmq4	4351	10596	-0.42	-0.42	0.01	-36.43	3300	Levant	domestic
Tqa2	1132	1034	0.05	0.05	0.02	2.09	4800	Levant	wild
Tri1	228055	165181	0.16	0.16	0.01	30.65	8116	Central Europe	domestic
Tsa1	104074	240162	-0.40	-0.40	0.01	-47.33	2920	Levant	domestic
Tsa3	3393	4131	-0.10	-0.10	0.01	-7.43	2900	Levant	domestic
Tyq1	9734	28052	-0.48	-0.48	0.01	-57.01	2200	Levant	domestic
Viz1	104764	92957	0.06	0.06	0.00	12.23	3400	Northern Europe	domestic
Viz2	182022	166856	0.04	0.04	0.00	8.97	3401	Northern Europe	wild
Win1	205379	195078	0.03	0.03	0.00	5.16	1800	Northern Europe	domestic
Yer1	10335	38934	-0.58	-0.58	0.01	-79.50	2050	Central Asia	wild
Yor1	209053	188476	0.05	0.05	0.00	10.69	1929	British&Irish Isles	wild
Yor2	202048	183170	0.05	0.05	0.01	9.71	1100	British&Irish Isles	wild
Yor3	189638	170103	0.05	0.05	0.01	10.80	650	British&Irish Isles	wild
Yor4	196150	178801	0.05	0.05	0.01	8.94	1050	British&Irish Isles	wild
Zah1	5303	15538	-0.49	-0.49	0.01	-57.32	1700	Levant	wild

Table 9.3.12- D(((Sub1,Test),Gyumri2),Yak). Values are rounded to two decimal places for this table.

Test	nABBA	nBABA	Dstat	jackEst	SE	Z	Years BP	Region	Wild/Domestic
Ace1	20017	19374	0.02	0.02	0.01	2.44	4200	Anatolia	domestic
Ash4	1686	4839	-0.48	-0.48	0.01	-35.52	3100	Levant	domestic
Baikal1	146491	306339	-0.35	-0.35	0.00	-80.80	12095	Southern Siberia	wild
Bed3	171865	212099	-0.10	-0.10	0.01	-20.43	11558	Central Europe	wild
Bed4	145065	175929	-0.10	-0.10	0.01	-19.09	11708	Central Europe	wild
Bel1	14584	14548	0.00	0.00	0.01	0.17	6925	Balkans	domestic
Bel2	22090	21629	0.01	0.01	0.01	1.59	6925	Balkans	domestic
Belorus1	141983	165934	-0.08	-0.08	0.01	-15.47	0	Eastern Europe	wild

Bes1	127673	327750	-0.44	-0.44	0.01	-53.53	2800	Mesopotamia	domestic
Bes2	131510	604922	-0.64	-0.64	0.01	-117.17	629	Mesopotamia	domestic
Bla1	3289	3309	0.00	0.00	0.01	-0.23	8100	Balkans	domestic
Bri1	152880	169519	-0.05	-0.05	0.01	-9.87	2300	Northern Europe	domestic
Bub1	52178	52914	-0.01	-0.01	0.01	-1.30	7600	Balkans	domestic
Bul1	8133	20837	-0.44	-0.44	0.01	-41.31	3700	Central Asia	domestic
Bun1	135298	143002	-0.03	-0.03	0.00	-5.60	2300	Northern Europe	domestic
Bun2	145112	157564	-0.04	-0.04	0.01	-8.18	2300	Northern Europe	domestic
CA317	3673	8278	-0.39	-0.39	0.01	-35.01	1300	Southern Caucasus	domestic
Cas1	10887	32279	-0.50	-0.50	0.01	-63.65	1400	Levant	domestic
Ch22	45923	45881	0.00	0.00	0.01	0.09	8000	Anatolia	domestic
Cla1	162483	182176	-0.06	-0.06	0.01	-11.32	2789	British&Irish Isles	domestic
Cla2	137826	148976	-0.04	-0.04	0.01	-7.73	2789	British&Irish Isles	domestic
CPC98	155546	187692	-0.09	-0.09	0.01	-18.31	6738	British&Irish Isles	wild
Dav1	163379	169002	-0.02	-0.02	0.01	-3.30	3500	Levant	domestic
Dav3	3051	3087	-0.01	-0.01	0.01	-0.42	4110	Levant	domestic
Dav4	2297	2448	-0.03	-0.03	0.02	-1.89	4000	Levant	domestic
Dav5	742	2151	-0.49	-0.49	0.02	-26.23	2300	Levant	domestic
Dro1	152942	165885	-0.04	-0.04	0.00	-8.32	1800	Northern Europe	domestic
Dub1	139892	149637	-0.03	-0.03	0.01	-6.59	1100	British&Irish Isles	domestic
Dyr1	145140	159989	-0.05	-0.05	0.01	-9.08	1000	Central Europe	domestic
Dzh1	158294	161683	-0.01	-0.01	0.01	-2.05	7800	Balkans	domestic
Dzh2	155605	154569	0.00	0.00	0.00	0.67	7600	Balkans	domestic
Els1	149368	161739	-0.04	-0.04	0.00	-7.97	1950	Northern Europe	domestic
Fal7	145683	183545	-0.12	-0.12	0.01	-21.46	800	Central Europe	wild
Far1	5694	5337	0.03	0.03	0.01	3.09	7500	Iran	domestic
Fir1	153114	170407	-0.05	-0.05	0.01	-10.42	1200	Northern Europe	domestic
Gyumri1	136867	277717	-0.34	-0.34	0.00	-73.76	13780	Southern Caucasus	wild
Has1	6325	7108	-0.06	-0.06	0.01	-5.12	3700	Iran	domestic
Has3	111511	110069	0.01	0.01	0.00	1.35	4470	Iran	domestic
Has4	118393	139418	-0.08	-0.08	0.01	-10.38	2900	Iran	domestic
Has5	6666	7391	-0.05	-0.05	0.01	-5.07	2300	Iran	domestic

Hou1	150146	163300	-0.04	-0.04	0.01	-8.39	1000	Northern Europe	domestic
Hou2	149910	162732	-0.04	-0.04	0.01	-7.97	850	Northern Europe	domestic
Hxh1	161059	164159	-0.01	-0.01	0.01	-1.71	7000	Central Europe	domestic
Hxh2	171498	217065	-0.12	-0.12	0.01	-23.05	7001	Central Europe	wild
Kalisz2	158019	187084	-0.08	-0.08	0.01	-16.55	0	Eastern Europe	wild
Kalisz3	2612	2990	-0.07	-0.07	0.01	-4.56	0	Eastern Europe	wild
Kaz1	151698	231803	-0.21	-0.21	0.01	-25.90	1000	Southern Caucasus	domestic
Kaz2	41162	75234	-0.29	-0.29	0.01	-36.26	1050	Southern Caucasus	domestic
Kaz3	60453	92479	-0.21	-0.21	0.01	-25.84	1050	Southern Caucasus	domestic
Kaz4	62378	105399	-0.26	-0.26	0.01	-30.43	1040	Southern Caucasus	domestic
Kho1	26083	115041	-0.63	-0.63	0.01	-120.03	950	Iran	domestic
Kie1	7911	7960	0.00	0.00	0.01	-0.33	5000	Eastern Europe	domestic
Kie2	35694	37477	-0.02	-0.02	0.01	-4.10	5001	Eastern Europe	domestic
Kir4	166557	178275	-0.03	-0.03	0.01	-6.76	4195	Central Europe	domestic
Kok1	1703	6343	-0.58	-0.58	0.01	-50.08	4000	Central Asia	domestic
Lud1	25075	25038	0.00	0.00	0.01	0.12	7500	Eastern Europe	domestic
Lud2	52547	51571	0.01	0.01	0.01	1.71	7500	Eastern Europe	domestic
Lud3	43285	44304	-0.01	-0.01	0.01	-2.08	7500	Eastern Europe	domestic
Lud4	30633	30133	0.01	0.01	0.01	1.26	7500	Eastern Europe	domestic
Mar1	6892	7207	-0.02	-0.02	0.01	-2.33	7000	Iran	domestic
Men1	144578	148725	-0.01	-0.01	0.01	-2.81	7900	Anatolia	domestic
Men2	127641	123810	0.02	0.02	0.01	2.96	7900	Anatolia	domestic
New1	160380	175538	-0.05	-0.05	0.01	-8.63	4600	British&Irish Isles	domestic
New2	155295	166069	-0.03	-0.03	0.00	-6.88	1550	British&Irish Isles	domestic
New3	159901	172055	-0.04	-0.04	0.00	-7.34	4200	British&Irish Isles	domestic
New4	155394	166525	-0.03	-0.03	0.00	-7.14	4200	British&Irish Isles	domestic
New5	159231	167347	-0.02	-0.02	0.00	-5.05	4337	British&Irish Isles	domestic
Otb1	149712	166346	-0.05	-0.05	0.01	-10.36	1800	Northern Europe	domestic
Plo1	21541	21119	0.01	0.01	0.01	1.55	7125	Balkans	domestic
Plo2	49670	48629	0.01	0.01	0.01	1.82	6950	Balkans	domestic
Plo3	145560	147914	-0.01	-0.01	0.01	-1.59	7000	Balkans	domestic
Plo4	146567	148359	-0.01	-0.01	0.01	-1.21	7000	Balkans	domestic
Plo5	14652	14238	0.01	0.01	0.01	2.04	6650	Balkans	domestic

Plo6	19315	18800	0.01	0.01	0.01	1.91	7126	Balkans	domestic
Plo7	18862	18473	0.01	0.01	0.01	1.50	7000	Balkans	domestic
Plo8	30646	30315	0.01	0.01	0.01	0.87	7001	Balkans	domestic
Qaz1	127952	125319	0.01	0.01	0.01	2.02	4800	Iran	domestic
Sac3	3566	3618	-0.01	-0.01	0.01	-0.56	7373	Iran	domestic
Sch1	131403	134998	-0.01	-0.01	0.00	-2.71	5000	Northern Europe	domestic
Ste1	100828	107075	-0.03	-0.03	0.01	-5.76	1400	Northern Europe	domestic
Stu1	25365	24784	0.01	0.01	0.01	1.81	6600	Balkans	domestic
Tango1	139439	181463	-0.13	-0.13	0.01	-24.35	0	Unknown	wild
Tango2	147562	168479	-0.07	-0.07	0.01	-12.85	4425	Unknown	wild
Th7	13026	17384	-0.14	-0.14	0.01	-20.69	8800	North Africa	wild
Tmq1	557	1557	-0.47	-0.47	0.02	-21.82	3150	Levant	domestic
Tmq2	622	1687	-0.46	-0.46	0.02	-23.07	3150	Levant	domestic
Tmq3	2959	8616	-0.49	-0.49	0.01	-43.45	2925	Levant	domestic
Tmq4	3888	9449	-0.42	-0.42	0.01	-35.41	3300	Levant	domestic
Tri1	147910	178385	-0.09	-0.09	0.01	-17.97	8116	Central Europe	wild
Tsa1	93054	217924	-0.40	-0.40	0.01	-47.23	2920	Levant	domestic
Tsa3	2943	3547	-0.09	-0.09	0.01	-6.31	2900	Levant	domestic
Tyq1	8674	25443	-0.49	-0.49	0.01	-56.09	2200	Levant	domestic
Viz1	85097	89724	-0.03	-0.03	0.00	-5.29	3400	Northern Europe	domestic
Viz2	144166	157271	-0.04	-0.04	0.01	-8.49	3401	Northern Europe	domestic
Win1	161887	182244	-0.06	-0.06	0.00	-11.94	1800	Northern Europe	domestic
Yer1	9319	35843	-0.59	-0.59	0.01	-78.77	2050	Central Asia	domestic
Yor1	161246	179044	-0.05	-0.05	0.00	-10.73	1929	British&Irish Isles	domestic
Yor2	156886	174065	-0.05	-0.05	0.00	-10.49	1100	British&Irish Isles	domestic
Yor3	148393	161544	-0.04	-0.04	0.01	-8.36	650	British&Irish Isles	domestic
Yor4	153114	168567	-0.05	-0.05	0.01	-9.29	1050	British&Irish Isles	domestic
Zah1	4836	14154	-0.49	-0.49	0.01	-53.38	1700	Levant	domestic

Table 9.3.13- D(((Sub1,Test),Gyumri1),Yak). Values are rounded to two decimal places for this table.

Test	nABBA	nBABA	Dstat	jackEst	SE	Z	Years BP	Region	Wild/Domestic
Ace1	18486	17798	0.02	0.02	0.01	2.81	4200	Anatolia	domestic
Ash4	1707	4453	-0.45	-0.45	0.01	-32.13	3100	Levant	domestic
Baikal1	367466	148247	0.43	0.43	0.01	74.02	12095	Southern Siberia	wild
Bed3	176639	192647	-0.04	-0.04	0.00	-9.49	11558	Central Europe	wild
Bed4	146732	157341	-0.03	-0.03	0.00	-7.65	11708	Central Europe	wild
Bel1	13888	13540	0.01	0.01	0.01	1.70	6925	Balkans	domestic
Bel2	20734	20124	0.01	0.01	0.01	2.44	6925	Balkans	domestic
Belorus1	141462	148925	-0.03	-0.03	0.00	-5.51	0	Eastern Europe	wild
Bes1	139992	311640	-0.38	-0.38	0.01	-48.39	2800	Mesopotamia	domestic
Bes2	163925	584418	-0.56	-0.56	0.01	-104.83	629	Mesopotamia	domestic
Bla1	3085	2991	0.02	0.02	0.01	1.14	8100	Balkans	domestic
Bri1	150062	157208	-0.02	-0.02	0.00	-4.84	2300	Northern Europe	domestic
Bub1	50075	50094	0.00	0.00	0.01	-0.04	7600	Balkans	domestic
Bul1	8689	19157	-0.38	-0.38	0.01	-36.95	3700	Central Asia	domestic
Bun1	132101	132021	0.00	0.00	0.00	0.07	2300	Northern Europe	domestic
Bun2	142823	144942	-0.01	-0.01	0.00	-1.64	2300	Northern Europe	domestic
CA317	3912	7953	-0.34	-0.34	0.01	-30.82	1300	Southern Caucasus	domestic
Cas1	11661	29896	-0.44	-0.44	0.01	-58.93	1400	Levant	domestic
Ch22	42702	43214	-0.01	-0.01	0.01	-1.17	8000	Anatolia	domestic
Cla1	159066	170824	-0.04	-0.04	0.00	-7.66	2789	British&Irish Isles	domestic
Cla2	132890	138385	-0.02	-0.02	0.00	-4.22	2789	British&Irish Isles	domestic
CPC98	158637	169661	-0.03	-0.03	0.00	-7.57	6738	British&Irish Isles	wild
Dav1	157286	158314	0.00	0.00	0.00	-0.68	3500	Levant	domestic
Dav3	2806	2769	0.01	0.01	0.01	0.47	4110	Levant	domestic
Dav4	2102	2189	-0.02	-0.02	0.02	-1.18	4000	Levant	domestic
Dav5	778	1978	-0.44	-0.44	0.02	-22.81	2300	Levant	domestic
Dro1	149335	154593	-0.02	-0.02	0.00	-3.75	1800	Northern Europe	domestic
Dub1	136447	139580	-0.01	-0.01	0.00	-2.53	1100	British&Irish Isles	domestic
Dyr1	143024	147414	-0.02	-0.02	0.00	-3.06	1000	Central Europe	domestic
Dzh1	151287	153022	-0.01	-0.01	0.00	-1.28	7800	Balkans	domestic

Dzh2	147094	147660	0.00	0.00	0.00	-0.40	7600	Balkans	domestic
Els1	145749	150262	-0.02	-0.02	0.00	-3.45	1950	Northern Europe	domestic
Fal7	148138	167893	-0.06	-0.06	0.00	-13.37	800	Central Europe	wild
Far1	5263	4884	0.04	0.04	0.01	3.35	7500	Iran	domestic
Fir1	151922	157022	-0.02	-0.02	0.00	-3.51	1200	Northern Europe	domestic
Gyumri2	136867	130557	0.02	0.02	0.00	5.23	7260	Southern Caucasus	wild
Has1	5963	6471	-0.04	-0.04	0.01	-3.68	3700	Iran	domestic
Has3	104696	101291	0.02	0.02	0.00	3.63	4470	Iran	domestic
Has4	113838	129210	-0.06	-0.06	0.01	-8.20	2900	Iran	domestic
Has5	6260	6898	-0.05	-0.05	0.01	-4.37	2300	Iran	domestic
Hou1	147096	152081	-0.02	-0.02	0.00	-3.47	1000	Northern Europe	domestic
Hou2	146711	151145	-0.01	-0.01	0.00	-3.03	850	Northern Europe	domestic
Hxh1	153188	156490	-0.01	-0.01	0.00	-2.25	7000	Central Europe	domestic
Hxh2	177196	196660	-0.05	-0.05	0.00	-10.75	7001	Central Europe	wild
Kalisz2	159474	169665	-0.03	-0.03	0.00	-6.94	0	Eastern Europe	wild
Kalisz3	2519	2758	-0.05	-0.05	0.01	-3.11	0	Eastern Europe	wild
Kaz1	153607	219354	-0.18	-0.18	0.01	-24.07	1000	Southern Caucasus	domestic
Kaz2	42504	71190	-0.25	-0.25	0.01	-32.20	1050	Southern Caucasus	domestic
Kaz3	61391	87406	-0.17	-0.17	0.01	-22.15	1050	Southern Caucasus	domestic
Kaz4	63289	98869	-0.22	-0.22	0.01	-26.87	1040	Southern Caucasus	domestic
Kho1	31985	108277	-0.54	-0.54	0.01	-94.10	950	Iran	domestic
Kie1	7301	7362	0.00	0.00	0.01	-0.44	5000	Eastern Europe	domestic
Kie2	33866	33720	0.00	0.00	0.01	0.39	5001	Eastern Europe	domestic
Kir4	164124	166398	-0.01	-0.01	0.00	-1.50	4195	Central Europe	domestic
Kok1	2005	5945	-0.50	-0.50	0.01	-40.86	4000	Central Asia	domestic
Lud1	23356	23305	0.00	0.00	0.01	0.17	7500	Eastern Europe	domestic
Lud2	48209	47965	0.00	0.00	0.01	0.47	7500	Eastern Europe	domestic
Lud3	40645	40357	0.00	0.00	0.01	0.65	7500	Eastern Europe	domestic
Lud4	28693	27812	0.02	0.02	0.01	2.57	7500	Eastern Europe	domestic
Mar1	6625	6553	0.01	0.01	0.01	0.56	7000	Iran	domestic
Men1	138215	140611	-0.01	-0.01	0.00	-1.92	7900	Anatolia	domestic

Men2	118474	117515	0.00	0.00	0.00	0.88	7900	Anatolia	domestic
New1	157032	163466	-0.02	-0.02	0.00	-4.46	4600	British&Irish Isles	domestic
New2	151096	155697	-0.01	-0.01	0.00	-3.24	1550	British&Irish Isles	domestic
New3	156427	161329	-0.02	-0.02	0.00	-3.23	4200	British&Irish Isles	domestic
New4	151260	154984	-0.01	-0.01	0.00	-2.63	4200	British&Irish Isles	domestic
New5	152505	157537	-0.02	-0.02	0.00	-3.58	4337	British&Irish Isles	domestic
Otb1	146740	154048	-0.02	-0.02	0.00	-5.08	1800	Northern Europe	domestic
Plo1	20269	20105	0.00	0.00	0.01	0.63	7125	Balkans	domestic
Plo2	46997	45402	0.02	0.02	0.01	3.21	6950	Balkans	domestic
Plo3	139392	138248	0.00	0.00	0.00	0.87	7000	Balkans	domestic
Plo4	140068	139600	0.00	0.00	0.00	0.35	7000	Balkans	domestic
Plo5	13912	13304	0.02	0.02	0.01	3.10	6650	Balkans	domestic
Plo6	18378	18171	0.01	0.01	0.01	0.82	7126	Balkans	domestic
Plo7	17618	16855	0.02	0.02	0.01	3.33	7000	Balkans	domestic
Plo8	28938	28586	0.01	0.01	0.01	0.99	7001	Balkans	domestic
Qaz1	118991	115898	0.01	0.01	0.00	2.85	4800	Iran	domestic
Sac3	3333	3390	-0.01	-0.01	0.01	-0.66	7373	Iran	domestic
Sch1	125789	125955	0.00	0.00	0.00	-0.15	5000	Northern Europe	domestic
Ste1	96972	98154	-0.01	-0.01	0.00	-1.30	1400	Northern Europe	domestic
Stu1	23643	22629	0.02	0.02	0.01	3.53	6600	Balkans	domestic
Tango1	185910	134760	0.16	0.16	0.01	26.82	0	Unknown	wild
Tango2	155468	146631	0.03	0.03	0.01	5.85	4425	Unknown	wild
Th7	14368	14671	-0.01	-0.01	0.01	-1.45	8800	North Africa	wild
Tmq1	641	1427	-0.38	-0.38	0.02	-16.84	3150	Levant	domestic
Tmq2	699	1593	-0.39	-0.39	0.02	-19.07	3150	Levant	domestic
Tmq3	3354	8214	-0.42	-0.42	0.01	-37.70	2925	Levant	domestic
Tmq4	4122	9009	-0.37	-0.37	0.01	-33.18	3300	Levant	domestic
Tri1	150611	160576	-0.03	-0.03	0.00	-7.20	8116	Central Europe	wild
Tsa1	97126	204081	-0.36	-0.36	0.01	-44.44	2920	Levant	domestic
Tsa3	2947	3312	-0.06	-0.06	0.01	-4.01	2900	Levant	domestic
Tyq1	9513	23945	-0.43	-0.43	0.01	-51.19	2200	Levant	domestic
Viz1	81712	82337	0.00	0.00	0.00	-0.79	3400	Northern Europe	domestic
Viz2	141861	145982	-0.01	-0.01	0.00	-3.08	3401	Northern Europe	domestic
Win1	160815	169636	-0.03	-0.03	0.00	-5.79	1800	Northern Europe	domestic

Yer1	10659	33150	-0.51	-0.51	0.01	-70.10	2050	Central Asia	domestic
Yor1	158942	167006	-0.02	-0.02	0.00	-5.49	1929	British&Irish Isles	domestic
Yor2	154588	161855	-0.02	-0.02	0.00	-4.98	1100	British&Irish Isles	domestic
Yor3	144898	150859	-0.02	-0.02	0.00	-4.33	650	British&Irish Isles	domestic
Yor4	150839	156915	-0.02	-0.02	0.00	-4.22	1050	British&Irish Isles	domestic
Zah1	5212	13116	-0.43	-0.43	0.01	-48.11	1700	Levant	domestic

Table 9.3.14- D(((Sub1,Test),Th7),Yak). Values are rounded to two decimal places for this table.

Test	nABBA	nBABA	Dstat	jackEst	SE	Z	Years BP	Region	Wild/Domestic
Ace1	2132	1970	0.04	0.04	0.02	2.37	4200	Anatolia	domestic
Baikal1	15661	27801	-0.28	-0.28	0.01	-44.96	12095	Southern Siberia	wild
Bed3	16811	19581	-0.08	-0.08	0.01	-11.24	11558	Central Europe	wild
Bed4	14090	16450	-0.08	-0.08	0.01	-10.80	11708	Central Europe	wild
Bel1	1751	1737	0.00	0.00	0.02	0.22	6925	Balkans	domestic
Bel2	2498	2449	0.01	0.01	0.01	0.67	6925	Balkans	domestic
Belorus1	13352	15425	-0.07	-0.07	0.01	-9.70	0	Eastern Europe	wild
Bes1	13067	32377	-0.42	-0.42	0.01	-47.58	2800	Mesopotamia	domestic
Bes2	13195	57668	-0.63	-0.63	0.01	-102.29	629	Mesopotamia	domestic
Bri1	14606	15508	-0.03	-0.03	0.01	-4.08	2300	Northern Europe	domestic
Bub1	5708	5718	0.00	0.00	0.01	-0.08	7600	Balkans	domestic
Bul1	923	2207	-0.41	-0.41	0.02	-22.48	3700	Central Asia	domestic
Bun1	13330	13823	-0.02	-0.02	0.01	-2.50	2300	Northern Europe	domestic
Bun2	14482	14841	-0.01	-0.01	0.01	-1.66	2300	Northern Europe	domestic
Cas1	1280	3223	-0.43	-0.43	0.02	-27.18	1400	Levant	domestic
Ch22	4765	4928	-0.02	-0.02	0.01	-1.54	8000	Anatolia	domestic
Cla1	15484	16890	-0.04	-0.04	0.01	-6.30	2789	British&Irish Isles	domestic
Cla2	13475	14116	-0.02	-0.02	0.01	-3.00	2789	British&Irish Isles	domestic
CPC98	15629	17998	-0.07	-0.07	0.01	-10.09	6738	British&Irish Isles	wild
Dav1	16360	15493	0.03	0.03	0.01	3.85	3500	Levant	domestic
Dro1	14587	15642	-0.03	-0.03	0.01	-5.00	1800	Northern Europe	domestic

Dub1	13892	14358	-0.02	-0.02	0.01	-2.30	1100	British&Irish Isles	domestic
Dyr1	13930	15110	-0.04	-0.04	0.01	-5.17	1000	Central Europe	domestic
Dzh1	15018	14962	0.00	0.00	0.01	0.26	7800	Balkans	domestic
Dzh2	14860	14950	0.00	0.00	0.01	-0.41	7600	Balkans	domestic
Els1	14431	15132	-0.02	-0.02	0.01	-3.27	1950	Northern Europe	domestic
Fal7	14098	17238	-0.10	-0.10	0.01	-13.59	800	Central Europe	wild
Fir1	14646	15749	-0.04	-0.04	0.01	-5.18	1200	Northern Europe	domestic
Gyumri1	14368	24927	-0.27	-0.27	0.01	-41.72	13780	Southern Caucasus	wild
Gyumri2	13026	13150	0.00	0.00	0.01	-0.65	7260	Southern Caucasus	wild
Has3	10751	10388	0.02	0.02	0.01	2.14	4470	Iran	domestic
Has4	11622	13745	-0.08	-0.08	0.01	-8.36	2900	Iran	domestic
Hou1	14641	15462	-0.03	-0.03	0.01	-3.68	1000	Northern Europe	domestic
Hou2	14848	15646	-0.03	-0.03	0.01	-3.51	850	Northern Europe	domestic
Hxh1	15040	15465	-0.01	-0.01	0.01	-1.93	7000	Central Europe	domestic
Hxh2	16462	20019	-0.10	-0.10	0.01	-14.25	7001	Central Europe	wild
Kalisz2	15093	17446	-0.07	-0.07	0.01	-10.26	0	Eastern Europe	wild
Kaz1	14531	21811	-0.20	-0.20	0.01	-21.71	1000	Southern Caucasus	domestic
Kaz2	4311	7638	-0.28	-0.28	0.01	-22.73	1050	Southern Caucasus	domestic
Kaz3	6490	9546	-0.19	-0.19	0.01	-17.67	1050	Southern Caucasus	domestic
Kaz4	6134	10132	-0.25	-0.25	0.01	-21.63	1040	Southern Caucasus	domestic
Kho1	2853	11310	-0.60	-0.60	0.01	-66.09	950	Iran	domestic
Kie2	3659	3687	0.00	0.00	0.01	-0.30	5001	Eastern Europe	domestic
Kir4	15801	16622	-0.03	-0.03	0.01	-3.63	4195	Central Europe	domestic
Lud1	2811	2677	0.02	0.02	0.01	1.74	7500	Eastern Europe	domestic
Lud2	5009	4985	0.00	0.00	0.01	0.21	7500	Eastern Europe	domestic
Lud3	4299	4189	0.01	0.01	0.01	1.11	7500	Eastern Europe	domestic
Lud4	3148	3042	0.02	0.02	0.01	1.26	7500	Eastern Europe	domestic
Men1	14143	14184	0.00	0.00	0.01	-0.20	7900	Anatolia	domestic
Men2	13008	12369	0.03	0.03	0.01	3.07	7900	Anatolia	domestic
New1	15330	16181	-0.03	-0.03	0.01	-3.55	4600	British&Irish Isles	domestic
New2	15119	15793	-0.02	-0.02	0.01	-2.97	1550	British&Irish Isles	domestic
New3	15309	15862	-0.02	-0.02	0.01	-2.33	4200	British&Irish Isles	domestic

New4	15136	15510	-0.01	-0.01	0.01	-1.66	4200	British&Irish Isles	domestic
New5	15144	15753	-0.02	-0.02	0.01	-2.60	4337	British&Irish Isles	domestic
Otb1	14373	15435	-0.04	-0.04	0.01	-4.99	1800	Northern Europe	domestic
Plo1	2573	2441	0.03	0.03	0.01	1.78	7125	Balkans	domestic
Plo2	5326	5243	0.01	0.01	0.01	0.74	6950	Balkans	domestic
Plo3	14062	14267	-0.01	-0.01	0.01	-1.00	7000	Balkans	domestic
Plo4	14086	14185	0.00	0.00	0.01	-0.49	7000	Balkans	domestic
Plo5	1776	1629	0.04	0.04	0.02	2.51	6650	Balkans	domestic
Plo6	2442	2244	0.04	0.04	0.01	2.85	7126	Balkans	domestic
Plo7	2175	2069	0.02	0.02	0.02	1.55	7000	Balkans	domestic
Plo8	3540	3507	0.00	0.00	0.01	0.38	7001	Balkans	domestic
Qaz1	12397	11860	0.02	0.02	0.01	2.78	4800	Iran	domestic
Sch1	13081	13281	-0.01	-0.01	0.01	-1.03	5000	Northern Europe	domestic
Ste1	10043	10441	-0.02	-0.02	0.01	-2.43	1400	Northern Europe	domestic
Stu1	2750	2664	0.02	0.02	0.01	1.08	6600	Balkans	domestic
Tango1	13226	16888	-0.12	-0.12	0.01	-16.71	0	Unknown	wild
Tango2	14015	15816	-0.06	-0.06	0.01	-8.32	4425	Unknown	wild
Tri1	15121	17340	-0.07	-0.07	0.01	-9.40	8116	Central Europe	wild
Tsa1	9454	20836	-0.38	-0.38	0.01	-36.01	2920	Levant	domestic
Tyq1	1079	2718	-0.43	-0.43	0.02	-25.30	2200	Levant	domestic
Viz1	8617	8661	0.00	0.00	0.01	-0.30	3400	Northern Europe	domestic
Viz2	13954	14919	-0.03	-0.03	0.01	-4.23	3401	Northern Europe	domestic
Win1	15300	16884	-0.05	-0.05	0.01	-6.79	1800	Northern Europe	domestic
Yer1	1020	3527	-0.55	-0.55	0.02	-36.59	2050	Central Asia	domestic
Yor1	15617	16416	-0.02	-0.02	0.01	-3.34	1929	British&Irish Isles	domestic
Yor2	15218	16096	-0.03	-0.03	0.01	-3.95	1100	British&Irish Isles	domestic
Yor3	14516	15155	-0.02	-0.02	0.01	-2.80	650	British&Irish Isles	domestic
Yor4	14971	15831	-0.03	-0.03	0.01	-3.74	1050	British&Irish Isles	domestic

Table 9.3.15- D(((Sub1,Test),Tango1),Yak). Values are rounded to two decimal places for this table.

Test	nABBA	nBABA	Dstat	jackEst	SE	Z	Years BP	Region	Wild/Domestic
Ace1	19121	18506	0.02	0.02	0.01	2.70	4200	Anatolia	domestic
Ash4	1668	4604	-0.47	-0.47	0.01	-33.25	3100	Levant	domestic
Baikal1	202103	257427	-0.12	-0.12	0.01	-16.42	12095	Southern Siberia	wild
Bed3	183921	192271	-0.02	-0.02	0.00	-4.76	11558	Central Europe	wild
Bed4	155583	159493	-0.01	-0.01	0.00	-2.58	11708	Central Europe	wild
Bel1	14438	13812	0.02	0.02	0.01	3.07	6925	Balkans	domestic
Bel2	21552	20366	0.03	0.03	0.01	4.72	6925	Balkans	domestic
Belorus1	150220	150538	0.00	0.00	0.00	-0.21	0	Eastern Europe	wild
Bes1	130830	316496	-0.42	-0.42	0.01	-52.66	2800	Mesopotamia	domestic
Bes2	139317	587897	-0.62	-0.62	0.01	-112.01	629	Mesopotamia	domestic
Bla1	3263	3039	0.04	0.04	0.01	2.70	8100	Balkans	domestic
Bri1	153804	159776	-0.02	-0.02	0.00	-4.04	2300	Northern Europe	domestic
Bub1	51699	50081	0.02	0.02	0.01	3.15	7600	Balkans	domestic
Bul1	8240	20047	-0.42	-0.42	0.01	-39.21	3700	Central Asia	domestic
Bun1	135590	134824	0.00	0.00	0.00	0.65	2300	Northern Europe	domestic
Bun2	146931	146776	0.00	0.00	0.00	0.12	2300	Northern Europe	domestic
CA317	3851	7972	-0.35	-0.35	0.01	-31.36	1300	Southern Caucasus	domestic
Cas1	11091	31132	-0.47	-0.47	0.01	-61.16	1400	Levant	domestic
Ch22	44348	44385	0.00	0.00	0.01	-0.08	8000	Anatolia	domestic
Cla1	164783	170120	-0.02	-0.02	0.00	-3.39	2789	British&Irish Isles	domestic
Cla2	139418	138904	0.00	0.00	0.00	0.41	2789	British&Irish Isles	domestic
CPC98	167328	170364	-0.01	-0.01	0.00	-1.88	6738	British&Irish Isles	wild
Dav1	157848	163702	-0.02	-0.02	0.00	-4.00	3500	Levant	domestic
Dav3	2995	2948	0.01	0.01	0.01	0.57	4110	Levant	domestic
Dav4	2213	2358	-0.03	-0.03	0.02	-1.89	4000	Levant	domestic
Dav5	673	2076	-0.51	-0.51	0.02	-28.85	2300	Levant	domestic
Dro1	154850	155020	0.00	0.00	0.00	-0.13	1800	Northern Europe	domestic
Dub1	141572	140381	0.00	0.00	0.00	0.88	1100	British&Irish Isles	domestic
Dyr1	146326	149748	-0.01	-0.01	0.00	-2.37	1000	Central Europe	domestic
Dzh1	154912	154578	0.00	0.00	0.00	0.23	7800	Central Europe	domestic

Dzh2	151270	148676	0.01	0.01	0.00	1.98	7600	Central Europe	domestic
Els1	151242	152338	0.00	0.00	0.00	-0.82	1950	Northern Europe	domestic
Fal7	155919	166999	-0.03	-0.03	0.01	-6.72	800	Central Europe	wild
Far1	5524	5104	0.04	0.04	0.01	3.79	7500	Iran	domestic
Fir1	155121	159640	-0.01	-0.01	0.00	-3.28	1200	Northern Europe	domestic
Gyumri1	185910	233649	-0.11	-0.11	0.01	-15.83	13780	Southern Caucasus	wild
Gyumri2	139439	136244	0.01	0.01	0.00	2.55	7260	Southern Caucasus	wild
Has1	6126	6775	-0.05	-0.05	0.01	-4.72	3700	Iran	domestic
Has3	108170	105527	0.01	0.01	0.00	2.67	4470	Iran	domestic
Has4	116505	133022	-0.07	-0.07	0.01	-8.86	2900	Iran	domestic
Has5	6502	7101	-0.04	-0.04	0.01	-4.16	2300	Iran	domestic
Hou1	151347	153793	-0.01	-0.01	0.00	-1.64	1000	Northern Europe	domestic
Hou2	150691	153016	-0.01	-0.01	0.00	-1.60	850	Northern Europe	domestic
Hxh1	156770	157373	0.00	0.00	0.00	-0.43	7000	Central Europe	domestic
Hxh2	184846	196343	-0.03	-0.03	0.01	-6.03	7001	Central Europe	wild
Kalisz2	168638	169993	0.00	0.00	0.00	-0.81	0	Eastern Europe	wild
Kalisz3	2758	2828	-0.01	-0.01	0.01	-0.84	0	Eastern Europe	wild
Kaz1	150019	223596	-0.20	-0.20	0.01	-26.16	1000	Southern Caucasus	domestic
Kaz2	41169	72760	-0.28	-0.28	0.01	-33.92	1050	Southern Caucasus	domestic
Kaz3	60429	88775	-0.19	-0.19	0.01	-23.99	1050	Southern Caucasus	domestic
Kaz4	62478	101704	-0.24	-0.24	0.01	-28.49	1040	Southern Caucasus	domestic
Kho1	27835	111443	-0.60	-0.60	0.01	-107.35	950	Iran	domestic
Kie1	7925	7615	0.02	0.02	0.01	2.22	5000	Eastern Europe	domestic
Kie2	36358	34370	0.03	0.03	0.01	4.95	5001	Eastern Europe	domestic
Kir4	165664	168482	-0.01	-0.01	0.00	-1.83	4195	Central Europe	domestic
Kok1	1859	6120	-0.53	-0.53	0.01	-43.64	4000	Central Asia	domestic
Lud1	25005	23995	0.02	0.02	0.01	3.33	7500	Eastern Europe	domestic
Lud2	50705	48907	0.02	0.02	0.01	3.37	7500	Eastern Europe	domestic
Lud3	42854	41318	0.02	0.02	0.01	3.24	7500	Eastern Europe	domestic
Lud4	29769	28690	0.02	0.02	0.01	3.06	7500	Eastern Europe	domestic
Mar1	6800	6900	-0.01	-0.01	0.01	-0.75	7000	Iran	domestic

Men1	141029	143166	-0.01	-0.01	0.00	-1.74	7900	Anatolia	domestic
Men2	122731	119733	0.01	0.01	0.00	2.81	7900	Anatolia	domestic
New1	160910	165268	-0.01	-0.01	0.00	-2.84	4600	British&Irish Isles	domestic
New2	156676	156905	0.00	0.00	0.00	-0.16	1550	British&Irish Isles	domestic
New3	160481	162288	-0.01	-0.01	0.00	-1.20	4200	British&Irish Isles	domestic
New4	156553	156290	0.00	0.00	0.00	0.18	4200	British&Irish Isles	domestic
New5	157312	159385	-0.01	-0.01	0.00	-1.46	4337	British&Irish Isles	domestic
Otb1	149019	156673	-0.03	-0.03	0.00	-5.58	1800	Northern Europe	domestic
Plo1	21140	20345	0.02	0.02	0.01	2.88	7125	Balkans	domestic
Plo2	48978	46308	0.03	0.03	0.00	5.66	6950	Balkans	domestic
Plo3	143928	140446	0.01	0.01	0.00	2.71	7000	Balkans	domestic
Plo4	144391	141312	0.01	0.01	0.00	2.31	7000	Balkans	domestic
Plo5	14322	13595	0.03	0.03	0.01	3.62	6650	Balkans	domestic
Plo6	19124	18223	0.02	0.02	0.01	3.67	7126	Balkans	domestic
Plo7	18355	17535	0.02	0.02	0.01	3.46	7000	Balkans	domestic
Plo8	29895	29063	0.01	0.01	0.01	2.42	7001	Balkans	domestic
Qaz1	122665	120524	0.01	0.01	0.00	1.99	4800	Iran	domestic
Sac3	3462	3482	0.00	0.00	0.01	-0.23	7373	Iran	domestic
Sch1	131183	128377	0.01	0.01	0.00	2.26	5000	Northern Europe	domestic
Ste1	101149	99988	0.01	0.01	0.00	1.22	1400	Northern Europe	domestic
Stu1	25055	23627	0.03	0.03	0.01	4.73	6600	Balkans	domestic
Tango2	157572	152478	0.02	0.02	0.00	3.50	4425	Unknown	wild
Th7	13226	15995	-0.09	-0.09	0.01	-12.83	8800	North Africa	wild
Tmq2	626	1655	-0.45	-0.45	0.02	-21.86	3150	Levant	domestic
Tmq3	3090	8379	-0.46	-0.46	0.01	-41.65	2925	Levant	domestic
Tmq4	3920	9138	-0.40	-0.40	0.01	-35.14	3300	Levant	domestic
Tri1	158286	161802	-0.01	-0.01	0.00	-2.32	8116	Central Europe	wild
Tsa1	93065	211206	-0.39	-0.39	0.01	-46.82	2920	Levant	domestic
Tsa3	2975	3468	-0.08	-0.08	0.01	-5.63	2900	Levant	domestic
Tyq1	8969	24690	-0.47	-0.47	0.01	-54.22	2200	Levant	domestic
Viz1	85702	84071	0.01	0.01	0.00	2.02	3400	Northern Europe	domestic
Viz2	144874	149078	-0.01	-0.01	0.00	-3.09	3401	Northern Europe	domestic
Win1	162785	171723	-0.03	-0.03	0.00	-5.95	1800	Northern Europe	domestic
Yer1	9512	34697	-0.57	-0.57	0.01	-78.27	2050	Central Asia	domestic

Yor1	163329	167882	-0.01	-0.01	0.00	-2.98	1929	British&Irish Isles	domestic
Yor2	158408	163387	-0.02	-0.02	0.00	-3.38	1100	British&Irish Isles	domestic
Yor3	149602	152132	-0.01	-0.01	0.00	-1.76	650	British&Irish Isles	domestic
Yor4	154982	158872	-0.01	-0.01	0.00	-2.64	1050	British&Irish Isles	domestic
Zah1	4784	13506	-0.48	-0.48	0.01	-53.28	1700	Levant	domestic

Table 9.3.16- D(((Sub1,Test),Tango2),Yak). Values are rounded to two decimal places for this table.

Test	nABBA	nBABA	Dstat	jackEst	SE	Z	Years BP	Region	Wild/Domestic
Ace1	20572	20178	0.01	0.01	0.01	1.53	4200	Anatolia	domestic
Ash4	1699	4974	-0.49	-0.49	0.01	-34.65	3100	Levant	domestic
Baikal1	167243	313500	-0.30	-0.30	0.01	-60.48	12095	Southern Siberia	wild
Bed3	220208	197971	0.05	0.05	0.01	9.04	11558	Central Europe	wild
Bed4	184421	163920	0.06	0.06	0.01	10.27	11708	Central Europe	wild
Bel1	16102	14894	0.04	0.04	0.01	5.08	6925	Balkans	domestic
Bel2	24015	22164	0.04	0.04	0.01	5.97	6925	Balkans	domestic
Belorus1	177804	153990	0.07	0.07	0.01	11.77	0	Eastern Europe	wild
Bes1	137351	345808	-0.43	-0.43	0.01	-53.02	2800	Mesopotamia	domestic
Bes2	141122	642595	-0.64	-0.64	0.01	-123.29	629	Mesopotamia	domestic
Bla1	3478	3364	0.02	0.02	0.01	1.32	8100	Balkans	domestic
Bri1	170822	172193	0.00	0.00	0.01	-0.78	2300	Northern Europe	domestic
Bub1	57713	54780	0.03	0.03	0.01	4.51	7600	Balkans	domestic
Bul1	8551	21544	-0.43	-0.43	0.01	-41.05	3700	Central Asia	domestic
Bun1	153216	144330	0.03	0.03	0.01	5.85	2300	Northern Europe	domestic
Bun2	163965	158461	0.02	0.02	0.01	3.34	2300	Northern Europe	domestic
CA317	3953	8622	-0.37	-0.37	0.01	-34.60	1300	Southern Caucasus	domestic
Cas1	11275	33425	-0.50	-0.50	0.01	-61.51	1400	Levant	domestic
Ch22	48026	48382	0.00	0.00	0.01	-0.65	8000	Anatolia	domestic
Cla1	186164	181669	0.01	0.01	0.01	2.33	2789	British&Irish Isles	domestic
Cla2	157300	148327	0.03	0.03	0.01	5.64	2789	British&Irish Isles	domestic

CPC98	199041	176408	0.06	0.06	0.01	10.48	6738	British&Irish Isles	wild
Dav1	170129	180353	-0.03	-0.03	0.00	-6.00	3500	Levant	domestic
Dav3	3020	3244	-0.04	-0.04	0.01	-2.85	4110	Levant	domestic
Dav4	2336	2496	-0.03	-0.03	0.02	-2.05	4000	Levant	domestic
Dav5	715	2284	-0.52	-0.52	0.02	-30.38	2300	Levant	domestic
Dro1	172559	167264	0.02	0.02	0.01	3.05	1800	Northern Europe	domestic
Dub1	158947	150327	0.03	0.03	0.01	5.35	1100	British&Irish Isles	domestic
Dyr1	161221	162538	0.00	0.00	0.01	-0.73	1000	Central Europe	domestic
Dzh1	169323	169229	0.00	0.00	0.01	0.05	7800	Balkans	domestic
Dzh2	163622	163460	0.00	0.00	0.00	0.10	7600	Balkans	domestic
Els1	168020	163464	0.01	0.01	0.01	2.68	1950	Northern Europe	domestic
Fal7	183923	174095	0.03	0.03	0.01	4.66	800	Central Europe	wild
Far1	5841	5448	0.03	0.03	0.01	3.25	7500	Iran	domestic
Fir1	173146	171311	0.01	0.01	0.01	1.04	1200	Northern Europe	domestic
Gyumri1	155468	283324	-0.29	-0.29	0.01	-57.07	13780	Southern Caucasus	wild
Gyumri2	147562	149547	-0.01	-0.01	0.00	-1.39	7260	Southern Caucasus	wild
Has1	6661	7377	-0.05	-0.05	0.01	-4.71	3700	Iran	domestic
Has3	116426	114804	0.01	0.01	0.01	1.36	4470	Iran	domestic
Has4	124125	145932	-0.08	-0.08	0.01	-10.10	2900	Iran	domestic
Has5	6934	7667	-0.05	-0.05	0.01	-4.90	2300	Iran	domestic
Hou1	168029	165598	0.01	0.01	0.01	1.38	1000	Northern Europe	domestic
Hou2	167410	165334	0.01	0.01	0.01	1.21	850	Northern Europe	domestic
Hxh1	174482	169404	0.01	0.01	0.01	2.79	7000	Central Europe	domestic
Hxh2	220246	202992	0.04	0.04	0.01	7.34	7001	Central Europe	wild
Kalisz2	201427	174411	0.07	0.07	0.01	12.65	0	Eastern Europe	wild
Kalisz3	3190	2845	0.06	0.06	0.01	4.09	0	Eastern Europe	wild
Kaz1	161172	244554	-0.21	-0.21	0.01	-26.27	1000	Southern Caucasus	domestic
Kaz2	44047	79422	-0.29	-0.29	0.01	-33.93	1050	Southern Caucasus	domestic
Kaz3	64931	97629	-0.20	-0.20	0.01	-24.93	1050	Southern Caucasus	domestic
Kaz4	66303	110747	-0.25	-0.25	0.01	-30.39	1040	Southern Caucasus	domestic
Kho1	27887	120407	-0.62	-0.62	0.01	-123.99	950	Iran	domestic
Kie1	8631	8255	0.02	0.02	0.01	2.38	5000	Eastern Europe	domestic

Kie2	41005	36504	0.06	0.06	0.01	9.93	5001	Eastern Europe	domestic
Kir4	181730	183827	-0.01	-0.01	0.00	-1.16	4195	Central Europe	domestic
Kok1	1789	6634	-0.58	-0.58	0.01	-50.58	4000	Central Asia	domestic
Lud1	27034	25477	0.03	0.03	0.01	4.52	7500	Eastern Europe	domestic
Lud2	55700	52389	0.03	0.03	0.01	5.42	7500	Eastern Europe	domestic
Lud3	46301	44747	0.02	0.02	0.01	2.85	7500	Eastern Europe	domestic
Lud4	32879	30647	0.04	0.04	0.01	5.72	7500	Eastern Europe	domestic
Mar1	7214	7447	-0.02	-0.02	0.01	-1.62	7000	Iran	domestic
Men1	154388	155773	0.00	0.00	0.01	-0.86	7900	Anatolia	domestic
Men2	132611	131276	0.01	0.01	0.01	1.01	7900	Anatolia	domestic
Mus1	536	1532	-0.48	-0.48	0.02	-23.52	3100	Levant	domestic
New1	179757	177244	0.01	0.01	0.01	1.32	4600	British&Irish Isles	domestic
New2	176817	167996	0.03	0.03	0.01	5.10	1550	British&Irish Isles	domestic
New3	178008	175232	0.01	0.01	0.01	1.52	4200	British&Irish Isles	domestic
New4	176068	167390	0.03	0.03	0.01	4.50	4200	British&Irish Isles	domestic
New5	176119	170708	0.02	0.02	0.01	2.85	4337	British&Irish Isles	domestic
Otb1	167999	167828	0.00	0.00	0.01	0.10	1800	Northern Europe	domestic
Plo1	23189	22000	0.03	0.03	0.01	3.98	7125	Balkans	domestic
Plo2	53603	49809	0.04	0.04	0.01	6.44	6950	Balkans	domestic
Plo3	158857	152149	0.02	0.02	0.01	4.20	7000	Balkans	domestic
Plo4	159349	152962	0.02	0.02	0.00	4.13	7000	Balkans	domestic
Plo5	15753	14554	0.04	0.04	0.01	5.67	6650	Balkans	domestic
Plo6	20931	19856	0.03	0.03	0.01	3.88	7126	Balkans	domestic
Plo7	20183	18788	0.04	0.04	0.01	5.10	7000	Balkans	domestic
Plo8	33135	31407	0.03	0.03	0.01	4.28	7001	Balkans	domestic
Qaz1	131855	131514	0.00	0.00	0.00	0.26	4800	Iran	domestic
Sac3	3653	3792	-0.02	-0.02	0.01	-1.46	7373	Iran	domestic
Sch1	146530	137189	0.03	0.03	0.00	6.69	5000	Northern Europe	domestic
Ste1	114201	107228	0.03	0.03	0.01	5.97	1400	Northern Europe	domestic
Stu1	27178	25289	0.04	0.04	0.01	5.68	6600	Balkans	domestic
Tango1	157572	181458	-0.07	-0.07	0.01	-12.03	0	Unknown	wild
Th7	14015	17927	-0.12	-0.12	0.01	-17.53	8800	North Africa	wild

Tmq1	547	1656	-0.50	-0.50	0.02	-24.21	3150	Levant	domestic
Tmq2	641	1788	-0.47	-0.47	0.02	-24.60	3150	Levant	domestic
Tmq3	3164	9189	-0.49	-0.49	0.01	-46.12	2925	Levant	domestic
Tmq4	4081	9979	-0.42	-0.42	0.01	-36.90	3300	Levant	domestic
Tri1	190442	166928	0.07	0.07	0.01	11.92	8116	Central Europe	wild
Tsa1	96843	228178	-0.40	-0.40	0.01	-48.76	2920	Levant	domestic
Tsa3	3075	3855	-0.11	-0.11	0.01	-8.00	2900	Levant	domestic
Tyq1	9202	26529	-0.48	-0.48	0.01	-58.09	2200	Levant	domestic
Viz1	95234	89888	0.03	0.03	0.01	5.60	3400	Northern Europe	domestic
Viz2	162169	159482	0.01	0.01	0.01	1.63	3401	Northern Europe	domestic
Win1	181010	185339	-0.01	-0.01	0.01	-2.28	1800	Northern Europe	domestic
Yer1	9789	37267	-0.58	-0.58	0.01	-81.35	2050	Central Asia	domestic
Yor1	183809	179906	0.01	0.01	0.01	2.04	1929	British&Irish Isles	domestic
Yor2	179313	174855	0.01	0.01	0.01	2.35	1100	British&Irish Isles	domestic
Yor3	168700	162409	0.02	0.02	0.01	3.53	650	British&Irish Isles	domestic
Yor4	173536	170915	0.01	0.01	0.01	1.41	1050	British&Irish Isles	domestic
Zah1	4969	14715	-0.50	-0.50	0.01	-54.48	1700	Levant	domestic

Table 9.3.17- D(((Sub1,Test),Baikal1),Yak). Values are rounded to two decimal places for this table.

Test	nABBA	nBABA	Dstat	jackEst	SE	Z	Years BP	Region	Wild/Domestic
Ace1	19762	18914	0.02	0.02	0.01	3.27	4200	Anatolia	domestic
Ash4	1906	4686	-0.42	-0.42	0.01	-30.88	3100	Levant	domestic
Bed3	193385	210794	-0.04	-0.04	0.00	-9.79	11558	Central Europe	wild
Bed4	158223	169682	-0.03	-0.03	0.00	-7.81	11708	Central Europe	wild
Bel1	15199	14845	0.01	0.01	0.01	1.71	6925	Balkans	domestic
Bel2	22767	21743	0.02	0.02	0.01	3.84	6925	Balkans	domestic
Belorus1	153559	160328	-0.02	-0.02	0.00	-4.50	0	Eastern Europe	wild
Bes1	154518	337608	-0.37	-0.37	0.01	-47.54	2800	Mesopotamia	domestic
Bes2	181439	635152	-0.56	-0.56	0.01	-101.42	629	Mesopotamia	domestic
Bla1	3358	3210	0.02	0.02	0.01	1.72	8100	Balkans	domestic
Bri1	164278	171018	-0.02	-0.02	0.00	-4.25	2300	Northern Europe	domestic
Bub1	55043	55303	0.00	0.00	0.01	-0.46	7600	Balkans	domestic

Bul1	9340	20356	-0.37	-0.37	0.01	-35.79	3700	Central Asia	domestic
Bun1	144372	144928	0.00	0.00	0.00	-0.44	2300	Northern Europe	domestic
Bun2	156924	158949	-0.01	-0.01	0.00	-1.44	2300	Northern Europe	domestic
CA317	4256	8474	-0.33	-0.33	0.01	-30.59	1300	Southern Caucasus	domestic
Cas1	12428	31337	-0.43	-0.43	0.01	-57.17	1400	Levant	domestic
Ch22	46571	46576	0.00	0.00	0.01	-0.01	8000	Anatolia	domestic
Cla1	174978	187640	-0.03	-0.03	0.00	-7.62	2789	British&Irish Isles	domestic
Cla2	145840	151460	-0.02	-0.02	0.00	-4.13	2789	British&Irish Isles	domestic
CPC98	172114	186315	-0.04	-0.04	0.00	-9.19	6738	British&Irish Isles	wild
Dav1	173133	172988	0.00	0.00	0.00	0.09	3500	Levant	domestic
Dav3	3049	2970	0.01	0.01	0.01	0.94	4110	Levant	domestic
Dav4	2208	2273	-0.01	-0.01	0.02	-0.85	4000	Levant	domestic
Dro1	162852	168344	-0.02	-0.02	0.00	-3.76	1800	Northern Europe	domestic
Dub1	149567	152152	-0.01	-0.01	0.00	-1.92	1100	British&Irish Isles	domestic
Dyr1	155948	161545	-0.02	-0.02	0.00	-3.57	1000	Central Europe	domestic
Dzh1	166037	168577	-0.01	-0.01	0.00	-1.68	7800	Balkans	domestic
Dzh2	160901	161558	0.00	0.00	0.00	-0.43	7600	Balkans	domestic
Els1	159077	164202	-0.02	-0.02	0.00	-3.50	1950	Northern Europe	domestic
Fal7	162408	183212	-0.06	-0.06	0.00	-12.70	800	Central Europe	wild
Far1	5547	5147	0.04	0.04	0.01	3.46	7500	Iran	domestic
Fir1	165293	171053	-0.02	-0.02	0.00	-3.57	1200	Northern Europe	domestic
Gyumri1	367466	141238	0.44	0.44	0.01	87.23	13780	Southern Caucasus	wild
Gyumri2	146491	140751	0.02	0.02	0.00	4.53	7260	Southern Caucasus	wild
Has1	6492	6969	-0.04	-0.04	0.01	-3.16	3700	Iran	domestic
Has3	113421	108601	0.02	0.02	0.00	4.89	4470	Iran	domestic
Has4	123802	139816	-0.06	-0.06	0.01	-8.08	2900	Iran	domestic
Has5	6799	7345	-0.04	-0.04	0.01	-3.73	2300	Iran	domestic
Hou1	161676	166258	-0.01	-0.01	0.00	-2.83	1000	Northern Europe	domestic
Hou2	160691	166084	-0.02	-0.02	0.00	-3.55	850	Northern Europe	domestic
Hxh1	168140	171793	-0.01	-0.01	0.00	-2.33	7000	Central Europe	domestic
Hxh2	194488	216103	-0.05	-0.05	0.00	-11.24	7001	Central Europe	wild
Kalisz2	173319	183726	-0.03	-0.03	0.00	-6.56	0	Eastern Europe	wild

Kalisz3	2720	2977	-0.05	-0.05	0.01	-3.18	0	Eastern Europe	wild
Kaz1	167737	238487	-0.17	-0.17	0.01	-23.49	1000	Southern Caucasus	domestic
Kaz2	46419	76936	-0.25	-0.25	0.01	-31.63	1050	Southern Caucasus	domestic
Kaz3	67645	95166	-0.17	-0.17	0.01	-21.95	1050	Southern Caucasus	domestic
Kaz4	68511	105585	-0.21	-0.21	0.01	-26.11	1040	Southern Caucasus	domestic
Kho1	34478	115056	-0.54	-0.54	0.01	-95.61	950	Iran	domestic
Kie1	7859	7775	0.01	0.01	0.01	0.58	5000	Eastern Europe	domestic
Kie2	36269	35933	0.00	0.00	0.01	0.85	5001	Eastern Europe	domestic
Kir4	180195	182878	-0.01	-0.01	0.00	-1.61	4195	Central Europe	domestic
Kok1	2097	6160	-0.49	-0.49	0.01	-39.92	4000	Central Asia	domestic
Lud1	25303	24990	0.01	0.01	0.01	1.03	7500	Eastern Europe	domestic
Lud2	51504	50850	0.01	0.01	0.01	1.20	7500	Eastern Europe	domestic
Lud3	42996	42870	0.00	0.00	0.01	0.27	7500	Eastern Europe	domestic
Lud4	30488	29682	0.01	0.01	0.01	2.34	7500	Eastern Europe	domestic
Mar1	7159	7060	0.01	0.01	0.01	0.76	7000	Iran	domestic
Men1	151045	154023	-0.01	-0.01	0.00	-2.16	7900	Anatolia	domestic
Men2	129745	128141	0.01	0.01	0.00	1.31	7900	Anatolia	domestic
New1	172072	179747	-0.02	-0.02	0.00	-4.84	4600	British&Irish Isles	domestic
New2	165912	170533	-0.01	-0.01	0.00	-3.05	1550	British&Irish Isles	domestic
New3	171551	176702	-0.01	-0.01	0.00	-3.20	4200	British&Irish Isles	domestic
New4	166072	169303	-0.01	-0.01	0.00	-2.08	4200	British&Irish Isles	domestic
New5	168136	172440	-0.01	-0.01	0.00	-2.88	4337	British&Irish Isles	domestic
Otb1	159337	168212	-0.03	-0.03	0.00	-5.75	1800	Northern Europe	domestic
Plo1	22273	21710	0.01	0.01	0.01	2.02	7125	Balkans	domestic
Plo2	51015	49064	0.02	0.02	0.01	3.80	6950	Balkans	domestic
Plo3	153010	150919	0.01	0.01	0.00	1.51	7000	Balkans	domestic
Plo4	153397	152285	0.00	0.00	0.00	0.78	7000	Balkans	domestic
Plo5	15031	14579	0.02	0.02	0.01	2.21	6650	Balkans	domestic
Plo6	20422	20026	0.01	0.01	0.01	1.47	7126	Balkans	domestic
Plo7	19034	18319	0.02	0.02	0.01	2.89	7000	Balkans	domestic
Plo8	31784	31410	0.01	0.01	0.01	1.02	7001	Balkans	domestic
Qaz1	128598	124719	0.02	0.02	0.00	3.31	4800	Iran	domestic
Sac3	3634	3563	0.01	0.01	0.01	0.78	7373	Iran	domestic

Sch1	137479	137901	0.00	0.00	0.00	-0.33	5000	Northern Europe	domestic
Ste1	105372	106196	0.00	0.00	0.00	-0.85	1400	Northern Europe	domestic
Stu1	25453	24356	0.02	0.02	0.01	3.48	6600	Balkans	domestic
Tango1	202103	143411	0.17	0.17	0.01	28.38	0	Unknown	wild
Tango2	167243	158210	0.03	0.03	0.01	5.34	4425	Unknown	wild
Th7	15661	16085	-0.01	-0.01	0.01	-1.97	8800	North Africa	wild
Tmq3	3674	8810	-0.41	-0.41	0.01	-39.19	2925	Levant	domestic
Tmq4	4435	9549	-0.37	-0.37	0.01	-33.85	3300	Levant	domestic
Tri1	165113	175654	-0.03	-0.03	0.00	-6.94	8116	Central Europe	wild
Tsa1	104453	217221	-0.35	-0.35	0.01	-43.92	2920	Levant	domestic
Tsa3	3219	3668	-0.07	-0.07	0.01	-4.90	2900	Levant	domestic
Tyq1	10310	25597	-0.43	-0.43	0.01	-50.61	2200	Levant	domestic
Viz1	87832	88586	0.00	0.00	0.00	-0.90	3400	Northern Europe	domestic
Viz2	154185	159402	-0.02	-0.02	0.00	-3.65	3401	Northern Europe	domestic
Win1	176123	186314	-0.03	-0.03	0.00	-6.15	1800	Northern Europe	domestic
Yer1	11407	34885	-0.51	-0.51	0.01	-68.89	2050	Central Asia	domestic
Yor1	174421	183768	-0.03	-0.03	0.00	-5.69	1929	British&Irish Isles	domestic
Yor2	169748	176871	-0.02	-0.02	0.00	-4.36	1100	British&Irish Isles	domestic
Yor3	158180	163968	-0.02	-0.02	0.00	-3.92	650	British&Irish Isles	domestic
Yor4	164907	171689	-0.02	-0.02	0.00	-4.58	1050	British&Irish Isles	domestic
Zah1	5625	14039	-0.43	-0.43	0.01	-47.89	1700	Levant	domestic

Table 9.3.18- D(((Sub1,Test),Hxh2),Yak). Values are rounded to two decimal places for this table.

Test	nABBA	nBABA	Dstat	jackEst	SE	Z	Years BP	Region	Wild/Domestic
Ace1	23768	22648	0.02	0.02	0.01	3.77	4200	Anatolia	domestic
Ash4	1862	5479	-0.49	-0.49	0.01	-38.34	3100	Levant	domestic
Baikal1	194488	376038	-0.32	-0.32	0.00	-68.24	12095	Southern Siberia	wild
Bed3	317586	216658	0.19	0.19	0.01	34.97	11558	Central Europe	wild
Bed4	248797	170120	0.19	0.19	0.01	36.73	11708	Central Europe	wild
Bel1	19139	17350	0.05	0.05	0.01	6.79	6925	Balkans	domestic

Bel2	28354	25662	0.05	0.05	0.01	8.11	6925	Balkans	domestic
Belorus1	232604	165566	0.17	0.17	0.01	31.76	0	Eastern Europe	wild
Bes1	167394	409129	-0.42	-0.42	0.01	-50.93	2800	Mesopotamia	domestic
Bes2	181462	773685	-0.62	-0.62	0.01	-110.35	629	Mesopotamia	domestic
Bir3	1023	1016	0.00	0.00	0.02	0.14	6000	Eastern Europe	domestic
Bla1	3945	3867	0.01	0.01	0.01	0.83	8100	Balkans	domestic
Bri1	213498	201991	0.03	0.03	0.01	5.18	2300	Northern Europe	domestic
Bub1	70579	65904	0.03	0.03	0.01	6.24	7600	Balkans	domestic
Bul1	9748	24309	-0.43	-0.43	0.01	-40.74	3700	Central Asia	domestic
Bun1	191255	167687	0.07	0.07	0.01	12.70	2300	Northern Europe	domestic
Bun2	209614	184874	0.06	0.06	0.01	12.08	2300	Northern Europe	domestic
CA317	4553	9961	-0.37	-0.37	0.01	-34.99	1300	Southern Caucasus	domestic
Cas1	12575	37046	-0.49	-0.49	0.01	-63.53	1400	Levant	domestic
Ch22	56730	56194	0.00	0.00	0.01	0.88	8000	Anatolia	domestic
Cla1	246055	218852	0.06	0.06	0.01	11.60	2789	British&Irish Isles	domestic
Cla2	200531	172598	0.07	0.07	0.01	13.81	2789	British&Irish Isles	domestic
CPC98	274555	187432	0.19	0.19	0.00	37.77	6738	British&Irish Isles	wild
Dav1	204853	216907	-0.03	-0.03	0.01	-5.53	3500	Levant	domestic
Dav3	3342	3568	-0.03	-0.03	0.01	-2.64	4110	Levant	domestic
Dav4	2483	2777	-0.06	-0.06	0.02	-3.49	4000	Levant	domestic
Dav5	867	2555	-0.49	-0.49	0.02	-28.63	2300	Levant	domestic
Dro1	219220	196292	0.06	0.06	0.01	10.83	1800	Northern Europe	domestic
Dub1	199818	176586	0.06	0.06	0.01	11.69	1100	British&Irish Isles	domestic
Dyr1	203855	189126	0.04	0.04	0.01	6.67	1000	Central Europe	domestic
Dzh1	209253	209013	0.00	0.00	0.01	0.10	7800	Balkans	domestic
Dzh2	202168	196159	0.02	0.02	0.01	2.99	7600	Balkans	domestic
Els1	213287	191240	0.05	0.05	0.00	10.92	1950	Northern Europe	domestic
Fal7	253198	194649	0.13	0.13	0.01	24.11	800	Central Europe	wild
Far1	6410	6292	0.01	0.01	0.01	0.89	7500	Iran	domestic
Fir1	218280	202637	0.04	0.04	0.01	6.83	1200	Northern Europe	domestic
Gyumri1	177196	334138	-0.31	-0.31	0.00	-62.72	13780	Southern Caucasus	wild
Gyumri2	171498	172646	0.00	0.00	0.00	-0.70	7260	Southern Caucasus	wild
Has1	7740	8410	-0.04	-0.04	0.01	-3.81	3700	Iran	domestic

Has3	135297	131661	0.01	0.01	0.00	2.74	4470	Iran	domestic
Has4	146491	168587	-0.07	-0.07	0.01	-8.72	2900	Iran	domestic
Has5	7829	8697	-0.05	-0.05	0.01	-5.03	2300	Iran	domestic
Hou1	212499	195705	0.04	0.04	0.01	7.76	1000	Northern Europe	domestic
Hou2	211693	195453	0.04	0.04	0.01	7.81	850	Northern Europe	domestic
Hxh1	217847	208442	0.02	0.02	0.01	4.00	7000	Central Europe	domestic
Kalisz2	266007	190276	0.17	0.17	0.00	33.67	0	Eastern Europe	wild
Kalisz3	4025	2920	0.16	0.16	0.01	12.51	0	Eastern Europe	wild
Kaz1	201029	292618	-0.19	-0.19	0.01	-23.67	1000	Southern Caucasus	domestic
Kaz2	52943	92996	-0.27	-0.27	0.01	-33.08	1050	Southern Caucasus	domestic
Kaz3	79136	115794	-0.19	-0.19	0.01	-23.32	1050	Southern Caucasus	domestic
Kaz4	78592	127605	-0.24	-0.24	0.01	-28.13	1040	Southern Caucasus	domestic
Kho1	32946	136510	-0.61	-0.61	0.01	-111.20	950	Iran	domestic
Kie1	9829	8973	0.05	0.05	0.01	5.24	5000	Eastern Europe	domestic
Kie2	48914	39922	0.10	0.10	0.01	17.58	5001	Eastern Europe	domestic
Kir4	233393	224428	0.02	0.02	0.00	3.95	4195	Central Europe	domestic
Kok1	2006	7177	-0.56	-0.56	0.01	-49.96	4000	Central Asia	domestic
Lud1	31147	29672	0.02	0.02	0.01	3.83	7500	Eastern Europe	domestic
Lud2	64240	59519	0.04	0.04	0.01	6.58	7500	Eastern Europe	domestic
Lud3	53120	50552	0.02	0.02	0.01	3.99	7500	Eastern Europe	domestic
Lud4	37441	34711	0.04	0.04	0.01	6.42	7500	Eastern Europe	domestic
Mar1	8453	8747	-0.02	-0.02	0.01	-1.92	7000	Iran	domestic
Men1	186065	190005	-0.01	-0.01	0.01	-2.06	7900	Anatolia	domestic
Men2	158527	156535	0.01	0.01	0.00	1.31	7900	Anatolia	domestic
Mus1	640	1794	-0.47	-0.47	0.02	-25.06	3100	Levant	domestic
New1	233918	215691	0.04	0.04	0.01	7.67	4600	British&Irish Isles	domestic
New2	227252	197223	0.07	0.07	0.01	13.62	1550	British&Irish Isles	domestic
New3	230016	209985	0.05	0.05	0.01	8.44	4200	British&Irish Isles	domestic
New4	223038	198270	0.06	0.06	0.01	11.21	4200	British&Irish Isles	domestic
New5	226321	202207	0.06	0.06	0.01	10.55	4337	British&Irish Isles	domestic
Otb1	213866	196634	0.04	0.04	0.01	8.01	1800	Northern Europe	domestic

Plo1	28140	25841	0.04	0.04	0.01	6.60	7125	Balkans	domestic
Plo2	62731	57877	0.04	0.04	0.01	7.24	6950	Balkans	domestic
Plo3	192240	181167	0.03	0.03	0.00	6.02	7000	Balkans	domestic
Plo4	194121	182464	0.03	0.03	0.01	5.86	7000	Balkans	domestic
Plo5	18725	17205	0.04	0.04	0.01	5.86	6650	Balkans	domestic
Plo6	25598	24010	0.03	0.03	0.01	4.70	7126	Balkans	domestic
Plo7	23611	21926	0.04	0.04	0.01	5.57	7000	Balkans	domestic
Plo8	39691	37394	0.03	0.03	0.01	4.81	7001	Balkans	domestic
Qaz1	152458	152314	0.00	0.00	0.01	0.09	4800	Iran	domestic
Sac3	4246	4411	-0.02	-0.02	0.01	-1.57	7373	Iran	domestic
Sch1	183108	159866	0.07	0.07	0.01	12.98	5000	Northern Europe	domestic
Ste1	140144	122288	0.07	0.07	0.01	13.15	1400	Northern Europe	domestic
Stu1	31580	28499	0.05	0.05	0.01	8.15	6600	Balkans	domestic
Tango1	184846	208744	-0.06	-0.06	0.01	-9.59	0	Unknown	wild
Tango2	220246	180470	0.10	0.10	0.01	18.57	4425	Unknown	wild
Th7	16462	20995	-0.12	-0.12	0.01	-17.25	8800	North Africa	wild
Tmq1	677	1896	-0.47	-0.47	0.02	-23.84	3150	Levant	domestic
Tmq2	773	2075	-0.46	-0.46	0.02	-25.70	3150	Levant	domestic
Tmq3	3651	10567	-0.49	-0.49	0.01	-45.73	2925	Levant	domestic
Tmq4	4650	11356	-0.42	-0.42	0.01	-38.91	3300	Levant	domestic
Tqa2	1197	1155	0.02	0.02	0.02	0.82	4800	Levant	domestic
Tri1	264686	176817	0.20	0.20	0.01	37.78	8116	Central Europe	wild
Tsa1	111938	259140	-0.40	-0.40	0.01	-47.55	2920	Levant	domestic
Tsa3	3696	4568	-0.11	-0.11	0.01	-8.01	2900	Levant	domestic
Tyq1	10514	30245	-0.48	-0.48	0.01	-56.90	2200	Levant	domestic
Viz1	115364	100450	0.07	0.07	0.01	13.10	3400	Northern Europe	domestic
Viz2	204662	186575	0.05	0.05	0.01	8.94	3401	Northern Europe	domestic
Win1	239203	223642	0.03	0.03	0.01	6.33	1800	Northern Europe	domestic
Yer1	11193	41372	-0.57	-0.57	0.01	-78.54	2050	Central Asia	domestic
Yor1	241762	214259	0.06	0.06	0.01	11.62	1929	British&Irish Isles	domestic
Yor2	229642	206783	0.05	0.05	0.01	9.94	1100	British&Irish Isles	domestic
Yor3	214170	189886	0.06	0.06	0.01	11.36	650	British&Irish Isles	domestic
Yor4	222246	200979	0.05	0.05	0.01	9.28	1050	British&Irish Isles	domestic
Zah1	5732	16580	-0.49	-0.49	0.01	-55.84	1700	Levant	domestic

Table 9.3.19- D(((Sub1,Test),CPC98),Yak). Values are rounded to two decimal places for this table.

Test	nABBA	nBABA	Dstat	jackEst	SE	Z	Years BP	Region	Wild/Domestic
Ace1	21713	20550	0.03	0.03	0.01	4.17	4200	Anatolia	domestic
Ash4	1737	5124	-0.49	-0.49	0.01	-36.92	3100	Levant	domestic
Baikal1	172114	338322	-0.33	-0.33	0.00	-70.97	12095	Southern Siberia	wild
Bed3	279047	185935	0.20	0.20	0.00	40.20	11558	Central Europe	wild
Bed4	229225	151649	0.20	0.20	0.00	41.50	11708	Central Europe	wild
Bel1	17624	15890	0.05	0.05	0.01	7.19	6925	Balkans	domestic
Bel2	26520	23527	0.06	0.06	0.01	9.25	6925	Balkans	domestic
Belorus1	209542	148112	0.17	0.17	0.00	34.67	0	Eastern Europe	wild
Bes1	152370	372790	-0.42	-0.42	0.01	-49.38	2800	Mesopotamia	domestic
Bes2	155150	688527	-0.63	-0.63	0.01	-116.04	629	Mesopotamia	domestic
Bla1	3655	3505	0.02	0.02	0.01	1.68	8100	Balkans	domestic
Bri1	188328	176350	0.03	0.03	0.01	6.23	2300	Northern Europe	domestic
Bub1	65292	59262	0.05	0.05	0.01	8.51	7600	Balkans	domestic
Bul1	8805	22397	-0.44	-0.44	0.01	-41.59	3700	Central Asia	domestic
Bun1	173621	150258	0.07	0.07	0.00	14.54	2300	Northern Europe	domestic
Bun2	189555	164051	0.07	0.07	0.00	14.44	2300	Northern Europe	domestic
CA317	4193	9109	-0.37	-0.37	0.01	-33.10	1300	Southern Caucasus	domestic
Cas1	11646	34054	-0.49	-0.49	0.01	-63.75	1400	Levant	domestic
Ch22	52282	50509	0.02	0.02	0.01	3.03	8000	Anatolia	domestic
Cla1	212360	186693	0.06	0.06	0.00	12.93	2789	British&Irish Isles	domestic
Cla2	181479	152205	0.09	0.09	0.01	17.23	2789	British&Irish Isles	domestic
Dav1	183168	192234	-0.02	-0.02	0.01	-4.64	3500	Levant	domestic
Dav3	3154	3266	-0.02	-0.02	0.01	-1.35	4110	Levant	domestic
Dav4	2250	2505	-0.05	-0.05	0.02	-3.21	4000	Levant	domestic
Dav5	771	2378	-0.51	-0.51	0.02	-30.26	2300	Levant	domestic
Dro1	195660	172113	0.06	0.06	0.01	12.46	1800	Northern Europe	domestic
Dub1	182001	155755	0.08	0.08	0.01	15.39	1100	British&Irish Isles	domestic
Dyr1	182576	168069	0.04	0.04	0.01	7.67	1000	Central Europe	domestic
Dzh1	182640	180974	0.00	0.00	0.01	0.84	7800	Balkans	domestic

Dzh2	178409	172807	0.02	0.02	0.00	3.24	7600	Balkans	domestic
Els1	190648	167789	0.06	0.06	0.01	12.61	1950	Northern Europe	domestic
Fal7	221070	168756	0.13	0.13	0.01	24.79	800	Central Europe	wild
Far1	6034	5780	0.02	0.02	0.01	2.07	7500	Iran	domestic
Fir1	192719	176377	0.04	0.04	0.00	8.94	1200	Northern Europe	domestic
Gyumri1	158637	300419	-0.31	-0.31	0.00	-65.45	13780	Southern Caucasus	wild
Gyumri2	155546	155037	0.00	0.00	0.00	0.34	7260	Southern Caucasus	wild
Has1	7021	7646	-0.04	-0.04	0.01	-3.85	3700	Iran	domestic
Has3	123127	119559	0.01	0.01	0.00	2.98	4470	Iran	domestic
Has4	132875	153900	-0.07	-0.07	0.01	-9.06	2900	Iran	domestic
Has5	7251	7990	-0.05	-0.05	0.01	-4.86	2300	Iran	domestic
Hou1	189540	172663	0.05	0.05	0.01	9.06	1000	Northern Europe	domestic
Hou2	190422	172274	0.05	0.05	0.01	9.68	850	Northern Europe	domestic
Hxh1	190749	180019	0.03	0.03	0.01	5.53	7000	Central Europe	domestic
Hxh2	274555	193122	0.17	0.17	0.00	36.41	7001	Central Europe	wild
Kalisz2	238209	169866	0.17	0.17	0.00	34.68	0	Eastern Europe	wild
Kalisz3	3670	2683	0.16	0.16	0.01	11.40	0	Eastern Europe	wild
Kaz1	174185	258463	-0.19	-0.19	0.01	-24.36	1000	Southern Caucasus	domestic
Kaz2	47828	84825	-0.28	-0.28	0.01	-33.11	1050	Southern Caucasus	domestic
Kaz3	71938	105369	-0.19	-0.19	0.01	-22.73	1050	Southern Caucasus	domestic
Kaz4	70605	115941	-0.24	-0.24	0.01	-28.60	1040	Southern Caucasus	domestic
Kho1	29909	126559	-0.62	-0.62	0.01	-115.00	950	Iran	domestic
Kie1	9253	8164	0.06	0.06	0.01	7.09	5000	Eastern Europe	domestic
Kie2	45370	36471	0.11	0.11	0.01	18.26	5001	Eastern Europe	domestic
Kir4	200062	192225	0.02	0.02	0.00	4.04	4195	Central Europe	domestic
Kok1	1925	6670	-0.55	-0.55	0.01	-46.26	4000	Central Asia	domestic
Lud1	28931	26819	0.04	0.04	0.01	5.83	7500	Eastern Europe	domestic
Lud2	58273	53406	0.04	0.04	0.01	7.51	7500	Eastern Europe	domestic
Lud3	48787	45327	0.04	0.04	0.01	5.93	7500	Eastern Europe	domestic
Lud4	35028	31651	0.05	0.05	0.01	8.76	7500	Eastern Europe	domestic
Mar1	7669	7872	-0.01	-0.01	0.01	-1.39	7000	Iran	domestic
Men1	166942	167654	0.00	0.00	0.00	-0.44	7900	Anatolia	domestic

Men2	146686	140991	0.02	0.02	0.00	3.97	7900	Anatolia	domestic
Mus1	627	1627	-0.44	-0.44	0.02	-21.59	3100	Levant	domestic
New1	202415	184028	0.05	0.05	0.01	9.04	4600	British&Irish Isles	domestic
New2	204964	172883	0.08	0.08	0.01	16.97	1550	British&Irish Isles	domestic
New3	201876	181973	0.05	0.05	0.01	9.78	4200	British&Irish Isles	domestic
New4	200703	174331	0.07	0.07	0.01	13.86	4200	British&Irish Isles	domestic
New5	200906	178049	0.06	0.06	0.00	12.36	4337	British&Irish Isles	domestic
Otb1	188476	173192	0.04	0.04	0.01	8.13	1800	Northern Europe	domestic
Plo1	26008	23430	0.05	0.05	0.01	7.71	7125	Balkans	domestic
Plo2	58908	53070	0.05	0.05	0.01	9.14	6950	Balkans	domestic
Plo3	174417	162004	0.04	0.04	0.00	7.66	7000	Balkans	domestic
Plo4	176886	161880	0.04	0.04	0.01	8.47	7000	Balkans	domestic
Plo5	17527	15542	0.06	0.06	0.01	8.76	6650	Balkans	domestic
Plo6	23897	21756	0.05	0.05	0.01	7.11	7126	Balkans	domestic
Plo7	22292	19779	0.06	0.06	0.01	8.93	7000	Balkans	domestic
Plo8	36776	33952	0.04	0.04	0.01	6.62	7001	Balkans	domestic
Qaz1	138954	137536	0.01	0.01	0.00	1.06	4800	Iran	domestic
Sac3	3782	3915	-0.02	-0.02	0.01	-1.37	7373	Iran	domestic
Sch1	166200	143581	0.07	0.07	0.00	14.95	5000	Northern Europe	domestic
Ste1	128973	109167	0.08	0.08	0.00	17.42	1400	Northern Europe	domestic
Stu1	29307	25852	0.06	0.06	0.01	10.14	6600	Balkans	domestic
Tango1	167328	188294	-0.06	-0.06	0.01	-9.23	0	Unknown	wild
Tango2	199041	162646	0.10	0.10	0.01	19.58	4425	Unknown	wild
Th7	15629	19354	-0.11	-0.11	0.01	-14.75	8800	North Africa	wild
Tmq1	632	1796	-0.48	-0.48	0.02	-23.59	3150	Levant	domestic
Tmq2	748	1939	-0.44	-0.44	0.02	-22.93	3150	Levant	domestic
Tmq3	3528	9810	-0.47	-0.47	0.01	-44.15	2925	Levant	domestic
Tmq4	4342	10555	-0.42	-0.42	0.01	-37.56	3300	Levant	domestic
Tqa2	1149	1056	0.04	0.04	0.02	1.90	4800	Levant	domestic
Tri1	242389	159320	0.21	0.21	0.00	44.03	8116	Central Europe	wild
Tsa1	101856	237900	-0.40	-0.40	0.01	-47.01	2920	Levant	domestic
Tsa3	3553	4227	-0.09	-0.09	0.01	-6.11	2900	Levant	domestic

Tyq1	9795	28072	-0.48	-0.48	0.01	-56.48	2200	Levant	domestic
Viz1	107384	91652	0.08	0.08	0.01	15.22	3400	Northern Europe	domestic
Viz2	183592	164164	0.06	0.06	0.01	10.82	3401	Northern Europe	domestic
Win1	205908	190719	0.04	0.04	0.00	7.70	1800	Northern Europe	domestic
Yer1	10213	37757	-0.57	-0.57	0.01	-76.92	2050	Central Asia	domestic
Yor1	211760	183444	0.07	0.07	0.00	14.64	1929	British&Irish Isles	domestic
Yor2	203659	180255	0.06	0.06	0.01	12.11	1100	British&Irish Isles	domestic
Yor3	192299	167089	0.07	0.07	0.01	13.55	650	British&Irish Isles	domestic
Yor4	199879	174886	0.07	0.07	0.01	12.80	1050	British&Irish Isles	domestic
Zah1	5310	15332	-0.49	-0.49	0.01	-53.26	1700	Levant	domestic

Table 9.3.20- D(((Test,Sub1),Th7),Yak). Values are rounded to two decimal places for this table.

Test	Dstat	Z	BABA	ABBA	SE
Lagune	0.07	2.53	586	512	0.03
N'Dama	0.07	2.62	602	527	0.03
Somba	0.04	1.54	595	550	0.03
Guernsey	0.00	0.10	553	551	0.02
Normande	-0.01	-0.27	547	555	0.02
Piedmontese	-0.01	-0.49	552	565	0.02
Simmental	-0.01	-0.51	553	567	0.02
Jersey	-0.01	-0.58	557	573	0.02
Alentejana	-0.01	-0.58	544	560	0.03
Muturu	-0.02	-0.69	568	587	0.02
Blonde d'Aquitaine	-0.02	-0.80	534	555	0.02
Limousin	-0.02	-0.83	541	563	0.02
Galloway	-0.02	-0.95	542	568	0.03
Highland	-0.02	-0.96	543	570	0.03
Holstein	-0.03	-1.31	542	576	0.02
Brown Swiss	-0.03	-1.32	542	577	0.02
Kerry	-0.04	-1.40	536	575	0.03
Norwegian Red Cattle	-0.04	-1.69	532	577	0.02

Charolais	-0.04	-1.77	536	582	0.02
Montbeliarde	-0.04	-1.61	531	576	0.03
Wagyu	-0.04	-1.82	525	573	0.02
Angus	-0.05	-2.10	543	600	0.02
Red Angus	-0.05	-2.21	541	602	0.02
Romagnola	-0.07	-2.74	527	601	0.02
Maremmana	-0.08	-3.21	528	624	0.03
Sikia	-0.10	-4.13	535	652	0.02
Anatolian Black	-0.23	-10.96	491	785	0.02
South Anatolian Red	-0.23	-10.93	495	796	0.02
East Anatolian Red	-0.25	-12.12	487	817	0.02
Taleshi	-0.34	-15.73	455	929	0.02
Sheko	-0.37	-18.38	467	1005	0.02
Gobra	-0.37	-18.50	461	1004	0.02
Maure	-0.38	-19.35	456	1010	0.02
Kenana	-0.46	-23.64	431	1154	0.02
Butana	-0.47	-23.71	421	1156	0.02
Sistani	-0.55	-30.87	377	1302	0.02
Brahman	-0.56	-33.98	375	1334	0.02
Gir	-0.58	-35.23	365	1389	0.02
Nelore	-0.59	-36.25	360	1402	0.02
Hariana	-0.59	-35.34	358	1399	0.02
Sahiwal	-0.60	-36.97	348	1392	0.02
Gaur	-0.89	-91.66	106	1823	0.01

Table 9.3.21- D(((Test,Sub1),Gyumri1),Yak). Values are rounded to two decimal places for this table.

Test	Dstat	Z	SE	BABA	ABBA
Alentejana	-0.03	-2.76	0.01	4904	5157
Anatolian Black	-0.21	-24.63	0.01	4563	7002
Angus	-0.05	-5.62	0.01	4866	5374

Blonde d'Aquitaine	-0.03	-2.70	0.01	4878	5131
Brahman	-0.51	-64.76	0.01	3876	11847
Brown Swiss	-0.02	-2.48	0.01	4904	5129
Butana	-0.42	-47.21	0.01	4162	10254
Charolais	-0.04	-5.00	0.01	4865	5294
East Anatolian Red	-0.23	-26.76	0.01	4522	7280
Galloway	-0.02	-2.20	0.01	4939	5146
Gaur	-0.85	-100.00	0.01	1312	16602
Gir	-0.52	-66.46	0.01	3837	12303
Gobra	-0.35	-39.54	0.01	4339	9065
Guernsey	-0.02	-2.57	0.01	4873	5104
Hariana	-0.53	-68.58	0.01	3786	12403
Highland	-0.03	-2.78	0.01	4955	5223
Holstein	-0.03	-3.73	0.01	4957	5287
Jersey	-0.03	-3.37	0.01	4935	5251
Kenana	-0.43	-47.91	0.01	4100	10210
Kerry	-0.02	-2.70	0.01	4942	5187
Lagune	-0.01	-0.93	0.01	4968	5063
Limousin	-0.03	-2.89	0.01	4896	5149
Maremmana	-0.09	-8.75	0.01	4709	5596
Maure	-0.36	-39.24	0.01	4326	9098
Montbeliarde	-0.02	-2.20	0.01	4944	5155
Muturu	-0.09	-9.56	0.01	4792	5754
N'Dama	-0.01	-0.59	0.01	4962	5016
Nelore	-0.52	-66.24	0.01	3877	12399
Normande	-0.02	-2.09	0.01	4920	5110
Norwegian Red Cattle	-0.03	-3.18	0.01	4914	5201
Piedmontese	-0.03	-3.15	0.01	4848	5120
Red Angus	-0.04	-5.01	0.01	4893	5343
Romagnola	-0.08	-8.56	0.01	4768	5551
Sahiwal	-0.53	-66.76	0.01	3816	12328
Sheko	-0.35	-39.45	0.01	4326	9017

Sikia	-0.09	-10.26	0.01	4805	5798
Simmental	-0.03	-3.32	0.01	4874	5177
Sistani	-0.49	-60.90	0.01	3919	11469
Somba	-0.03	-3.14	0.01	4916	5223
South Anatolian Red	-0.23	-25.53	0.01	4549	7190
Taleshi	-0.32	-34.33	0.01	4328	8354
Wagyu	0.00	-0.50	0.01	4950	4997

Table 9.3.22- D(((Test,Sub1),Baikal1),Yak). Values are rounded to two decimal places for this table.

Test	Dstat	Z	SE	BABA	ABBA
Wagyu	0.01	0.70	0.01	5308	5241
N'Dama	0.00	0.15	0.01	5307	5293
Lagune	0.00	-0.50	0.01	5304	5356
Normande	-0.01	-1.35	0.01	5266	5391
Guernsey	-0.01	-1.52	0.01	5211	5352
Galloway	-0.01	-1.53	0.01	5290	5435
Jersey	-0.01	-1.66	0.01	5322	5481
Montbeliarde	-0.02	-1.80	0.01	5250	5415
Kerry	-0.02	-1.95	0.01	5309	5490
Piedmontese	-0.02	-2.31	0.01	5196	5396
Simmental	-0.02	-2.29	0.01	5247	5456
Limousin	-0.02	-2.43	0.01	5232	5443
Blonde d'Aquitaine	-0.02	-2.36	0.01	5227	5441
Alentejana	-0.02	-2.40	0.01	5225	5445
Norwegian Red Cattle	-0.02	-2.62	0.01	5262	5495
Brown Swiss	-0.02	-2.66	0.01	5226	5465
Highland	-0.02	-2.60	0.01	5251	5494
Somba	-0.02	-2.71	0.01	5242	5503

Holstein	-0.03	-3.08	0.01	5290	5562
Red Angus	-0.03	-4.11	0.01	5242	5610
Angus	-0.04	-4.54	0.01	5224	5631
Charolais	-0.04	-4.67	0.01	5200	5605
Romagnola	-0.07	-7.91	0.01	5132	5868
Maremmana	-0.08	-8.81	0.01	5061	5953
Muturu	-0.09	-9.43	0.01	5126	6081
Sikia	-0.09	-10.15	0.01	5160	6144
Anatolian Black	-0.20	-24.38	0.01	4896	7403
South Anatolian Red	-0.22	-25.49	0.01	4890	7575
East Anatolian Red	-0.23	-26.93	0.01	4858	7710
Taleshi	-0.31	-35.08	0.01	4644	8819
Sheko	-0.34	-38.88	0.01	4665	9516
Gobra	-0.35	-39.63	0.01	4658	9607
Maure	-0.35	-39.29	0.01	4633	9608
Butana	-0.42	-47.56	0.01	4483	10896
Kenana	-0.42	-48.43	0.01	4411	10807
Sistani	-0.48	-60.72	0.01	4250	12119
Brahman	-0.50	-64.61	0.01	4190	12512
Nelore	-0.52	-66.02	0.01	4174	13124
Gir	-0.52	-67.15	0.01	4140	13025
Sahiwal	-0.52	-66.21	0.01	4117	13048
Hariana	-0.52	-67.53	0.01	4104	13118
Gaur	-0.85	-100.00	0.01	1401	17587

Table 9.3.23- D(((Test,Sub1),Kalisz2),Yak). Values are rounded to two decimal places for this table.

Test	Dstat	Z	SE	BABA	ABBA
Highland	0.05	6.12	0.01	6960	6249
Kerry	0.05	5.77	0.01	6889	6238
Galloway	0.05	5.67	0.01	6897	6260
Guernsey	0.05	5.40	0.01	6814	6195

Jersey	0.05	5.40	0.01	6894	6292
Norwegian Red Cattle	0.04	4.46	0.01	6798	6308
Simmental	0.03	3.93	0.01	6756	6316
Normande	0.03	3.57	0.01	6713	6312
Blonde d'Aquitaine	0.03	3.33	0.01	6693	6319
Limousin	0.03	3.51	0.01	6685	6318
Montbeliarde	0.03	3.16	0.01	6687	6331
Alentejana	0.03	3.17	0.01	6689	6335
Holstein	0.03	3.12	0.01	6808	6457
Piedmontese	0.03	3.19	0.01	6647	6308
Brown Swiss	0.03	2.90	0.01	6666	6338
Red Angus	0.02	2.73	0.01	6745	6439
Angus	0.02	2.37	0.01	6732	6469
Charolais	0.01	1.63	0.01	6684	6514
Wagyu	0.00	-0.03	0.01	6430	6434
Romagnola	-0.05	-5.48	0.01	6316	6949
N'Dama	-0.05	-6.25	0.01	6066	6771
Maremmana	-0.06	-6.03	0.01	6267	7012
Lagune	-0.06	-6.07	0.01	6071	6812
Somba	-0.07	-8.16	0.01	6044	6982
Sikia	-0.07	-8.56	0.01	6300	7288
Muturu	-0.13	-15.21	0.01	5851	7674
Anatolian Black	-0.23	-27.99	0.01	5634	8992
South Anatolian Red	-0.25	-31.14	0.01	5551	9259
East Anatolian Red	-0.26	-32.33	0.01	5514	9382
Taleshi	-0.35	-39.95	0.01	5147	10797
Sheko	-0.41	-51.11	0.01	4896	11740
Gobra	-0.42	-51.29	0.01	4883	11822
Maure	-0.42	-51.20	0.01	4841	11836
Kenana	-0.49	-63.24	0.01	4539	13264
Butana	-0.49	-61.16	0.01	4521	13372

Sistani	-0.56	-77.50	0.01	4181	14815
Brahman	-0.58	-84.12	0.01	4098	15241
Nelore	-0.60	-88.42	0.01	3956	15966
Gir	-0.60	-87.89	0.01	3922	15906
Sahiwal	-0.61	-87.89	0.01	3906	15902
Hariana	-0.61	-91.37	0.01	3882	16020
Gaur	-0.88	-100.00	0.01	1282	20712

Table 9.3.24- D(((Test,Sub1),Tango1),Yak). Values are rounded to two decimal places for this table.

Test	Dstat	Z	SE	BABA	ABBA
Galloway	-0.01	-1.40	0.01	5527	5658
Jersey	-0.02	-2.17	0.01	5508	5708
Guernsey	-0.02	-2.36	0.01	5428	5650
Highland	-0.02	-2.25	0.01	5484	5719
Simmental	-0.02	-2.56	0.01	5448	5689
Normande	-0.02	-2.56	0.01	5421	5670
Kerry	-0.02	-2.78	0.01	5452	5719
Limousin	-0.03	-3.35	0.01	5400	5699
Blonde d'Aquitaine	-0.03	-3.21	0.01	5395	5695
Montbeliarde	-0.03	-3.24	0.01	5409	5720
Brown Swiss	-0.03	-3.29	0.01	5403	5715
Alentejana	-0.03	-3.34	0.01	5380	5702
Piedmontese	-0.03	-3.62	0.01	5358	5680
Norwegian Red Cattle	-0.03	-3.51	0.01	5421	5750
Wagyu	-0.03	-3.49	0.01	5339	5665
Red Angus	-0.03	-3.59	0.01	5445	5795
Holstein	-0.03	-3.95	0.01	5470	5844
Angus	-0.04	-4.69	0.01	5425	5872
Charolais	-0.04	-5.62	0.01	5384	5883
N'Dama	-0.05	-4.96	0.01	5257	5759
Lagune	-0.05	-4.86	0.01	5217	5747

Somba	-0.07	-7.64	0.01	5180	5963
Romagnola	-0.08	-9.50	0.01	5230	6170
Maremmana	-0.09	-9.78	0.01	5177	6207
Sikia	-0.11	-12.26	0.01	5192	6474
Muturu	-0.13	-14.45	0.01	5037	6532
Anatolian Black	-0.25	-30.56	0.01	4723	7841
South Anatolian Red	-0.26	-31.38	0.01	4717	8026
East Anatolian Red	-0.27	-33.33	0.01	4695	8143
Taleshi	-0.36	-41.90	0.01	4356	9337
Sheko	-0.41	-49.88	0.01	4254	10109
Gobra	-0.41	-48.99	0.01	4245	10218
Maure	-0.41	-50.63	0.01	4230	10224
Kenana	-0.49	-60.12	0.01	3978	11475
Butana	-0.49	-58.01	0.01	3950	11516
Sistani	-0.56	-76.68	0.01	3608	12861
Brahman	-0.58	-84.08	0.01	3554	13214
Nelore	-0.60	-86.02	0.01	3460	13839
Gir	-0.60	-88.08	0.01	3434	13761
Sahiwal	-0.60	-87.35	0.01	3404	13798
Hariana	-0.61	-89.13	0.01	3382	13868
Gaur	-0.88	-100.00	0.01	1147	18096

Table 9.3.25 - D(((Test,Sub1),Tango2),Yak). Values are rounded to two decimal places for this table.

Test	Dstat	Z	SE	BABA	ABBA
Galloway	0.02	1.73	0.01	6368	6173
Highland	0.01	1.01	0.01	6362	6247
Guernsey	0.01	0.86	0.01	6215	6125
Kerry	0.01	0.78	0.01	6285	6198
Simmental	0.00	0.26	0.01	6256	6229
Normande	0.00	0.25	0.01	6187	6160

Norwegian Red Cattle	0.00	0.13	0.01	6258	6244
Jersey	0.00	0.12	0.01	6280	6268
Blonde d'Aquitaine	0.00	-0.52	0.01	6151	6205
Holstein	-0.01	-0.59	0.01	6278	6341
Montbeliarde	-0.01	-0.59	0.01	6195	6259
Alentejana	-0.01	-0.82	0.01	6153	6242
Limousin	-0.01	-0.86	0.01	6144	6233
Piedmontese	-0.01	-0.88	0.01	6120	6208
Brown Swiss	-0.01	-0.83	0.01	6128	6219
Red Angus	-0.01	-0.93	0.01	6218	6320
Angus	-0.02	-1.81	0.01	6207	6406
Charolais	-0.02	-2.14	0.01	6182	6406
Wagyu	-0.03	-2.83	0.01	5958	6265
N'Dama	-0.07	-7.56	0.01	5700	6520
Romagnola	-0.07	-8.46	0.01	5883	6784
Lagune	-0.07	-7.48	0.01	5667	6564
Maremmana	-0.08	-8.83	0.01	5819	6833
Somba	-0.09	-9.84	0.01	5612	6742
Sikia	-0.10	-11.54	0.01	5842	7132
Muturu	-0.15	-16.60	0.01	5460	7408
Anatolian Black	-0.25	-31.00	0.01	5233	8771
South Anatolian Red	-0.27	-33.63	0.01	5162	8996
East Anatolian Red	-0.28	-33.55	0.01	5142	9101
Taleshi	-0.37	-42.68	0.01	4749	10421
Sheko	-0.43	-52.47	0.01	4561	11349
Gobra	-0.43	-53.61	0.01	4543	11465
Maure	-0.44	-53.42	0.01	4504	11477
Kenana	-0.51	-63.89	0.01	4182	12845
Butana	-0.51	-61.92	0.01	4191	12910
Sistani	-0.58	-78.73	0.01	3844	14346
Brahman	-0.59	-86.03	0.01	3767	14763
Gir	-0.62	-89.77	0.01	3610	15394
Nelore	-0.62	-90.91	0.01	3614	15458

Sahiwal	-0.62	-89.57	0.01	3585	15402
Hariana	-0.63	-90.77	0.01	3568	15487
Gaur	-0.89	-100.00	0.01	1178	20086

Table 9.3.26- D(((Test,Sub1),Fal7),Yak). Values are rounded to two decimal places for this table.

Test	Dstat	Z	SE	BABA	ABBA
Galloway	0.05	5.90	0.01	6765	6120
Highland	0.05	5.32	0.01	6753	6141
Kerry	0.05	5.41	0.01	6720	6132
Norwegian Red Cattle	0.04	4.86	0.01	6678	6144
Jersey	0.04	4.87	0.01	6690	6179
Guernsey	0.04	4.57	0.01	6574	6079
Simmental	0.03	4.10	0.01	6585	6154
Normande	0.03	3.29	0.01	6557	6176
Holstein	0.03	3.20	0.01	6643	6289
Blonde d'Aquitaine	0.03	3.10	0.01	6532	6191
Limousin	0.02	2.98	0.01	6497	6188
Piedmontese	0.02	2.95	0.01	6468	6162
Red Angus	0.02	2.75	0.01	6583	6280
Alentejana	0.02	2.49	0.01	6483	6210
Montbeliarde	0.02	2.32	0.01	6503	6233
Angus	0.02	2.38	0.01	6580	6318
Brown Swiss	0.02	2.03	0.01	6449	6229
Charolais	0.01	1.48	0.01	6543	6387
Wagyu	0.00	-0.55	0.01	6223	6284
Romagnola	-0.05	-6.08	0.01	6147	6852
N'Dama	-0.06	-6.70	0.01	5852	6641
Maremmana	-0.06	-6.96	0.01	6060	6880
Lagune	-0.07	-6.74	0.01	5822	6671

Sikia	-0.08	-8.88	0.01	6089	7156
Somba	-0.09	-9.22	0.01	5773	6851
Muturu	-0.15	-15.91	0.01	5604	7517
Anatolian Black	-0.24	-28.34	0.01	5420	8825
South Anatolian Red	-0.26	-30.48	0.01	5311	9073
East Anatolian Red	-0.27	-31.66	0.01	5313	9180
Taleshi	-0.37	-41.34	0.01	4835	10561
Sheko	-0.42	-49.15	0.01	4684	11436
Gobra	-0.43	-50.45	0.01	4647	11545
Maure	-0.43	-49.95	0.01	4622	11556
Butana	-0.50	-58.70	0.01	4322	12971
Kenana	-0.50	-60.21	0.01	4285	12979
Sistani	-0.57	-74.77	0.01	3948	14503
Brahman	-0.59	-82.27	0.01	3875	14882
Gir	-0.62	-86.65	0.01	3674	15495
Nelore	-0.62	-87.08	0.01	3701	15609
Sahiwal	-0.62	-84.91	0.01	3678	15555
Hariana	-0.62	-87.86	0.01	3619	15616
Gaur	-0.89	-100.00	0.01	1204	20126

9.4. Chapter 6 Supplementary tables

Table 9.4.1- Procrustes projection PCA analyses.

ID	Number of Loci Covered	Average Coverage	Procrustes Similarity	PC1	PC2	Place	Date
Ace1	80507	0.130023	0.999445	-191.71	118.662	Anatolia	Bronze
Ash4	7256	0.0109868	0.996785	254.161	78.62	Levant	Iron
Azer1	924	0.00138895	0.975616	-179.561	69.7775	Iran	Chalcolithic
Bel1	59484	0.0942395	0.999312	-234.916	-7.32581	Balkans	Neolithic
Bel2	90808	0.147717	0.999499	-230.401	9.53754	Balkans	Neolithic
Bes1	586075	2.34338	0.999915	117.018	31.6011	Iraq	Iron
Bes2	664468	16.0422	0.999997	428.532	-1.52139	Iraq	Post Iron
Bir1	1123	0.00168808	0.979183	-210.191	68.0987	Eastern Europe	Neolithic
Bir2	932	0.00140398	0.976656	-211.98	38.5328	Eastern Europe	Neolithic
Bir3	2137	0.00322134	0.988965	-119.79	29.7363	Eastern Europe	Neolithic
Bla1	14266	0.021694	0.997955	-232.899	18.7128	Balkans	Neolithic
Bla2	2354	0.00354452	0.989668	-292.421	-22.412	Balkans	Neolithic
Bub1	201455	0.371772	0.999402	-262.044	-11.3078	Balkans	Neolithic
Bul1	36138	0.0560149	0.99918	145.898	31.2585	Central Asia	Bronze
CA317	16311	0.0248703	0.998493	67.685	63.1315	Georgia	Post Iron
Cas1	49916	0.0785807	0.999323	224.296	65.8951	Levant	Post Iron
Dan1	127	0.000190905	0.852293	-114.034	51.8392	Levant	Bronze
Dav1	653241	6.13694	0.999972	-158.438	254.698	Levant	Bronze
Dav2	2935	0.00442238	0.992347	-160.857	239.154	Levant	Bronze
Dav3	11729	0.0178534	0.997878	-150.659	235.705	Levant	Bronze
Dav4	8861	0.0134295	0.997302	-129.141	259.382	Levant	Bronze
Dav5	3047	0.00459375	0.992485	274.179	60.8777	Levant	Post Iron
Far1	23367	0.0359067	0.998716	-177.276	124.526	Iran	Neolithic
Gil1	464	0.00070199	0.954328	-121.365	185.567	Levant	Chalcolithic
Has1	25335	0.0390033	0.99876	-176.977	72.9036	Iran	Bronze
Has3	459653	1.43132	0.999812	-190.097	88.5519	Iran	Bronze
Has4	495237	1.62411	0.999858	-151.558	82.3203	Iran	Iron

Has5	26520	0.040753	0.998915	-157.363	88.3649	Iran	Post Iron
Kaz1	635125	3.47015	0.999944	-88.8081	68.5824	Georgia	Post Iron
Kaz2	178549	0.313221	0.9997	-23.1391	59.3073	Georgia	Post Iron
Kaz3	258849	0.496051	0.999764	-82.9062	64.8021	Georgia	Post Iron
Kaz4	268558	0.52181	0.999715	-42.2659	56.62	Georgia	Post Iron
Kho1	135555	0.229647	0.999628	415.331	-17.3479	Iran	Post Iron
Kok1	8652	0.0130973	0.997151	338.46	-19.3277	Central Asia	Iron
Mar1	27565	0.0423809	0.998904	-183.096	108.134	Iran	Chalcolithic
Men1	622577	3.24944	0.999939	-197.255	78.5744	Anatolia	Neolithic
Men2	544060	2.06074	0.999882	-197.264	74.7924	Anatolia	Neolithic
Mon1	753	0.00113341	0.970748	-187.608	114.17	Central Asia	Chalcolithic
Mus1	2257	0.00340322	0.989817	199.256	92.0751	Levant	Iron
Nah1	220	0.000330702	0.910817	-125.845	272.324	Levant	Bronze
Plo1	87285	0.141449	0.999528	-218.956	6.31062	Balkans	Neolithic
Plo2	209219	0.387371	0.999641	-236.267	1.41096	Balkans	Neolithic
Plo3	623676	3.05477	0.99993	-229.226	4.67666	Balkans	Neolithic
Plo4	626867	3.12413	0.999935	-225.422	11.093	Balkans	Neolithic
Plo5	60485	0.0954781	0.999389	-237.043	2.2726	Balkans	Neolithic
Plo6	77751	0.125438	0.999529	-246.144	-2.89511	Balkans	Neolithic
Plo7	78152	0.125655	0.999418	-233.245	6.9377	Balkans	Neolithic
Plo8	125603	0.215741	0.999599	-230.159	0.420188	Balkans	Neolithic
Qaz1	522422	1.94853	0.999867	-178.753	117.777	Iran	Bronze
Sac3	14279	0.0217046	0.998198	-188.753	116.157	Iran	Neolithic
Stu1	105553	0.174795	0.999429	-231.368	8.68323	Balkans	Neolithic
Sub1	664328	15.48	0.999995	-195.33	70.7665	Anatolia	Neolithic
Tda1	772	0.00116948	0.971152	-170.704	244.287	Levant	Bronze
Thr1	908	0.00137692	0.97545	-177.28	319.841	Levant	Neolithic
Tmq1	2245	0.00340472	0.989853	179.123	71.3798	Levant	Iron
Tmq2	2644	0.00399548	0.990968	194.274	108.833	Levant	Iron
Tmq3	13456	0.020484	0.998196	221.928	78.4505	Levant	Iron
Tmq4	17090	0.0260713	0.998447	117.864	81.0613	Levant	Iron
Tqa1	1968	0.00296429	0.988699	-150.853	251.656	Levant	Bronze
Tqa2	3640	0.00548815	0.993524	-145.699	289.672	Levant	Bronze
Tqa3	2668	0.00402554	0.991562	-174.822	266	Levant	Bronze

Tsa1	418389	1.12309	0.9998	103.398	104.342	Levant	Iron
Tsa2	1424	0.00214205	0.984623	189.127	56.8965	Levant	Iron
Tsa3	11555	0.0175497	0.997911	-131.663	348.71	Levant	Iron
Tyq1	40936	0.0635413	0.999185	212.51	90.1729	Levant	Post Iron
Yer1	44520	0.0696232	0.999226	351.678	-9.84235	Central Asia	Post Iron
Zah1	22217	0.0340533	0.998728	220.34	49.2311	Levant	Post Iron

Table 9.4.2 -ADMIXTURE table for figures 6.3 & 6.4 (ancient samples)

Origin	Sample ID	Taurine	Indicine	Date BC/AD
Neolithic				
Anatolia	Men2	99%	1%	6048-5893 BC
Anatolia	Men1	99%	1%	c.5500 BC
Anatolia	Sub1	99%	1%	6221-6024 BC
Iran	Sac3	99%	1%	5673 BC
Iran	Far1	100%	0%	6000-5500 BC
Moldova	Bir3	86%	14%	c. 5200 - 3500 BC
Moldova	Bir1	100%	0%	c. 5200 - 3500 BC
Moldova	Bir2	100%	0%	c. 5200 - 3500 BC
Serbia	Bel1	99%	1%	5050/4925-4900/4800 BC
Serbia	Plo1	99%	1%	5275/5125-5100/5000 BC
Serbia	Plo7	100%	0%	5100/5000-5025/4950 BC
Serbia	Bel2	100%	0%	5050/4925-4900/4800 BC
Serbia	Stu1	100%	0%	4800-4500 BC

Serbia	Bla1	100%	0%	6200-6000 BC
Serbia	Bla2	100%	0%	6200-6000 BC
Serbia	Bub1	100%	0%	c.6000-5600 BC
Serbia	Plo2	100%	0%	5025/4950-4850-4650 BC
Serbia	Plo3	100%	0%	5100/5000-5025/4950 BC
Serbia	Plo4	100%	0%	5100/5000-5025/4950 BC
Serbia	Plo5	100%	0%	4850/4650-4600/4500 BC
Serbia	Plo6	100%	0%	5275/5125-5100/5000 BC
Serbia	Plo8	100%	0%	5100/5000-5025/4950 BC
Southern Levant	Thr1	92%	8%	5100-4300 BC
Chalcolithic				
Iran	Azer1	100%	0%	4260-4050 BC
Iran	Mar1	97%	3%	c.5000 BC
Southern Levant	Gil1	76%	24%	c.4300–3300 BC
Turkmenistan	Mon1	91%	9%	5100-4500 cal BC
Bronze Age				
Anatolia	Ace1	98%	2%	c. 2200 BC
Iran	Has3	98%	2%	2470 BC
Iran	Qaz1	97%	3%	2880-2830 BC
Iran	Has1	94%	6%	1900-1600 BC
Southern Levant	Dan1	100%	0%	3500-3000 BC
Southern Levant	Dav2	100%	0%	2200-2000 BC

Southern Levant	Dav1	96%	4%	1929-1753 BC
Southern Levant	Tqa3	95%	5%	3150-2200 BC
Southern Levant	Dav3	93%	7%	2200-2000 BC
Southern Levant	Tda1	92%	8%	3050 BC
Southern Levant	Tqa2	91%	9%	3150-2200 BC
Southern Levant	Tqa1	90%	10%	3150-2200 BC
Southern Levant	Dav4	90%	10%	2200-2000 BC
Southern Levant	Nah1	48%	52%	3300-3050 BC
Uzbekistan	Bul1	56%	44%	2000-1700 BC
Iron Age				
Iran	Has4	92%	8%	1050-800 BC
Iraq	Bes1	61%	39%	911–609 BC
Southern Levant	Tsa3	93%	7%	925-720 BC
Southern Levant	Tsa1	63%	37%	925-720 BC
Southern Levant	Tmq4	60%	40%	1400-1200 BC
Southern Levant	Tmq1	55%	45%	1200-1150 BC
Southern Levant	Tsa2	54%	46%	1200-1000BC
Southern Levant	Mus1	53%	47%	1200-1000 BC
Southern Levant	Tyq1	49%	51%	332-167 BC
Southern Levant	Tmq3	45%	55%	1000-925 BC
Southern Levant	Ash4	45%	55%	1200–1000 BC

Southern Levant	Tmq2	44%	56%	1200-1150 BC
Uzbekistan	Kok1	38%	62%	1500-3000 BC
Post Iron Age				
Georgia	Kaz1	85%	15%	AD 950
Georgia	Kaz3	83%	17%	AD 900
Georgia	Kaz4	79%	21%	AD 910
Georgia	Kaz2	78%	22%	AD 900
Georgia	CA317	67%	33%	AD 651-766
Iran	Has5	93%	7%	550-275 BC
Iran	Kho1	28%	72%	300 BC - AD 1300
Iraq	Bes2	27%	73%	AD 1292-1399
Southern Levant	Zah1	48%	52%	c.63 BC - AD 330
Southern Levant	Cas1	48%	52%	AD 324-638
Southern Levant	Dav5	34%	66%	332-167 BC
Uzbekistan	Yer1	34%	66%	c.50 BC

Table 9.4.3 - ADMIXTURE Chapter 6 Figure 6.4. Modern 700K populations only. ADMIXTURE proportions correspond to the median value for each breed. Values are rounded to 2 decimal places for this table.

Breed Code	Name	No of individuals	Country	Latitude	Longitude	Taurine	Indicine
ALE	Alentejana	9	Portugal	38.95	-7.666667	1.00	0.00
ANB	Anatolian Black	13	Turkey	38.847305	35.326303	0.65	0.35
ANG	Angus	42	Scotland	55.953056	-3.188889	1.00	0.00
BLO	Blonde	5	France	48.85	2.35	1.00	0.00

	d'Aquitaine						
BRM	Brahman	46	India	23.116108	79.437682	0.05	0.95
BSW	Brown Swiss	22	Switzerland	46.875323	8.092078	1.00	0.00
BUT	Butana	7	Ethiopia	9.03	38.74	0.23	0.77
CHL	Charolais (UK)	37	France	48.85	2.35	0.99	0.01
EAR	East Anatolian Red	12	Turkey	38.847305	35.326303	0.63	0.37
GAL	Galloway	9	Scotland	55.953056	-3.188889	1.00	0.00
GIR	Gir	29	India	23.116108	79.437682	0.00	1.00
GNS	Guernsey	21	Guernsey	49.45	-2.6	1.00	0.00
GOB	Gobra	10	Senegal	14.348622	-14.562787	0.40	0.60
HAR	Hariana	10	India	23.116108	79.437682	0.00	1.00
HIG	Highland	8	Scotland	55.953056	-3.188889	1.00	0.00
HOL	Holstein (FR)	60	Netherlands?	52.366667	4.883333	1.00	0.00
JER	Jersey (FR)	38	Jersey	49.212714	2.132474	1.00	0.00
KEN	Kenana	10	Ethiopia	9.03	38.74	0.23	0.77
KER	Kerry	9	Ireland	52.060038	-9.505326	1.00	0.00
LAG	Lagune	5	Ghana	8.018138	-1.109819	0.93	0.07
LMS	Limousin	50	France	48.85	2.35	1.00	0.00
MAR	Maremmana	4	Italy	42.9983	12.447301	0.90	0.10
MAU	Maure	10	Mali	17.649168	-1.294065	0.39	0.61
MON	Montbeliarde	5	France	48.85	2.35	1.00	0.00
MUR	Murutu	11	Nigeria	9.70394	8.048066	0.93	0.07
NDA	N'Dama	32	Guinea	10.383333	-12.083333	0.94	0.06
NEL	Nelore	31	India	23.116108	79.437682	0.00	1.00
NOR	Normande	5	France	48.85	2.35	1.00	0.00
NRC	Norwegian Red Cattle	17	Norway	61.863647	10.086065	1.00	0.00
OGR	Gaur	3	South Asia/ South East Asia	25.149424	90.257418	0.05	0.95
OYK	Yak	2	Central Asia/Tibete/Mongolia/Russia	33	88	0.06	0.94
PMT	Piedmontese	21	Italy	42.9983	12.447301	1.00	0.00
RGU	Red Angus	10	Scotland	55.953056	-3.188889	1.00	0.00
RMG	Romagnola	21	Italy	42.9983	12.447301	0.92	0.08

SAH	Sahiwal	10	Pakistan	29.935612	69.194106	0.00	1.00
SAR	South Anatolian Red	13	Turkey	38.847305	35.326303	0.64	0.36
SHK	Sheko	16	Ethiopia	9.03	38.74	0.39	0.61
SIK	Sikia	5	Greece	39.511042	22.337491	0.88	0.12
SIM	Simmental	10	Switzerland	46.875323	8.092078	1.00	0.00
SIS	Sistani	5	Iran	31	62	0.06	0.94
SOM	Somba	10	Benin/Togo	9.000939	1.626503	0.91	0.09
TAL	Taleshi	5	Iran	37.801424	48.906695	0.50	0.50
WAG	Wagyu	13	Japan	36.508534	138.573993	0.97	0.03

Table 9.4.4 - ADMIXTURE Chapter 6. Modern 700K populations only. ADMIXTURE proportions showed for each modern individual, for each population. Values are rounded to 2 decimal places for this table.

Breed Code	Individual	Taurine	Indicine
ALE	AL10	1.00	0.00
ALE	AL12	1.00	0.00
ALE	AL13	1.00	0.00
ALE	AL17	0.99	0.01
ALE	AL18	1.00	0.00
ALE	AL19	1.00	0.00
ALE	AL23	1.00	0.00
ALE	AL25	1.00	0.00
ALE	AL26	1.00	0.00
ANB	AB01	0.65	0.35
ANB	AB08	0.65	0.35
ANB	AB10	0.65	0.35
ANB	AB14	0.64	0.36
ANB	AB17	0.84	0.16
ANB	AB21	0.76	0.24
ANB	AB28	0.65	0.35
ANB	AB29	0.67	0.33
ANB	AB32	0.67	0.33
ANB	AB36	0.65	0.35

ANB	AB38	0.65	0.35
ANB	AB40	0.66	0.34
ANB	AB41	0.65	0.35
ANG	ANG_000017	1.00	0.00
ANG	ANG_000022	1.00	0.00
ANG	ANG_001	1.00	0.00
ANG	ANG_002	1.00	0.00
ANG	ANG_003	1.00	0.00
ANG	ANG_004	1.00	0.00
ANG	ANG_005	1.00	0.00
ANG	ANG_006	1.00	0.00
ANG	ANG_007	1.00	0.00
ANG	ANG_008	1.00	0.00
ANG	ANG_009	1.00	0.00
ANG	ANG_001400	1.00	0.00
ANG	ANG_001778	1.00	0.00
ANG	ANG_001781	1.00	0.00
ANG	ANG_010	1.00	0.00
ANG	ANG_011	1.00	0.00
ANG	ANG_012	1.00	0.00
ANG	ANG_013	1.00	0.00
ANG	ANG_014	1.00	0.00
ANG	ANG_015	1.00	0.00
ANG	ANG_016	1.00	0.00
ANG	ANG_017	1.00	0.00
ANG	ANG_018	1.00	0.00
ANG	ANG_019	1.00	0.00
ANG	ANG_020	1.00	0.00
ANG	ANG_021	1.00	0.00
ANG	ANG_022	1.00	0.00
ANG	ANG_023	1.00	0.00
ANG	ANG_024	1.00	0.00

ANG	ANG_026	1.00	0.00
ANG	ANG_027	1.00	0.00
ANG	ANG_028	1.00	0.00
ANG	ANG_029	1.00	0.00
ANG	ANG_031	1.00	0.00
ANG	ANG_032	1.00	0.00
ANG	ANG_033	1.00	0.00
ANG	ANG_034	1.00	0.00
ANG	ANG_035	1.00	0.00
ANG	ANG_036	1.00	0.00
ANG	ANG_038	1.00	0.00
ANG	ANG_039	1.00	0.00
ANG	ANG_041	1.00	0.00
BLO	BLO_001	1.00	0.00
BLO	BLO_002	1.00	0.00
BLO	BLO_003	1.00	0.00
BLO	BLO_004	1.00	0.00
BLO	BLO_005	1.00	0.00
BRM	BRM_000014	0.04	0.96
BRM	BRM_001	0.02	0.98
BRM	BRM_002	0.03	0.97
BRM	BRM_003	0.04	0.96
BRM	BRM_004	0.15	0.85
BRM	BRM_005	0.06	0.94
BRM	BRM_006	0.07	0.93
BRM	BRM_007	0.02	0.98
BRM	BRM_008	0.05	0.95
BRM	BRM_009	0.06	0.94
BRM	BRM_010	0.07	0.93
BRM	BRM_011	0.04	0.96
BRM	BRM_012	0.04	0.96
BRM	BRM_013	0.12	0.88
BRM	BRM_014	0.04	0.96
BRM	BRM_015	0.11	0.89

BRM	BRM_016	0.13	0.87
BRM	BRM_017	0.14	0.86
BRM	BRM_018	0.11	0.89
BRM	BRM_019	0.05	0.95
BRM	BRM_021	0.04	0.96
BRM	BRM_022	0.04	0.96
BRM	BRM_023	0.04	0.96
BRM	BRM_024	0.06	0.94
BRM	BRM_025	0.03	0.97
BRM	BRM_026	0.08	0.92
BRM	BRM_027	0.06	0.94
BRM	BRM_028	0.08	0.92
BRM	BRM_029	0.08	0.92
BRM	BRM_030	0.07	0.93
BRM	BRM_031	0.05	0.95
BRM	BRM_032	0.07	0.93
BRM	BRM_033	0.04	0.96
BRM	BRM_034	0.06	0.94
BRM	BRM_035	0.09	0.91
BRM	BRM_036	0.03	0.97
BRM	BRM_037	0.05	0.95
BRM	BRM_038	0.05	0.95
BRM	BRM_039	0.03	0.97
BRM	BRM_040	0.05	0.95
BRM	BRM_041	0.02	0.98
BRM	BRM_042	0.06	0.94
BRM	BRM_043	0.06	0.94
BRM	BRM_044	0.05	0.95
BRM	BRM_045	0.02	0.98
BRM	BRM_046	0.08	0.92
BSW	BSW_000024	1.00	0.00
BSW	BSW_001	1.00	0.00

BSW	BSW_002	1.00	0.00
BSW	BSW_003	1.00	0.00
BSW	BSW_004	1.00	0.00
BSW	BSW_005	1.00	0.00
BSW	BSW_006	1.00	0.00
BSW	BSW_007	1.00	0.00
BSW	BSW_008	1.00	0.00
BSW	BSW_009	1.00	0.00
BSW	BSW_010	1.00	0.00
BSW	BSW_011	1.00	0.00
BSW	BSW_012	1.00	0.00
BSW	BSW_013	1.00	0.00
BSW	BSW_014	1.00	0.00
BSW	BSW_015	1.00	0.00
BSW	BSW_016	1.00	0.00
BSW	BSW_017	1.00	0.00
BSW	BSW_018	1.00	0.00
BSW	BSW_019	1.00	0.00
BSW	BSW_020	1.00	0.00
BSW	BSW_022	1.00	0.00
BUT	BUT12	0.23	0.77
BUT	BUT13	0.23	0.77
BUT	BUT15	0.23	0.77
BUT	BUT16	0.24	0.76
BUT	BUT17	0.23	0.77
BUT	BUT18	0.23	0.77
BUT	BUT21	0.23	0.77
CHL	CHL_000019	0.98	0.02
CHL	CHL_001	1.00	0.00
CHL	CHL_002	1.00	0.00
CHL	CHL_003	1.00	0.00
CHL	CHL_004	1.00	0.00
CHL	CHL_005	0.97	0.03
CHL	CHL_006	0.99	0.01

CHL	CHL_007	0.99	0.01
CHL	CHL_008	0.99	0.01
CHL	CHL_009	0.98	0.02
CHL	CHL_010	0.99	0.01
CHL	CHL_011	0.97	0.03
CHL	CHL_012	0.99	0.01
CHL	CHL_013	1.00	0.00
CHL	CHL_014	0.96	0.04
CHL	CHL_015	0.99	0.01
CHL	CHL_016	0.97	0.03
CHL	CHL_017	0.97	0.03
CHL	CHL_018	0.99	0.01
CHL	CHL_019	0.97	0.03
CHL	CHL_020	0.98	0.02
CHL	CHL_021	0.98	0.02
CHL	CHL_022	0.96	0.04
CHL	CHL_023	0.99	0.01
CHL	CHL_024	0.95	0.05
CHL	CHL_025	0.96	0.04
CHL	CHL_026	0.96	0.04
CHL	CHL_027	0.99	0.01
CHL	CHL_028	0.96	0.04
CHL	CHL_030	0.96	0.04
CHL	CHL_031	0.97	0.03
CHL	CHL_032	0.97	0.03
CHL	CHL_033	1.00	0.00
CHL	CHL_034	1.00	0.00
CHL	CHL_035	1.00	0.00
CHL	CHL_036	1.00	0.00
CHL	CHL_037	1.00	0.00
EAR	EA23	0.62	0.38
EAR	EA24	0.63	0.37

EAR	EA25	0.62	0.38
EAR	EA26	0.62	0.38
EAR	EA27	0.65	0.35
EAR	EAR9	0.65	0.35
EAR	EAR11	0.65	0.35
EAR	EAR13	0.70	0.30
EAR	EAR14	0.66	0.34
EAR	EAR17	0.64	0.36
EAR	EAR30	0.63	0.37
EAR	EAR31	0.62	0.38
GAL	GALL8022	1.00	0.00
GAL	GALL8025	1.00	0.00
GAL	GALL8034	1.00	0.00
GAL	GALL8039	1.00	0.00
GAL	GALL8042	1.00	0.00
GAL	GALL8043X	1.00	0.00
GAL	GALL8044	1.00	0.00
GAL	GALL8046	1.00	0.00
GAL	GALL8057	1.00	0.00
GIR	GIR20	0.00	1.00
GIR	GIR22	0.00	1.00
GIR	GIR_000016	0.00	1.00
GIR	GIR_001	0.00	1.00
GIR	GIR_002	0.00	1.00
GIR	GIR_003	0.00	1.00
GIR	GIR_004	0.00	1.00
GIR	GIR_005	0.00	1.00
GIR	GIR_006	0.00	1.00
GIR	GIR_007	0.00	1.00
GIR	GIR_008	0.00	1.00
GIR	GIR_009	0.00	1.00
GIR	GIR_010	0.00	1.00
GIR	GIR_011	0.00	1.00
GIR	GIR_012	0.00	1.00

GIR	GIR_014	0.00	1.00
GIR	GIR_015	0.00	1.00
GIR	GIR_016	0.00	1.00
GIR	GIR_017	0.00	1.00
GIR	GIR_018	0.00	1.00
GIR	GIR_019	0.00	1.00
GIR	GIR_020	0.00	1.00
GIR	GIR_021	0.00	1.00
GIR	GIR_022	0.00	1.00
GIR	GIR_023	0.00	1.00
GIR	GIR_024	0.00	1.00
GIR	GIR_025	0.00	1.00
GIR	GIR_026	0.00	1.00
GIR	GIR_027	0.00	1.00
GNS	GNS_000011	1.00	0.00
GNS	GNS_000012	1.00	0.00
GNS	GNS_000015	1.00	0.00
GNS	GNS_000021	1.00	0.00
GNS	GNS_001	1.00	0.00
GNS	GNS_002	1.00	0.00
GNS	GNS_003	1.00	0.00
GNS	GNS_004	1.00	0.00
GNS	GNS_005	1.00	0.00
GNS	GNS_006	1.00	0.00
GNS	GNS_007	1.00	0.00
GNS	GNS_008	1.00	0.00
GNS	GNS_009	1.00	0.00
GNS	GNS_010	1.00	0.00
GNS	GNS_013	1.00	0.00
GNS	GNS_014	1.00	0.00
GNS	GNS_016	1.00	0.00
GNS	GNS_017	1.00	0.00

GNS	GNS_018	1.00	0.00
GNS	GNS_019	1.00	0.00
GNS	GNS_020	1.00	0.00
GOB	G0-Z48	0.42	0.58
GOB	G0-Z54	0.40	0.60
GOB	GO-Z49	0.33	0.67
GOB	GO-Z50	0.40	0.60
GOB	GO-Z51	0.39	0.61
GOB	GO-Z52	0.39	0.61
GOB	GO-Z53	0.38	0.62
GOB	GO-Z55	0.40	0.60
GOB	GO-Z56	0.40	0.60
GOB	GO-Z58	0.40	0.60
HAR	HAR1	0.00	1.00
HAR	HAR2	0.00	1.00
HAR	HAR3	0.00	1.00
HAR	HAR4	0.00	1.00
HAR	HAR5	0.00	1.00
HAR	HAR6	0.00	1.00
HAR	HAR7	0.00	1.00
HAR	HAR8	0.00	1.00
HAR	HAR9	0.00	1.00
HAR	HAR10	0.00	1.00
HIG	H8012	1.00	0.00
HIG	H8052	1.00	0.00
HIG	H8053	1.00	0.00
HIG	H8055	1.00	0.00
HIG	H8059	1.00	0.00
HIG	HI10	1.00	0.00
HIG	HI13	1.00	0.00
HIG	HI14	1.00	0.00
HOL	HOL_000006	1.00	0.00
HOL	HOL_000007	1.00	0.00
HOL	HOL_000008	1.00	0.00

HOL	HOL_000013	1.00	0.00
HOL	HOL_000015	1.00	0.00
HOL	HOL_000016	1.00	0.00
HOL	HOL_000017	1.00	0.00
HOL	HOL_000019	1.00	0.00
HOL	HOL_000020	1.00	0.00
HOL	HOL_000021	1.00	0.00
HOL	HOL_000023	1.00	0.00
HOL	HOL_000027	1.00	0.00
HOL	HOL_000038	1.00	0.00
HOL	HOL_000041	1.00	0.00
HOL	HOL_000042	1.00	0.00
HOL	HOL_000043	1.00	0.00
HOL	HOL_001	1.00	0.00
HOL	HOL_002	1.00	0.00
HOL	HOL_003	1.00	0.00
HOL	HOL_004	1.00	0.00
HOL	HOL_005	1.00	0.00
HOL	HOL_006	1.00	0.00
HOL	HOL_007	1.00	0.00
HOL	HOL_008	1.00	0.00
HOL	HOL_009	1.00	0.00
HOL	HOL_010	1.00	0.00
HOL	HOL_011	1.00	0.00
HOL	HOL_012	1.00	0.00
HOL	HOL_013	1.00	0.00
HOL	HOL_017	1.00	0.00
HOL	HOL_018	1.00	0.00
HOL	HOL_019	1.00	0.00
HOL	HOL_021	1.00	0.00
HOL	HOL_025	1.00	0.00
HOL	HOL_029	1.00	0.00

HOL	HOL_031	1.00	0.00
HOL	HOL_032	1.00	0.00
HOL	HOL_034	1.00	0.00
HOL	HOL_035	1.00	0.00
HOL	HOL_036	1.00	0.00
HOL	HOL_037	1.00	0.00
HOL	HOL_038	1.00	0.00
HOL	HOL_039	1.00	0.00
HOL	HOL_040	1.00	0.00
HOL	HOL_042	1.00	0.00
HOL	HOL_043	1.00	0.00
HOL	HOL_047	1.00	0.00
HOL	HOL_048	1.00	0.00
HOL	HOL_049	1.00	0.00
HOL	HOL_050	1.00	0.00
HOL	HOL_051	1.00	0.00
HOL	HOL_052	1.00	0.00
HOL	HOL_053	1.00	0.00
HOL	HOL_054	1.00	0.00
HOL	HOL_055	1.00	0.00
HOL	HOL_056	1.00	0.00
HOL	HOL_057	1.00	0.00
HOL	HOL_058	1.00	0.00
HOL	HOL_059	1.00	0.00
HOL	HOL_060	1.00	0.00
JER	JER_000003	1.00	0.00
JER	JER_000020	1.00	0.00
JER	JER_000027	1.00	0.00
JER	JER_001	1.00	0.00
JER	JER_002	1.00	0.00
JER	JER_003	1.00	0.00
JER	JER_004	1.00	0.00
JER	JER_005	1.00	0.00
JER	JER_006	1.00	0.00

JER	JER_007	1.00	0.00
JER	JER_008	1.00	0.00
JER	JER_009	1.00	0.00
JER	JER_010	1.00	0.00
JER	JER_011	1.00	0.00
JER	JER_012	1.00	0.00
JER	JER_014	1.00	0.00
JER	JER_015	1.00	0.00
JER	JER_016	1.00	0.00
JER	JER_017	1.00	0.00
JER	JER_018	1.00	0.00
JER	JER_019	1.00	0.00
JER	JER_020	1.00	0.00
JER	JER_021	1.00	0.00
JER	JER_022	1.00	0.00
JER	JER_023	1.00	0.00
JER	JER_024	1.00	0.00
JER	JER_026	1.00	0.00
JER	JER_027	1.00	0.00
JER	JER_028	1.00	0.00
JER	JER_029	1.00	0.00
JER	JER_030	1.00	0.00
JER	JER_031	1.00	0.00
JER	JER_033	1.00	0.00
JER	JER_034	1.00	0.00
JER	JER_035	1.00	0.00
JER	JER_036	1.00	0.00
JER	JER_037	1.00	0.00
JER	JER_038	1.00	0.00
KEN	K19B	0.23	0.77
KEN	K20	0.24	0.76
KEN	K21	0.22	0.78

KEN	K22B	0.24	0.76
KEN	K23	0.23	0.77
KEN	K24A	0.24	0.76
KEN	K25	0.23	0.77
KEN	K32	0.24	0.76
KEN	K33	0.24	0.76
KEN	K34	0.23	0.77
KER	KER16	1.00	0.00
KER	KER17	1.00	0.00
KER	KER18	1.00	0.00
KER	KER19	1.00	0.00
KER	KER20	1.00	0.00
KER	KER21	1.00	0.00
KER	KER22	1.00	0.00
KER	KER23	1.00	0.00
KER	KER24	1.00	0.00
LAG	LAG_9410	0.93	0.07
LAG	LAG_9416	0.93	0.07
LAG	LAG_9428	0.94	0.06
LAG	LAG_9433	0.93	0.07
LAG	LAG_9445	0.93	0.07
LMS	LMS_000002	1.00	0.00
LMS	LMS_000015	1.00	0.00
LMS	LMS_000017	1.00	0.00
LMS	LMS_000025	1.00	0.00
LMS	LMS_000027	1.00	0.00
LMS	LMS_000028	1.00	0.00
LMS	LMS_000031	1.00	0.00
LMS	LMS_001	1.00	0.00
LMS	LMS_003	1.00	0.00
LMS	LMS_004	1.00	0.00
LMS	LMS_005	1.00	0.00
LMS	LMS_006	1.00	0.00
LMS	LMS_007	1.00	0.00

LMS	LMS_008	1.00	0.00
LMS	LMS_009	1.00	0.00
LMS	LMS_010	1.00	0.00
LMS	LMS_011	1.00	0.00
LMS	LMS_012	1.00	0.00
LMS	LMS_013	1.00	0.00
LMS	LMS_014	1.00	0.00
LMS	LMS_015	1.00	0.00
LMS	LMS_017	1.00	0.00
LMS	LMS_019	1.00	0.00
LMS	LMS_020	1.00	0.00
LMS	LMS_021	1.00	0.00
LMS	LMS_022	1.00	0.00
LMS	LMS_023	1.00	0.00
LMS	LMS_024	1.00	0.00
LMS	LMS_025	1.00	0.00
LMS	LMS_027	1.00	0.00
LMS	LMS_030	1.00	0.00
LMS	LMS_031	1.00	0.00
LMS	LMS_033	1.00	0.00
LMS	LMS_034	1.00	0.00
LMS	LMS_035	1.00	0.00
LMS	LMS_036	1.00	0.00
LMS	LMS_037	1.00	0.00
LMS	LMS_038	1.00	0.00
LMS	LMS_039	1.00	0.00
LMS	LMS_040	1.00	0.00
LMS	LMS_041	1.00	0.00
LMS	LMS_042	1.00	0.00
LMS	LMS_043	1.00	0.00
LMS	LMS_044	1.00	0.00
LMS	LMS_045	1.00	0.00

LMS	LMS_046	1.00	0.00
LMS	LMS_047	1.00	0.00
LMS	LMS_048	1.00	0.00
LMS	LMS_049	1.00	0.00
LMS	LMS_050	1.00	0.00
MAR	39.00	0.90	0.10
MAR	40.00	0.90	0.10
MAR	42.00	0.90	0.10
MAR	43.00	0.91	0.09
MAU	MAU-Z36	0.39	0.61
MAU	MAU-Z38	0.39	0.61
MAU	MAU-Z39	0.38	0.62
MAU	MAU-Z40	0.38	0.62
MAU	MAU-Z44	0.39	0.61
MAU	MAU-Z45	0.38	0.62
MAU	MAU-Z48	0.38	0.62
MAU	MAU-Z57	0.40	0.60
MAU	MAU-Z59	0.36	0.64
MAU	MAU-Z60	0.38	0.62
MON	MON_001	1.00	0.00
MON	MON_002	1.00	0.00
MON	MON_003	1.00	0.00
MON	MON_004	1.00	0.00
MON	MON_005	1.00	0.00
MUR	MT1	0.91	0.09
MUR	MT2	0.94	0.06
MUR	MT3	0.52	0.48
MUR	MT4	0.53	0.47
MUR	MT5	0.62	0.38
MUR	MT6	0.94	0.06
MUR	MT7	0.94	0.06
MUR	MT25	0.92	0.08
MUR	MT26	0.93	0.07
MUR	MT27	0.95	0.05

MUR	MT28	0.95	0.05
NDA	NDA_001	0.94	0.06
NDA	NDA_002	0.94	0.06
NDA	NDA_003	0.94	0.06
NDA	NDA_004	0.94	0.06
NDA	NDA_005	0.94	0.06
NDA	NDA_006	0.94	0.06
NDA	NDA_007	0.94	0.06
NDA	NDA_008	0.94	0.06
NDA	NDA_009	0.94	0.06
NDA	NDA_010	0.94	0.06
NDA	NDA_011	0.94	0.06
NDA	NDA_012	0.94	0.06
NDA	NDA_013	0.94	0.06
NDA	NDA_014	0.95	0.05
NDA	NDA_015	0.94	0.06
NDA	NDA_016	0.94	0.06
NDA	NDA_017	0.94	0.06
NDA	NDA_018	0.94	0.06
NDA	NDA_019	0.94	0.06
NDA	NDA_020	0.94	0.06
NDA	NDA_021	0.94	0.06
NDA	NDA_022	0.94	0.06
NDA	NDA_023	0.94	0.06
NDA	NDG54	0.92	0.08
NDA	NDG55	0.94	0.06
NDA	NDG56	0.94	0.06
NDA	NDG57	0.94	0.06
NDA	NDG58	0.94	0.06
NDA	NDG59	0.94	0.06
NDA	NDG60	0.94	0.06
NDA	NDG62	0.95	0.05

NDA	NDG63	0.94	0.06
NEL	NEL_001	0.00	1.00
NEL	NEL_002	0.00	1.00
NEL	NEL_003	0.00	1.00
NEL	NEL_004	0.00	1.00
NEL	NEL_005	0.00	1.00
NEL	NEL_006	0.00	1.00
NEL	NEL_007	0.00	1.00
NEL	NEL_008	0.00	1.00
NEL	NEL_009	0.00	1.00
NEL	NEL_010	0.00	1.00
NEL	NEL_011	0.00	1.00
NEL	NEL_012	0.00	1.00
NEL	NEL_013	0.00	1.00
NEL	NEL_014	0.01	0.99
NEL	NEL_015	0.00	1.00
NEL	NEL_016	0.00	1.00
NEL	NEL_017	0.01	0.99
NEL	NEL_018	0.00	1.00
NEL	NEL_019	0.00	1.00
NEL	NEL_020	0.00	1.00
NEL	NEL_021	0.00	1.00
NEL	NEL_022	0.00	1.00
NEL	NEL_023	0.00	1.00
NEL	NEL_024	0.00	1.00
NEL	NEL_025	0.00	1.00
NEL	NEL_026	0.00	1.00
NEL	NEL_027	0.00	1.00
NEL	NEL_028	0.00	1.00
NEL	NEL_029	0.00	1.00
NEL	NEL_030	0.00	1.00
NEL	NEL_031	0.00	1.00
NOR	NOR_001	1.00	0.00
NOR	NOR_002	1.00	0.00

NOR	NOR_003	1.00	0.00
NOR	NOR_004	1.00	0.00
NOR	NOR_005	1.00	0.00
NRC	NRC_001	1.00	0.00
NRC	NRC_002	1.00	0.00
NRC	NRC_003	1.00	0.00
NRC	NRC_004	1.00	0.00
NRC	NRC_005	1.00	0.00
NRC	NRC_006	1.00	0.00
NRC	NRC_007	1.00	0.00
NRC	NRC_008	1.00	0.00
NRC	NRC_009	1.00	0.00
NRC	NRC_010	1.00	0.00
NRC	NRC_011	1.00	0.00
NRC	NRC_012	1.00	0.00
NRC	NRC_013	1.00	0.00
NRC	NRC_014	1.00	0.00
NRC	NRC_015	1.00	0.00
NRC	NRC_016	1.00	0.00
NRC	NRC_017	1.00	0.00
OGR	Gaur2	0.05	0.95
OGR	OGR_001	0.05	0.95
OGR	OGR_002	0.05	0.95
OYK	OYK_001	0.06	0.94
OYK	OYK_002	0.06	0.94
PMT	PMT_001	0.99	0.01
PMT	PMT_002	0.99	0.01
PMT	PMT_003	1.00	0.00
PMT	PMT_004	1.00	0.00
PMT	PMT_005	0.99	0.01
PMT	PMT_006	1.00	0.00
PMT	PMT_007	1.00	0.00

PMT	PMT_008	1.00	0.00
PMT	PMT_009	1.00	0.00
PMT	PMT_010	0.99	0.01
PMT	PMT_011	1.00	0.00
PMT	PMT_012	1.00	0.00
PMT	PMT_013	1.00	0.00
PMT	PMT_014	1.00	0.00
PMT	PMT_015	1.00	0.00
PMT	PMT_016	1.00	0.00
PMT	PMT_017	1.00	0.00
PMT	PMT_018	1.00	0.00
PMT	PMT_019	0.99	0.01
PMT	PMT_020	0.99	0.01
PMT	PMT_021	0.99	0.01
RGU	RGU_000012	1.00	0.00
RGU	RGU_001	1.00	0.00
RGU	RGU_002	1.00	0.00
RGU	RGU_003	1.00	0.00
RGU	RGU_004	1.00	0.00
RGU	RGU_005	1.00	0.00
RGU	RGU_006	1.00	0.00
RGU	RGU_007	1.00	0.00
RGU	RGU_008	1.00	0.00
RGU	RGU_010	1.00	0.00
RMG	RMG_000002	0.92	0.08
RMG	RMG_000008	0.92	0.08
RMG	RMG_000017	0.92	0.08
RMG	RMG_002	0.92	0.08
RMG	RMG_003	0.91	0.09
RMG	RMG_004	0.92	0.08
RMG	RMG_005	0.90	0.10
RMG	RMG_007	0.91	0.09
RMG	RMG_008	0.91	0.09
RMG	RMG_009	0.92	0.08

RMG	RMG_010	0.92	0.08
RMG	RMG_011	0.92	0.08
RMG	RMG_012	0.91	0.09
RMG	RMG_013	0.91	0.09
RMG	RMG_015	0.92	0.08
RMG	RMG_016	0.91	0.09
RMG	RMG_017	0.91	0.09
RMG	RMG_018	0.91	0.09
RMG	RMG_019	0.92	0.08
RMG	RMG_020	0.92	0.08
RMG	RMG_021	0.92	0.08
SAH	SAH1A	0.00	1.00
SAH	SAH2A	0.00	1.00
SAH	SAH3B	0.00	1.00
SAH	SAH4B	0.00	1.00
SAH	SAH5A	0.00	1.00
SAH	SAH6B	0.00	1.00
SAH	SAH7A	0.00	1.00
SAH	SAH8B	0.00	1.00
SAH	SAH9A	0.00	1.00
SAH	SAH10A	0.00	1.00
SAR	SAR1	0.65	0.35
SAR	SAR2	0.70	0.30
SAR	SAR4	0.64	0.36
SAR	SAR5	0.63	0.37
SAR	SAR11	0.67	0.33
SAR	SAR12	0.62	0.38
SAR	SAR13	0.63	0.37
SAR	SAR14	0.65	0.35
SAR	SAR15	0.61	0.39
SAR	SAR21	0.70	0.30
SAR	SAR33	0.69	0.31

SAR	SAR37	0.63	0.37
SAR	SAR39	0.60	0.40
SHK	SHK_001	0.37	0.63
SHK	SHK_002	0.38	0.62
SHK	SHK_003	0.39	0.61
SHK	SHK_004	0.38	0.62
SHK	SHK_005	0.42	0.58
SHK	SHK_006	0.41	0.59
SHK	SHK_007	0.38	0.62
SHK	SHK_008	0.37	0.63
SHK	SHK_009	0.42	0.58
SHK	SHK_010	0.41	0.59
SHK	SHK_011	0.40	0.60
SHK	SHK_012	0.38	0.62
SHK	SHK_013	0.37	0.63
SHK	SHK_014	0.40	0.60
SHK	SHK_015	0.40	0.60
SHK	SHK_016	0.38	0.62
SIK	SK1	0.85	0.15
SIK	SK2	0.96	0.04
SIK	SK3	0.85	0.15
SIK	SK4	0.88	0.12
SIK	SK5	0.89	0.11
SIM	SIM_001	1.00	0.00
SIM	SIM_002	0.99	0.01
SIM	SIM_003	1.00	0.00
SIM	SIM_004	1.00	0.00
SIM	SIM_005	1.00	0.00
SIM	SIM_006	1.00	0.00
SIM	SIM_007	1.00	0.00
SIM	SIM_008	1.00	0.00
SIM	SIM_009	1.00	0.00
SIM	SIM_010	1.00	0.00
SIS	S20	0.05	0.95

SIS	S22	0.05	0.95
SIS	S23	0.06	0.94
SIS	S32	0.06	0.94
SIS	S46	0.34	0.66
SOM	3,201.00	0.90	0.10
SOM	3,224.00	0.91	0.09
SOM	3,232.00	0.90	0.10
SOM	3,248.00	0.92	0.08
SOM	3,421.00	0.92	0.08
SOM	3,437.00	0.89	0.11
SOM	3,441.00	0.89	0.11
SOM	3,454.00	0.90	0.10
SOM	3,482.00	0.91	0.09
SOM	3,496.00	0.92	0.08
TAL	T5	0.50	0.50
TAL	T20	0.49	0.51
TAL	T21	0.50	0.50
TAL	T22	0.50	0.50
TAL	T28	0.48	0.52
WAG	WAG_001	0.97	0.03
WAG	WAG_002	0.96	0.04
WAG	WAG_003	0.97	0.03
WAG	WAG_004	0.98	0.02
WAG	WAG_005	0.96	0.04
WAG	WAG_006	0.98	0.02
WAG	WAG_007	0.97	0.03
WAG	WAG_008	0.96	0.04
WAG	WAG_009	0.98	0.02
WAG	WAG_010	0.98	0.02
WAG	WAG_011	0.96	0.04
WAG	WAG_012	0.98	0.02
WAG	WAG_013	0.97	0.03

Table 9.4.5 - D statistics for ancient individuals for test D(((Test,Limousin),Sahiwal),Yak)

(((Test,LMS),SAH),Yak)	Dstat	Z	SE	BABA	ABBA	Number of SNPs present in all Populations
Ace1	0.00	0.14	0.02	504	501	12217
Ash4	0.13	2.25	0.06	68	53	1143
Azer1	0.17	1.15	0.15	6	5	140
Bel1	-0.03	-1.79	0.02	365	391	9536
Bel2	-0.01	-0.35	0.02	573	580	14749
Bes1	0.07	9.34	0.01	4865	4236	92352
Bes2	0.11	13.34	0.01	6748	5367	104197
Bir1	0.29	1.98	0.15	10	5	165
Bir2	0.28	1.71	0.16	7	4	134
Bir3	0.01	0.10	0.12	15	14	327
Bla1	-0.06	-1.31	0.04	77	86	2242
Bla2	0.20	2.37	0.09	24	16	474
Bub1	0.00	0.41	0.01	1429	1416	35969
Bul1	0.12	4.51	0.03	311	245	5510
CA317	0.07	1.73	0.04	126	111	2471
Cas1	0.13	5.78	0.02	457	348	7515
Dan1	0.36	1.13	0.32	2	1	25
Dav1	0.01	2.02	0.01	4258	4140	102459
Dav2	0.00	0.03	0.12	15	15	408
Dav3	-0.03	-0.55	0.05	66	69	1790
Dav4	0.01	0.21	0.06	52	51	1276
Dav5	0.06	0.74	0.09	30	26	469
Far1	-0.01	-0.27	0.03	141	144	3540
Gil1	-0.32	-1.31	0.24	2	4	86
Has1	0.06	1.83	0.03	175	155	4038
Has3	0.03	3.11	0.01	2959	2811	71311
Has4	0.02	2.91	0.01	3312	3160	77836
Has5	0.00	0.06	0.03	168	168	4209
Kaz1	0.04	5.21	0.01	4456	4115	99191
Kaz2	0.05	4.06	0.01	1310	1179	27509

Kaz3	0.03	2.76	0.01	1802	1691	40370
Kaz4	0.04	3.94	0.01	1909	1758	41028
Kho1	0.08	5.88	0.01	1309	1106	21148
Kok1	0.11	2.13	0.05	83	67	1289
Mar1	0.02	0.56	0.03	176	170	4252
Men1	0.02	2.63	0.01	4023	3867	97927
Men2	0.02	2.58	0.01	3559	3416	86261
Mon1	-0.11	-0.55	0.20	5	6	102
Mus1	0.07	0.68	0.10	19	16	377
Nah1	0.55	1.73	0.32	2	1	31
Plo1	-0.01	-0.39	0.02	558	565	14053
Plo2	0.00	0.23	0.01	1311	1304	33274
Plo3	0.02	2.38	0.01	3970	3840	97958
Plo4	0.01	1.77	0.01	3992	3887	98568
Plo5	-0.03	-1.43	0.02	373	395	9672
Plo6	0.01	0.53	0.02	506	496	12966
Plo7	0.00	0.13	0.02	489	487	12356
Plo8	0.02	1.06	0.01	826	801	20269
Qaz1	0.02	2.09	0.01	3332	3223	81374
Sac3	0.01	0.30	0.04	92	89	2219
Stu1	0.01	0.41	0.02	651	642	16572
Sub1	0.02	2.27	0.01	4276	4137	104187
Tda1	0.06	0.31	0.19	6	5	123
Thr1	0.17	1.16	0.15	6	8	155
Tmq1	0.14	1.38	0.10	24	18	360
Tmq2	0.06	0.66	0.09	21	19	430
Tmq3	0.13	3.03	0.04	129	100	2284
Tmq4	0.09	2.42	0.04	151	125	2710
Tqa1	0.07	0.60	0.11	13	12	328
Tqa2	0.05	0.70	0.08	29	26	564
Tqa3	0.00	0.02	0.10	19	19	445
Tsa1	0.07	7.94	0.01	3403	2940	64913

Tsa2	0.16	1.01	0.16	11	8	199
Tsa3	0.05	1.01	0.05	87	79	1942
Tyq1	0.08	3.25	0.03	355	300	6313
Yer1	0.11	5.12	0.02	423	336	6656
Zah1	0.10	2.75	0.04	197	162	3390

Table 9.4.6 - D statistics for ancient individuals for test D(((Highland,Test),Sahiwal),Yak)

(Highland,Test),SAH),Yak)	nABBA	nBABA	Dstat	jackEst	SE	Z
Ace1	16332	16264	0.00	0.00	0.01	0.30
Ash4	3589	2642	0.15	0.15	0.01	10.60
Azer1	184	204	-0.05	-0.05	0.05	-0.96
Bel1	12220	12596	-0.02	-0.02	0.01	-2.08
Bel2	18551	18452	0.00	0.00	0.01	0.40
Bes1	269283	189988	0.17	0.17	0.01	24.47
Bes2	509777	314945	0.24	0.24	0.01	31.80
Bir1	250	283	-0.06	-0.06	0.05	-1.36
Bir2	199	235	-0.08	-0.08	0.05	-1.66
Bir3	606	812	-0.15	-0.15	0.03	-5.17
Bla1	2657	2784	-0.02	-0.02	0.01	-1.62
Bla2	624	592	0.03	0.03	0.03	0.89
Bub1	45681	46413	-0.01	-0.01	0.01	-1.49
Bul1	15948	11577	0.16	0.16	0.01	15.95
CA317	6437	5018	0.12	0.12	0.01	10.29
Cas1	25290	16461	0.21	0.21	0.01	23.65
Dan1	41	40	0.01	0.01	0.11	0.11
Dav1	148421	148861	0.00	0.00	0.00	-0.34
Dav2	554	621	-0.06	-0.06	0.03	-1.93
Dav3	2458	2580	-0.02	-0.02	0.01	-1.64
Dav4	2030	1976	0.01	0.01	0.02	0.82
Dav5	1599	1187	0.15	0.15	0.02	7.44
Far1	4544	4587	0.00	0.00	0.01	-0.39
Gil1	125	159	-0.12	-0.12	0.06	-1.96

Has1	5880	5609	0.02	0.02	0.01	2.20
Has3	93339	94420	-0.01	-0.01	0.00	-1.20
Has4	117713	108540	0.04	0.04	0.01	6.85
Has5	6050	5539	0.04	0.04	0.01	4.14
Kaz1	197549	168713	0.08	0.08	0.01	12.79
Kaz2	62757	48772	0.13	0.13	0.01	17.77
Kaz3	77237	64958	0.09	0.09	0.01	12.79
Kaz4	84859	69804	0.10	0.10	0.01	14.31
Kho1	89614	56421	0.23	0.23	0.01	28.96
Kok1	4885	3261	0.20	0.20	0.01	14.56
Mar1	5828	5983	-0.01	-0.01	0.01	-1.30
Men1	136667	137273	0.00	0.00	0.00	-0.45
Men2	114748	112554	0.01	0.01	0.00	2.05
Mon1	150	147	0.01	0.01	0.06	0.17
Mus1	1216	840	0.18	0.18	0.02	7.96
Nah1	52	73	-0.17	-0.17	0.09	-1.86
Plo1	18023	18698	-0.02	-0.02	0.01	-2.78
Plo2	40964	41279	0.00	0.00	0.01	-0.73
Plo3	128169	127797	0.00	0.00	0.00	0.29
Plo4	128863	129013	0.00	0.00	0.00	-0.12
Plo5	12124	12196	0.00	0.00	0.01	-0.38
Plo6	16642	16933	-0.01	-0.01	0.01	-1.21
Plo7	15506	15860	-0.01	-0.01	0.01	-1.59
Plo8	25735	26249	-0.01	-0.01	0.01	-1.65
Qaz1	107756	106604	0.01	0.01	0.00	1.19
Sac3	3225	3084	0.02	0.02	0.01	1.67
Stu1	20143	20674	-0.01	-0.01	0.01	-1.98
Sub1	153305	154225	0.00	0.00	0.00	-0.66
Tda1	167	173	-0.02	-0.02	0.06	-0.32
Thr1	196	225	-0.07	-0.07	0.05	-1.37
Tmq1	1247	907	0.16	0.16	0.02	6.72
Tmq2	1349	988	0.15	0.15	0.02	6.82

Tmq3	6911	4856	0.17	0.17	0.01	15.12
Tmq4	7611	5415	0.17	0.17	0.01	14.76
Tqa1	419	435	-0.02	-0.02	0.03	-0.55
Tqa2	852	815	0.02	0.02	0.02	0.90
Tqa3	549	577	-0.02	-0.02	0.03	-0.82
Tsa1	174468	125298	0.16	0.16	0.01	23.01
Tsa2	699	588	0.09	0.09	0.03	2.92
Tsa3	3086	2942	0.02	0.02	0.01	1.66
Tyq1	19933	13869	0.18	0.18	0.01	20.39
Yer1	27090	17340	0.22	0.22	0.01	25.90
Zah1	10709	7699	0.16	0.16	0.01	16.03

Table 9.4.7 - Ancient populations for f3 statistics. (NE= Near East).

ID	Ancient Population	ID	Ancient Population
Ace1	NE_Bronze	**Mar1**	NE_Neolithic
Ash4	NE_Iron	**Men1**	Anatolia_Neolithic
Azer1	NE_Bronze	**Men2**	Anatolia_Neolithic
Bel1	Europe_Neolithic	**Mon1**	CentralAsia
Bel2	Europe_Neolithic	**Mus1**	NE_Iron
Bes1	NE_Iron	**Nah1**	NE_Bronze
Bes2	NE_PostIron	**Plo1**	Europe_Neolithic
Bir1	Europe_Neolithic	**Plo2**	Europe_Neolithic
Bir2	Europe_Neolithic	**Plo3**	Europe_Neolithic
Bir3	Europe_Neolithic	**Plo4**	Europe_Neolithic
Bla1	Europe_Neolithic	**Plo5**	Europe_Neolithic
Bla2	Europe_Neolithic	**Plo6**	Europe_Neolithic
Bub1	Europe_Neolithic	**Plo7**	Europe_Neolithic
Bul1	CentralAsia	**Plo8**	Europe_Neolithic
CA317	NE_PostIron	**Qaz1**	NE_Bronze
Cas1	NE_PostIron	**Sac3**	NE_Neolithic
Dan1	NE_Bronze	**Stu1**	Europe_Neolithic
Dav1	NE_Bronze	**Sub1**	Anatolia_Neolithic

Dav2	NE_Bronze	**Tda1**	NE_Bronze
Dav3	NE_Bronze	**Thr1**	NE_Neolithic
Dav4	NE_Bronze	**Tmq1**	NE_Iron
Dav5	NE_PostIron	**Tmq2**	NE_Iron
Far1	NE_Neolithic	**Tmq3**	NE_Iron
Gil1	NE_Bronze	**Tmq4**	NE_Iron
Has1	NE_Bronze	**Tqa1**	NE_Bronze
Has3	NE_Bronze	**Tqa2**	NE_Bronze
Has4	NE_Iron	**Tqa3**	NE_Bronze
Has5	NE_PostIron	**Tsa1**	NE_Iron
Kaz1	NE_PostIron	**Tsa2**	NE_Iron
Kaz2	NE_PostIron	**Tsa3**	NE_Iron
Kaz3	NE_PostIron	**Tyq1**	NE_PostIron
Kaz4	NE_PostIron	**Yer1**	CentralAsia
Kho1	NE_PostIron	**Zah1**	NE_PostIron
Kok1	CentralAsia		

Table 9.4.8- F4 ratios. Samples are shown in decreasing Years BP.

Test	f4ratio	std_error	Z	Region	Years BP
Sub1	0.075927	0.034489	2.201	Anatolia	8000
Bub1	0.018593	0.045481	0.409	Balkans	7600
Far1	-0.04519	0.189444	-0.239	Iran	7500
Sac3	0.079959	0.265038	0.302	Iran	7373
Plo6	0.045414	0.088314	0.514	Balkans	7126
Plo1	-0.03292	0.08927	-0.369	Balkans	7125
Men2	0.0936	0.037136	2.52	Anatolia	7092
Plo8	0.064263	0.059992	1.071	Balkans	7001
Mar1	0.096027	0.169775	0.566	Iran	7000
Men1	0.092037	0.036378	2.53	Anatolia	7000
Plo3	0.075523	0.032595	2.317	Balkans	7000
Plo4	0.060307	0.034927	1.727	Balkans	7000

Plo7	0.011221	0.086201	0.13	Balkans	7000
Plo2	0.012611	0.053235	0.237	Balkans	6950
Bel1	-0.185768	0.110397	-1.683	Balkans	6900
Bel2	-0.026247	0.080018	-0.328	Balkans	6900
Plo5	-0.136957	0.099551	-1.376	Balkans	6650
Stu1	0.024205	0.061735	0.392	Balkans	6600
Has3	0.121093	0.039282	3.083	Iran	4470
Ace1	0.01362	0.086773	0.157	Anatolia	4200
Qaz1	0.073692	0.035794	2.059	Iran	4170
Dav3	-0.133922	0.270988	-0.494	Levant	4110
Dav4	0.113298	0.443134	0.256	Levant	4000
Kok1	0.534068	0.221975	2.406	Central_Asia	4000
Bul1	0.627981	0.128685	4.88	Central_Asia	3700
Has1	0.314255	0.189028	1.662	Iran	3700
Dav1	0.06579	0.033045	1.991	Levant	3500
Tmq3	0.78667	0.266327	2.954	Levant	3200
Tmq4	0.550095	0.217914	2.524	Levant	3200
Tsa3	0.238677	0.244598	0.976	Levant	3000
Has4	0.110104	0.038618	2.851	Iran	2900
Tsa1	0.398428	0.045496	8.757	Levant	2900
Bes1	0.395369	0.039524	10.003	Mesopotamia	2800
Tyq1	0.458214	0.124482	3.681	Levant	2500
Has5	0.013463	0.177191	0.076	Iran	2300
Ash4	0.540283	0.217287	2.486	Levant	2100
Yer1	0.616285	0.103392	5.961	Central_Asia	2050
Zah1	0.572071	0.191607	2.986	Levant	1700
Cas1	0.618789	0.097597	6.34	Levant	1400
CA317	0.329858	0.181953	1.813	Southern_Caucasus	1300
Kaz3	0.151769	0.052744	2.877	Southern_Caucasus	1100
Kho1	0.580363	0.079562	7.294	Iran	1000
Kaz2	0.257248	0.061358	4.193	Southern_Caucasus	1000
Kaz4	0.215642	0.05403	3.991	Southern_Caucasus	1000
Kaz1	0.195174	0.037618	5.188	Southern_Caucasus	900
Bes2	0.758692	0.041402	18.325	Mesopotamia	629

9.5. Supplementary Figures

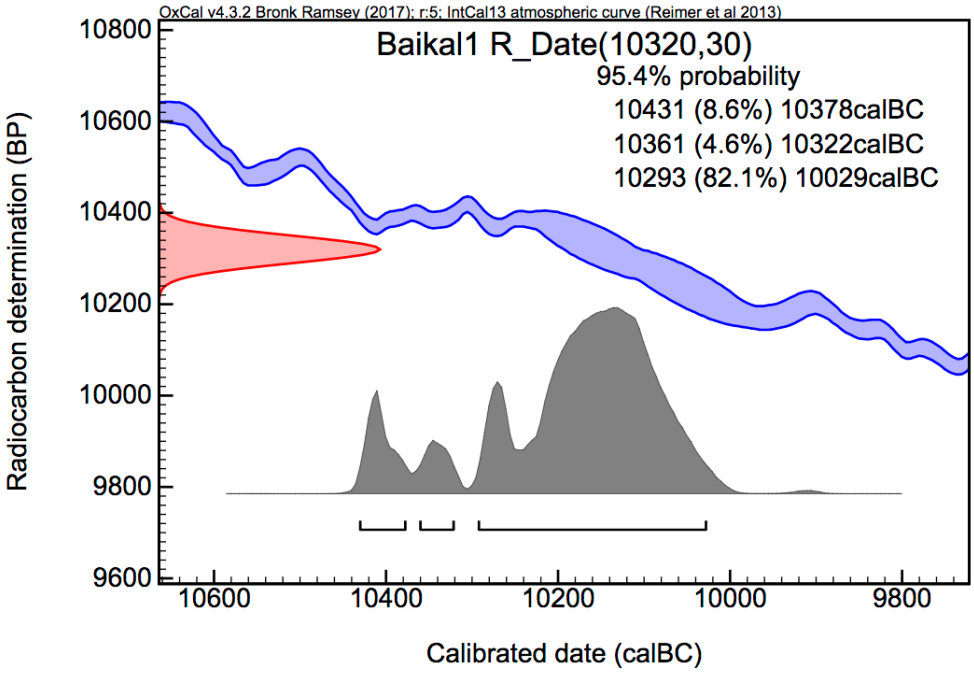


Figure 9.5.1 - Radiocarbon dates calibration for Baikal1.

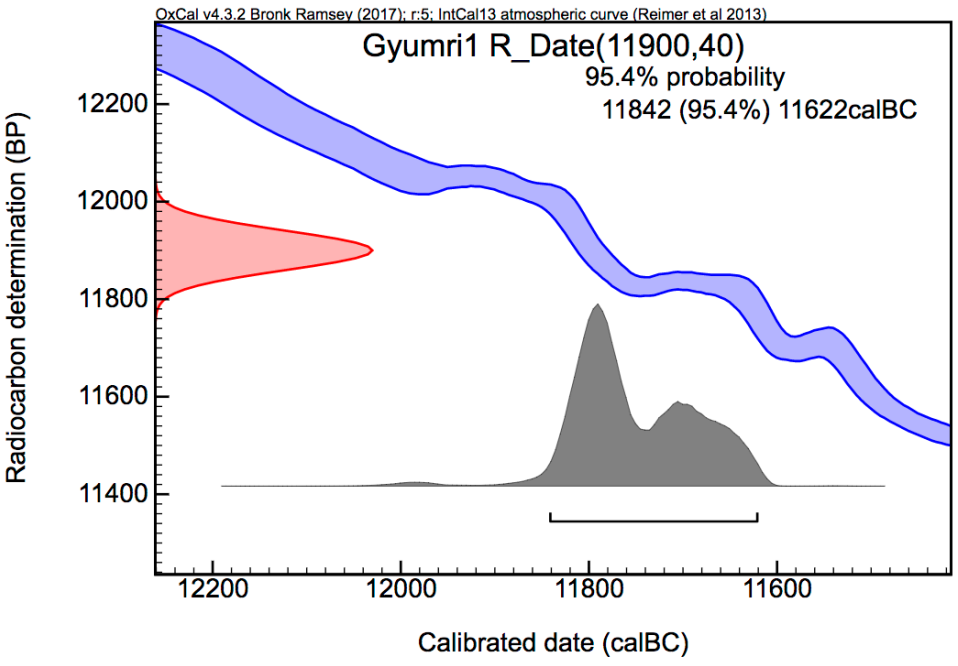


Figure 9.5.2 - Radiocarbon dates calibration for Gyumri1.

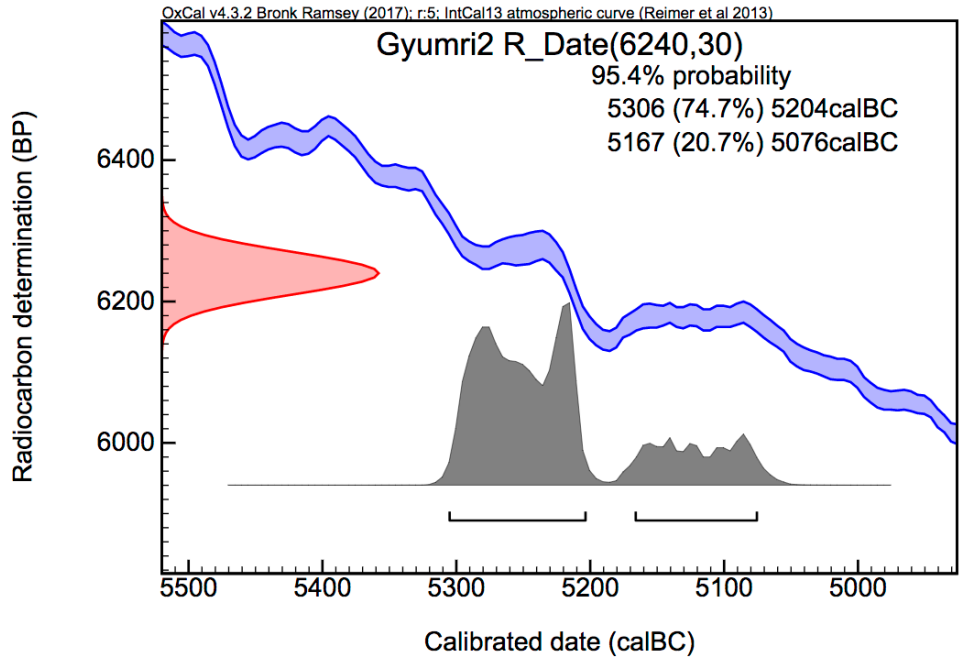


Figure 9.5.3 - Radiocarbon dates calibration for Gyumri2.

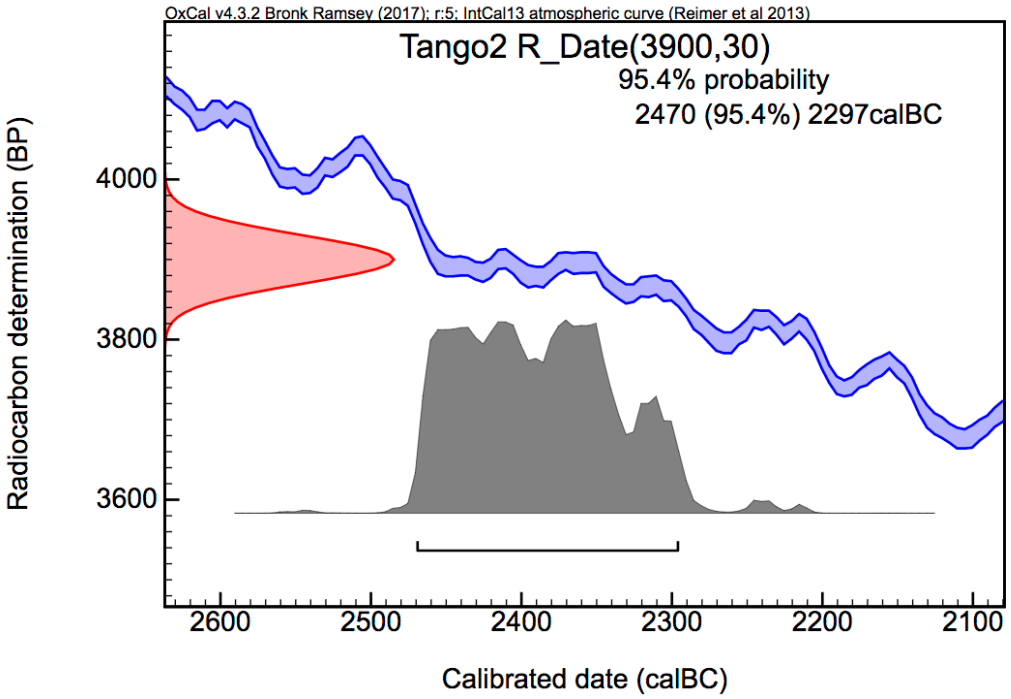


Figure 9.5.4 - Radiocarbon dates calibration for Tango2.

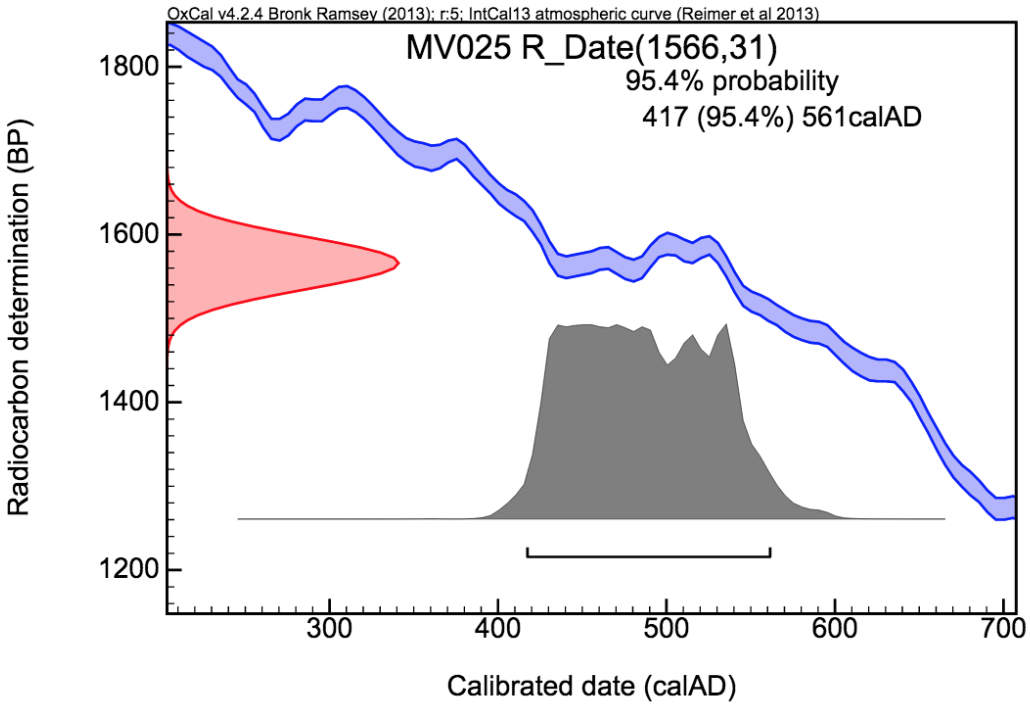


Figure 9.5.5 - Radiocarbon dates calibration for Win1.

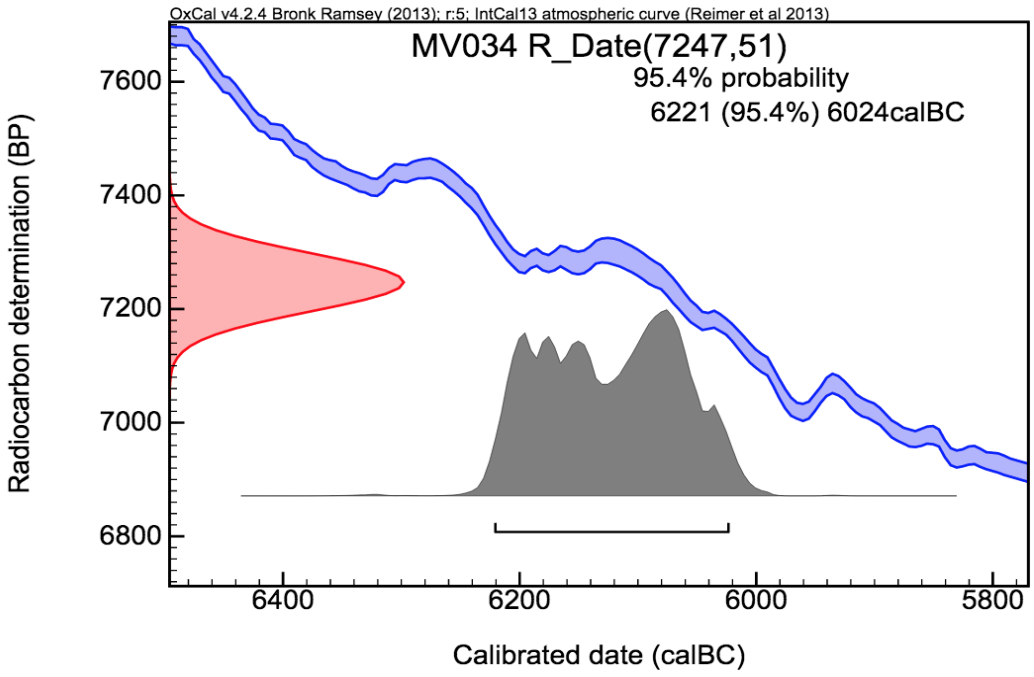


Figure 9.5.6 - Radiocarbon dates calibration for Sub1.

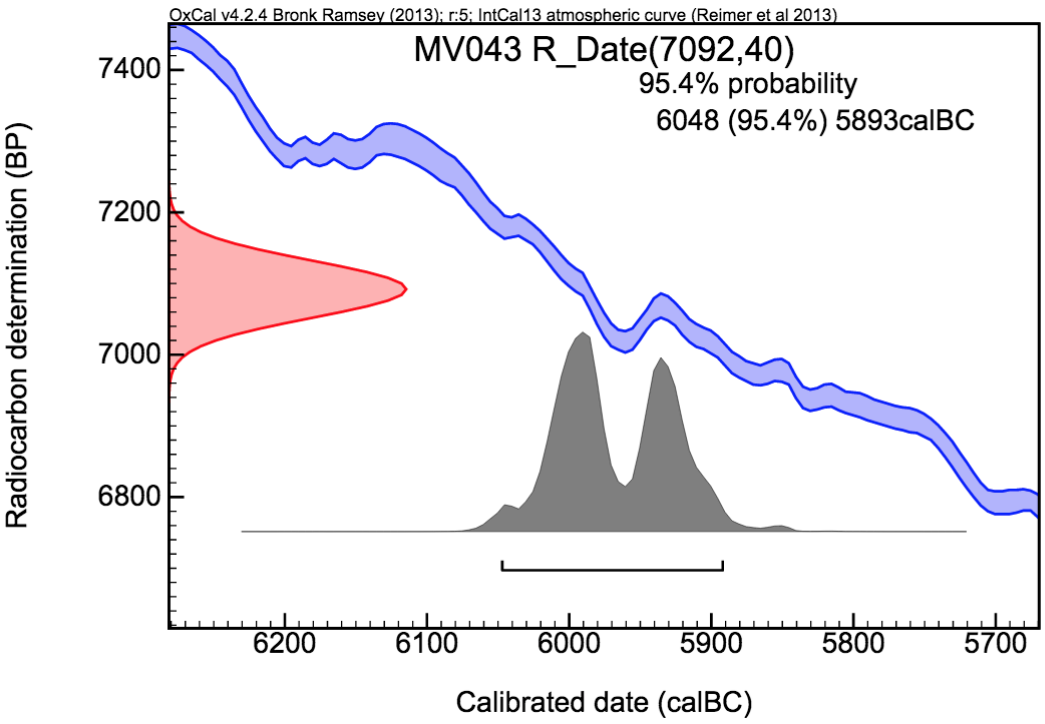


Figure 9.5.7 - Radiocarbon dates calibration for Men2.

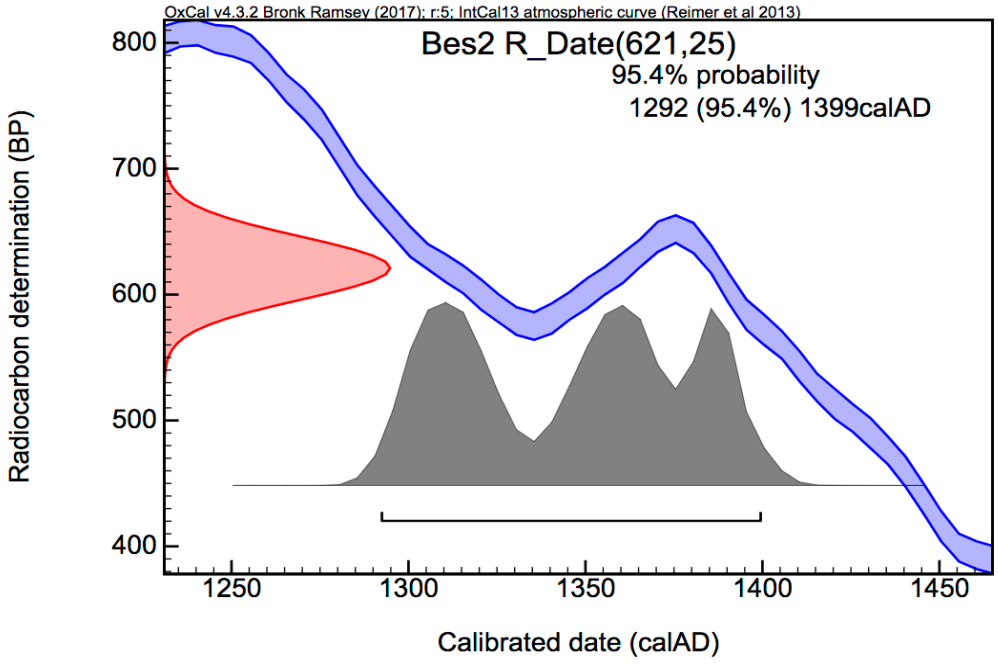


Figure 9.5.8 - Radiocarbon dates calibration for Bes2.

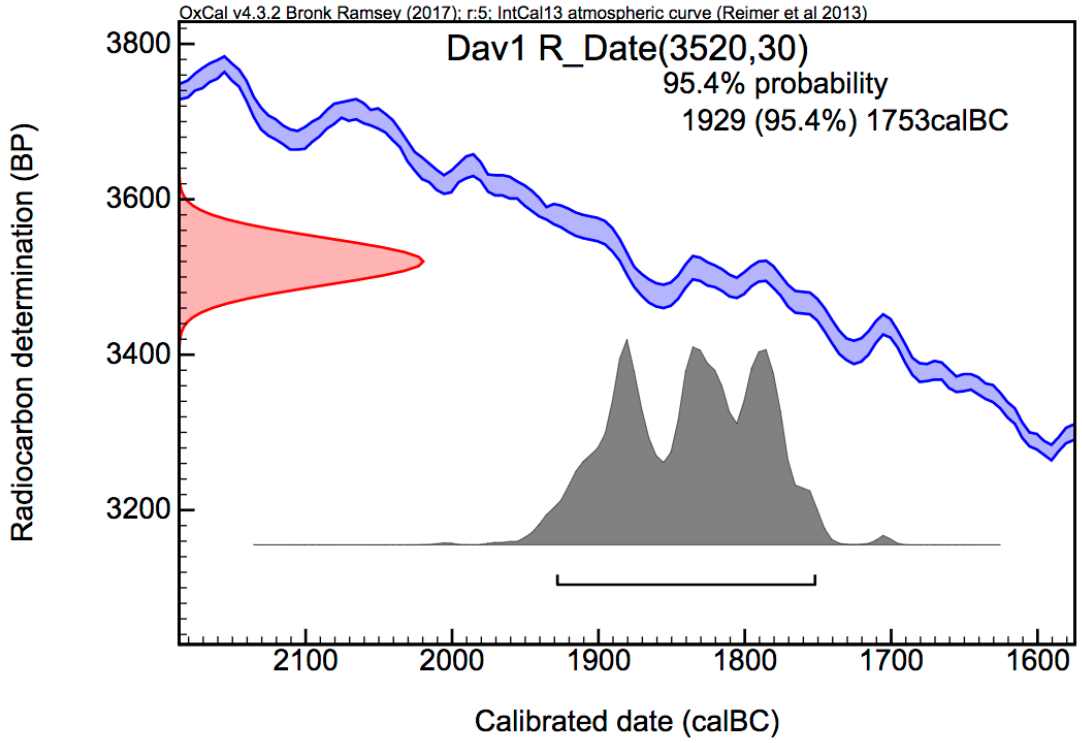


Figure 9.5.9 - Radiocarbon date calibration for Dav1.

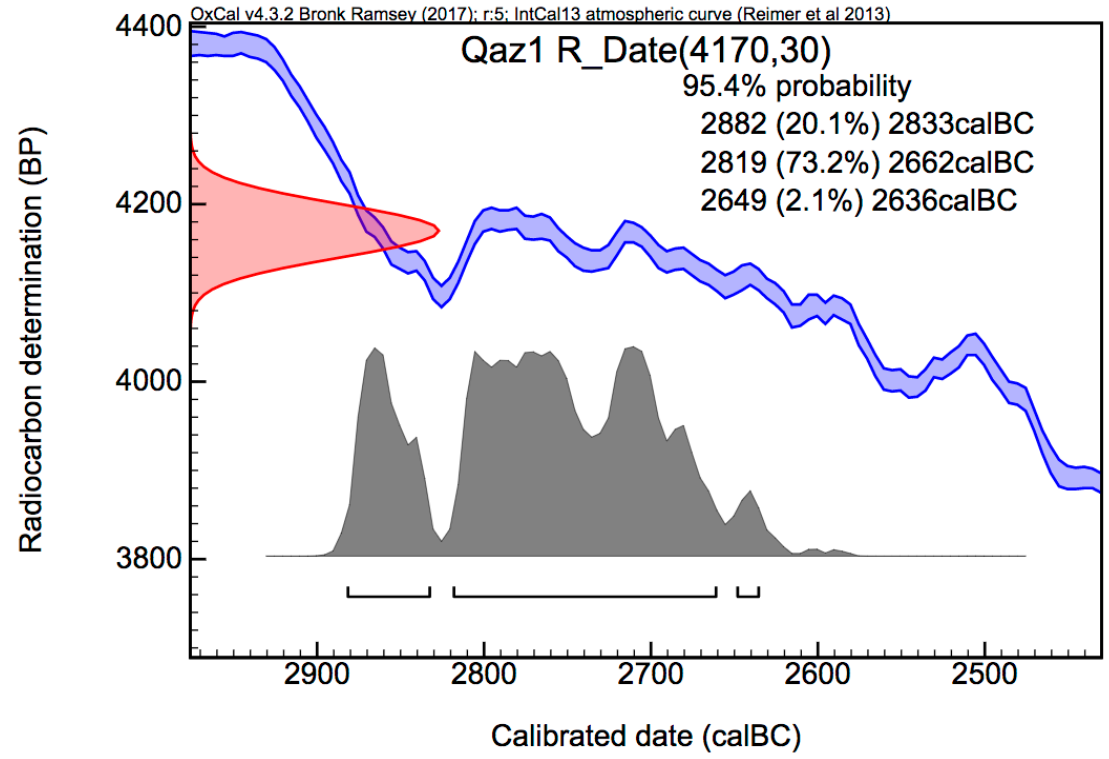


Figure 9.5.10 - Radiocarbon date calibration for Qaz1.

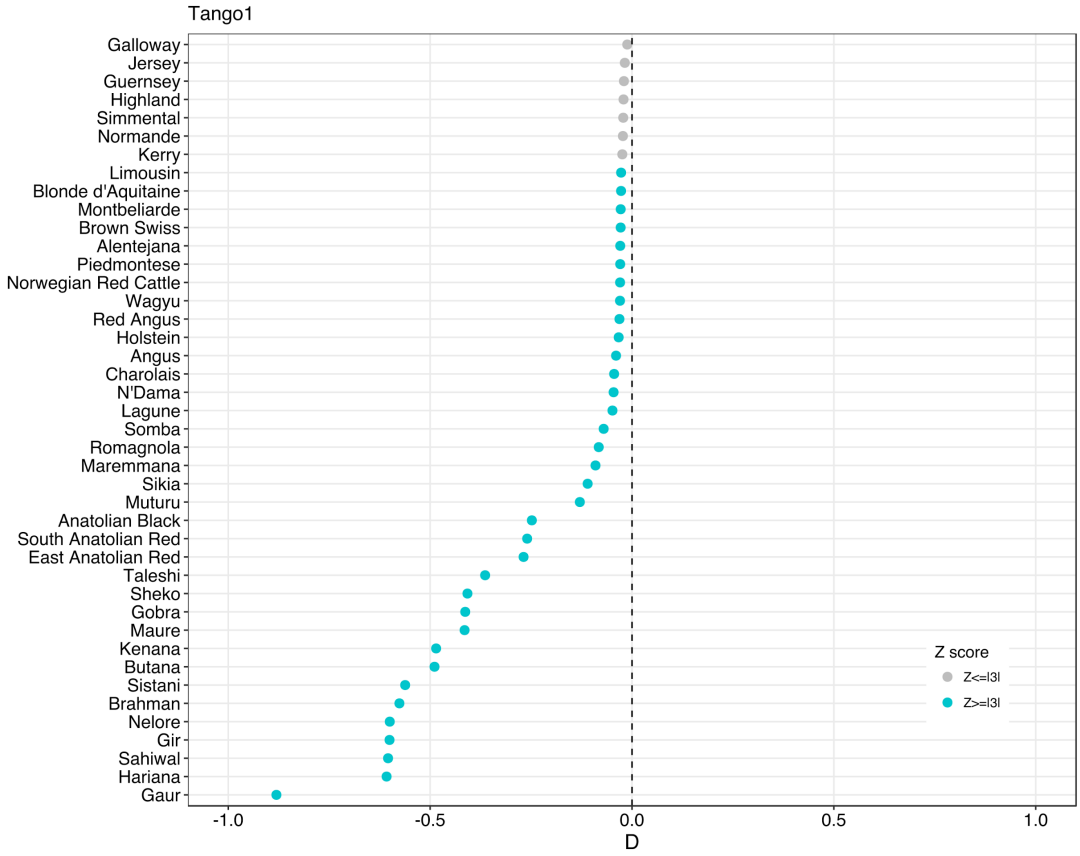


Figure 9.5.11 - D statistic for (((Test,Sub1),Tango1),Yak). Tango1 aurochs from unknown geographical origin and Test being all modern cattle breed populations from the 700K dataset. Positive D values indicate gene flow either from Tango1 to Test or from Yak to Sub1. Statistical significance is coloured: significant (blue), non significant (grey).

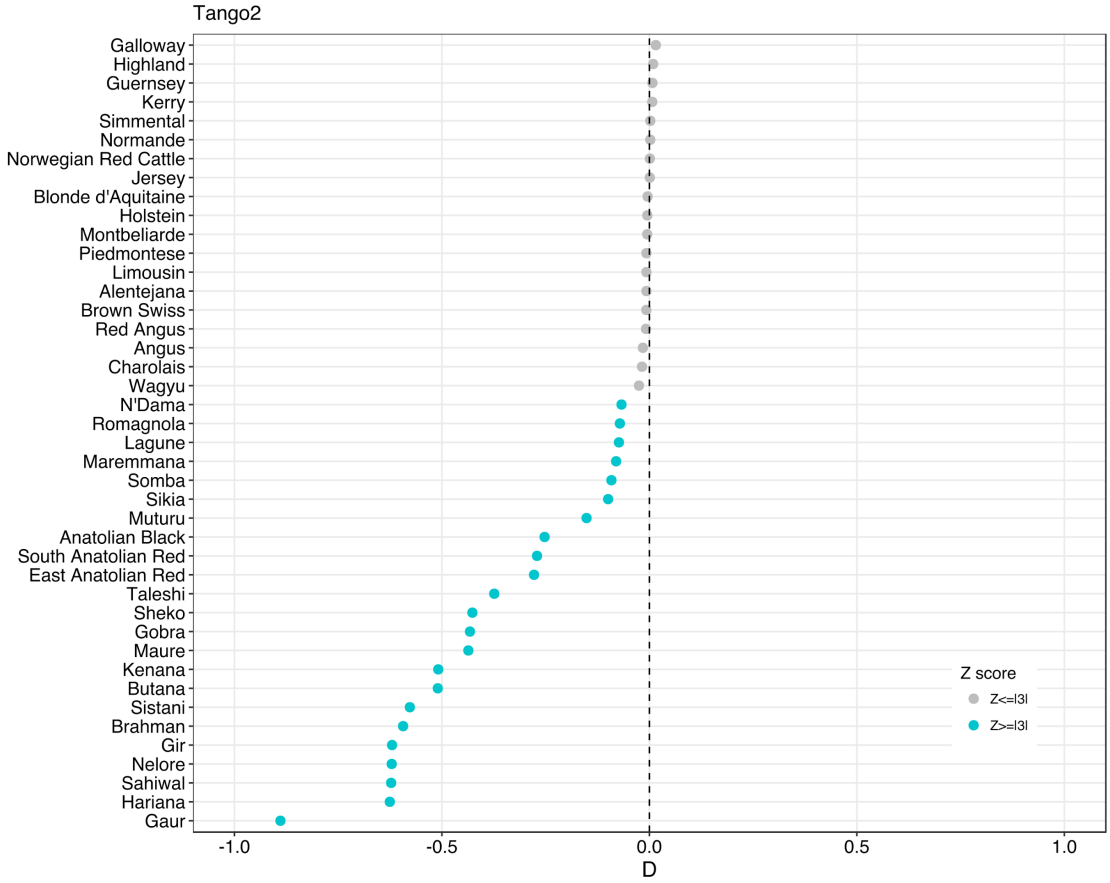


Figure 9.5.12. D statistic for (((Test,Sub1),Tango2),Yak). Tango1 aurochs from unknown geographical origin and Test being all modern cattle breed populations from the 700K dataset. Positive D values indicate gene flow either from Tango1 to Test or from Yak to Sub1. Statistical significance is coloured: significant (blue), non significant (grey).