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# The mtDNA D-Loop Legacy of Cattle: Fluctuations in Diversity from the Neolithic to Early Medieval Times in Switzerland

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**Abstract:** Fluctuations in the size of taurine cattle (*Bos taurus*) have been regularly demonstrated using archaeozoological data from across time and space in Europe, and have been linked to cultural, social and economic changes, but little is known about whether phenotypic change is accompanied by changes in genetic diversity. Here, we performed PCR-typed analysis of the partial mtDNA d-loop fragments of 99 cattle from the Neolithic to Early Medieval times from a number of different sites across Switzerland, combining newly presented data with previously published data ($n = 20$). We found that most cattle included (84) were members of the common European macro-haplogroup T3. However, cattle belonging to the haplogroups T1, T2, Q and P were identified as early as the Neolithic period, before 2690 cal. BCE. The highest diversity was found in the Neolithic period, during the 1st century CE and during the 7th–8th centuries CE. Bottleneck phases with low genetic diversity were detected during the Late Iron Age and from the fifth to the seventh century CE. Based on the $F_{ST}$ values, Horgen, Corded Ware and cattle populations from the seventh to the ninth century CE were plotted away from the clusters of all other populations. The periods with larger-sized cattle correspond with those of high mtDNA d-loop diversity. Phenotype and genotype both appear to respond to the same socio-economic and cultural processes.

**Keywords:** ancient DNA; haplogroup; haplotype; *Bos taurus*; Bronze Age; Iron Age; archaeozoology; Roman colonies; biometry; body size

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## 1. Introduction

The mobility of people and livestock and the extent of cultural impact on livestock husbandry since domestication around 10,000 years ago have shaped the genotypes and phenotypes in domestic animals through time. Taurine domestic cattle (*Bos taurus*) spread across Europe with farmers and reached the Alpine foreland and the area now occupied by modern day Switzerland during the second half of the sixth millennium BCE [1]. Since then, cattle have consistently been of large economic importance as providers of meat, milk, traction power, hide and other raw materials [1].

Genetically, mitochondrial (mtDNA) diversity patterns in extant cattle—and in other domesticates—largely reflect the past maternal history of livestock, and their spread with migrating people since domestication is something that has been reflected by this [2–6]. In the case of taurine cattle, large global datasets exist for both extant and extinct mtDNA variations. Yet, their mitochondrial phylogeny is still subject to ongoing research [4]. The recently revised mtDNA phylogenies are most commonly used with data from the mtDNA d-loop [7–9]. Typically, three haplogroups have been identified for Europe: T, Q and R. Haplogroup T is mainly represented by subhaplogroup T3, with minor frequencies of T2, T1 and T5, with all having different core areas of geographic distribution [3,7,10–12]. Within this context, mitochondrial diversity patterns within Europe have been attributed to dispersals of cattle from the Near East during the Neolithic period [13] with sporadic introgressions of European aurochs [4].

Ancient DNA studies have traditionally paid much attention to the process of domestication and the early spread of, e.g., cattle, [5,14–16]. However, in recent years, the focus has increasingly been turning to the cultural impact of cattle during later time periods across Europe and the Near East, for example, from Iberia, Austria, the Baltic region, Sweden, Hungary, Lithuania, Switzerland, Scotland and the Eastern Mediterranean region [17–25].

In this paper, we present some data from Switzerland, discussing diachronic changes in cattle from the Neolithic through to the Early Medieval period. Here, we give a brief overview of the cultural periods included in this study.

The Neolithic period in Switzerland is characterized by the so-called lake-dwelling phenomenon, which included many wetland sites forming part of the UNESCO world heritage entitled "Prehistoric Pile Dwellings around the Alps" (https://www.palafittes.org/homepage.html, accessed on 1 April 2023). A number of phases of cattle husbandry have previously been defined, broadly following the cultural changes [26,27] starting at around 4400 cal BCE. During the earliest phases, the cattle economy seemed to have focused on meat, but during the period from around 4000–3400 cal BCE (the Cortaillod and Pfyn cultures), we see the first evidence for the use of secondary products, such as milk and labour, indicating a diversification in the economy [28–30]. During the Horgen culture (3400–2800 cal BCE), proportions of cattle decreased (with pigs having more of a focus) and cattle also became smaller [28], a pattern that was reversed around 2800–2500 cal BCE, where an increase in cattle prevalence and body size is seen broadly concurrent with the arrival and influence of the Corded Ware Culture in eastern Switzerland, and the Auvenier Cordé in western areas [26,31,32]. There is evidence for specialised use of cattle for labour [28,33] and possibly for the introduction of a new cattle population into the area [32].

The Bronze Age (ca 2200–1300 BCE) is characterized by metallurgical innovations and a resulting intensification of trade networks. Lake dwellings disappeared [34] and settlements were established in marginal areas, such as the alpine region. Among the domestic animals, cattle were the most common animal in most regions, especially in the eastern part of Switzerland. In addition to the food economy, cattle were also crucial for trade and transport [35,36].

In the Iron Age (from the fifth century BCE), proto-urban centres, *oppida*, were founded in the Northern part of Switzerland [37]. Cattle were as important as in the Bronze Age, although their body size was rather small. However, during the late Iron Age, their significance grew, together with their body size. The most likely explanation for the latter is an already increasing Roman influence in Switzerland [38]. Despite the fact that most people of the Late Iron Age still had problems digesting fresh milk, organic residue analysis on ceramic sherds confirms the production of dairy products, such as cheese [39,40].

The rise of the Roman Empire was transformative for many parts of Europe, with major innovations in animal husbandry, as documented by historical sources along with archaeozoological data [41–44]. In Switzerland, cities arose, which were first built from wood and later (around 50 CE) by stone. These were surrounded by large networks of farming sites, the *villae rusticae*, where domestic animals were kept [45] to provide for the cities. For cattle, MacKinnon in 2010 [46] suggested the establishment of geographical "breeds" in Roman Italy, which were selected for their appearance (size and colour), working capacity or milking ability. Morphometric data from cattle remains in Europe indicate a general size increase with regional variations in speed, extent and onset. Several explanations for these changes have been discussed, including the import of new cattle and/or local improvement in husbandry, and it appears that cattle improvement at this time was a complex and regional process [47–53].

With the start of the Early Medieval period, after the collapse of the Roman Empire and the departure of Roman administration and military at the end of the fourth century CE, cattle became less frequent and experienced a considerable reduction in size [42,54–56]. This process continued until the High Middle Ages (11th–12th century CE) and has been independently observed in both male and female cattle [42,54]. It has been suggested that these changes were due to the development of feudal structures from a market-oriented production to an economy more dependent on self-subsistence. This might have led to changes in management practices, limited regional livestock mobility, and little or no genetic improvement of livestock [42].

The aim of this study was to explore whether some of the broad cultural changes mentioned above were accompanied by shifts in the genetic signature in regional cattle herds. We examined nucleotide diversity within the mitochondrial (mtDNA) d-loop in cattle from the Neolithic to the Early Medieval period in Switzerland. The data were collected over many years across a number of projects. They represent specific local patterns, and future work on cattle may reveal whether our findings can be generalized across the whole of Switzerland and beyond.

## 2. Materials and Methods

### *2.1. Archaeological Cattle*

The prehistoric cattle samples included in this study are from the Horgen layers at the site of Twann (canton Bern), the Corded Ware layers at the site of Zurich Versicherung Mythenquai (canton Zürich), and the Late Iron Age site Basel-Gasfabrik (canton Basel-Stadt). The data from the Roman period are from Augusta Raurica (cantons Basel-Landschaft and Aargau), and the Early Medieval cattle data included are from Lausen and Reinach (canton Basel-Landschaft). The analyses were complemented with previous published results from the Bronze Age site of Savognin Padnal (canton Grison) and one additional individual from Horgen Twann [57,58]. The size data were modified from [32,42,59] (Figure 1). The layers and sites were dated either typologically based on material culture or by dendrochronology (Twann, Zürich). The details for all sites are given in (Supplementary Material Table S1, Supplemental Text S1).

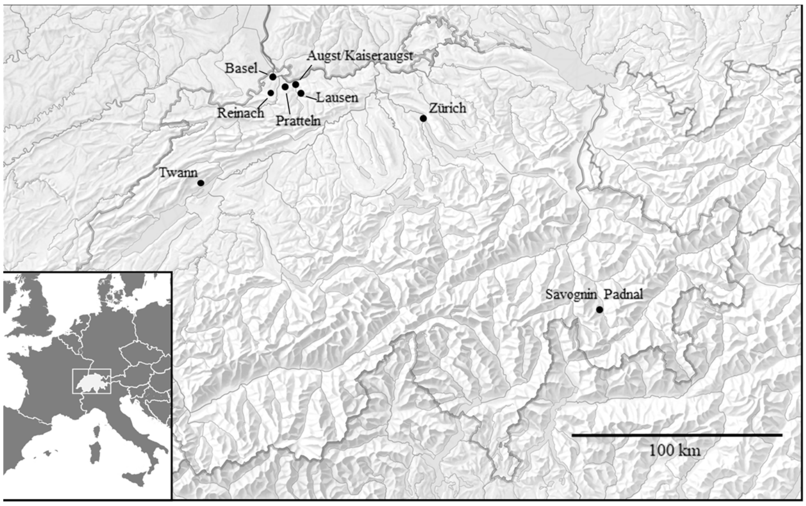

**Figure 1.** Location of sites of cattle samples in Switzerland included in this study. Details of each sample are given in Table S1. Data from Savognin Padnal are previously published [57] © swisstopo.

## *2.2. Methods*

The lab work was carried out over a time period of more than 20 years, during which the methods used were adapted, namely the reduction of amplicon length, focusing on a targeted d-loop region; a change from a self-made silica-based extraction and cloning [60,61] to the use of a Qiagen Blood and Tissue Kit and direct sequencing [58] with more powder; an increase in cycles from 35 up to 70; and an increase in AmpliTaq, reflecting the advances in aDNA research and availability of sequence information from mtDNA. Below the different methods for the cattle samples from different sites are briefly described. Because of the very different methodological approaches used through time, amplification success rates have not been compared.

### 2.2.1. DNA Extraction and PCR Amplification

Late Iron Age and Early Roman period R1: the archaeological bone samples were prepared and processed as described in detail using the primer ANnumber [60,61] (Table S2).

Horgen, Corded Ware, Roman R2, R3, R4, EEM, and LEM: extraction was performed with a Qiagen Blood and Tissue Kit optimized for teeth and bone samples with the primer Hnumber following [58,62] (Table S2).

DNA preservation is unfavorable in the waterlogged sediments from Twann and Zürich [58] (for Twann, 6 out of 16 specimens, and for Zürich Versicherung, 5 out of 32 specimens were successful), resulting in few reproducible PCRs of mtDNA d-loop targets. The same applies to Basel-Gasfabrik, where cattle bones were preserved dry. Low amplification success was also observed for human remains from the same site [63].

We argue that, even with the small sample size, overall diversity is still captured because the genetic diversity between the time periods covered even by a small number of samples is very different and not dominated by the expected dominant T3 haplotype.

We followed the authenticity criteria established by the IPAS [58,62], in particular physically separated labs for sample preparation, DNA extraction and PCR set-up of aDNA, with dedicated equipment and lab ware.

### 2.2.2. Sequence Analysis and Haplotype Identification

Concatenated sequences from all target regions were aligned with Bioedit v7.2.5 [64] and MEGA-X [65] and compared to the reference sequence V00654 [66]. Haplogroup assignation was undertaken by eye with diagnostic positions according to Achilli et al. (2009) [8] and Bonfiglio et al. (2012) [7] based on the individual length and the position of the sequence generated within the d-loop (pos. 16041–16271 and 33–198) (Table S3). The identification of members of the T1 haplogroup based on short d-loop fragments is problematic [4] due to recurrent mutations or diagnostic motifs outside the d-loop. We defined T1 using SNPs at position 16050 together with position 16113. However, Bonfiglio et al. (2012) [7] reported rare T1 types missing either SNP 16050 or SNP 16113, namely T1e and T1f based on mitogenomes. We assigned “cf T1” (Latin *conferre*) in cases where exact identification was not possible, but plausible.

### 2.2.3. Population Parameters

Population parameters of 189 bp (pos. 16041–16271) from the concatenated sequences in common for all sequences were calculated using Arlequin 3.5.2.2 [67] based on pairwise distances, using alpha distribution of gamma 0.11 [68].

A median-joining network was calculated using Network (version 10.2) (http://www.fluxus-technology.com, accessed on 1 January 2023) [69]. This was based on 189 bp shared between all units and using the default settings and a weight of 10 for all 35 SNPs. The only exceptions were SNPs at positions 16129 and 16255, which were set to 1 to reduce median vectors and cubes. The cattle individual with haplogroup P was not included [58].

Archaeological cattle were grouped chronologically, following, in case of Roman and Medieval times, Grau Sologestoa et al. (2021) [42] (Table S1): 3093–3072 cal BCE (Ho, Horgen), 2720–2690 cal BCE (CW, Corded Ware), 1950–800 BCE (BA, Bronze Age) [57], 170/150–100/90 BCE (IA, Late Iron Age), R1 (1st half of 1st century CE), R2 (2nd half of 1st century CE), R3 (2nd century CE), R4 (3rd–4th century CE), EEM (5th–7th century CE), and LEM (7th–8th century CE). Due to the nature of the typological dating methods used, some samples have dates that overlap time groups (see Table S1).

AMOVA statistics and linearised Slatkin's $F_{ST}$ based on pairwise distances from archaeological cattle were computed using Arlequin (version 3.5.2.2) [67] and analysed via non-metric multidimensional scaling (MDS) using the PAST software version 4.0 [70] with the Euclidean similarity index.

All sequences were deposited with Genbank, accession numbers OQ446331-OQ446408.

### *2.3. Biometry*

In order to contextualise our genetic results within their archaeozoological context, cattle biometrical data from across Switzerland were collected from available publications and plotted for the same time periods as for the genetic data [32,42,59]. The biometrical analysis was based on the log-ratio technique (also known as the "LSI technique"), a size index scaling technique that transforms logarithmically (in this paper, with logarithm base 10-LSI10) the ratio between the measurements taken from archaeological specimens and standard measurements taken from an individual or the mean of a given population, either modern or archaeological. The value resulting from this calculation is the "logarithmic size index" or LSI value. The biometrical analysis was performed in R using the purposely designed package Zoolog [71]. Only widths were considered since they are the most frequently represented axis. Only one measurement per bone and axis was used in the analysis, and only measurements taken on fully fused bones were considered. Zoolog prioritizes the most abundant, more replicable, and less age-dependent measurements. The set of standard measurements used belong to individuals of known sex, age and origin (https://ipna.duw.unibas.ch/fileadmin/user_uload/ipna_duw/PDF_s/PDF/LSIStandards_IPASUniversityBasel.xlsx, accessed on 1 April 2023).

## **3. Results**

### *3.1. Haplogroup and Haplotype Identifications*

In total, 79 cattle bone samples from different time periods were newly sequenced and combined with 20 previously published samples [57,58,60]. Based on diagnostic SNPs [7,8], 84 cattle belong to subhaplogroup T3; of these, 52 are affiliated to the main European T3 haplotype, and the other 32 are different variants of T3. Additionally, two individuals belong to haplogroup T1, five to cf. T1, four to haplogroup T2, three to haplogroup Q and one to haplogroup P (Table S3).

Within the 12 Neolithic (Horgen from Twann and Corded Ware from Zürich) samples, we find cattle belonging to haplogroups T3, T2, cf T1 (SNP 16113), Q (SNP 15953) and P, which represents a high diversity, being present about 2000 years after the first cattle appeared in Switzerland. Interestingly, the two sites differ in haplotype composition: at Twann in the west of Switzerland, three cattle carry cf.T1 haplotype and a small cattle has a P haplotype [58], whereas in the central part (Zürich), T2 and Q were identified. In the Bronze Age sample, T2 and Q cattle were also found, in addition to T3. In the five cattle from the late Iron Age, only T3 haplotypes occurred. In the Roman periods (R1– R4), T3, T2 and two cattle with cf. T1 (either TKH12 SNP 16050 or B32 SNP 16113) are present. In cattle from Early Medieval times (EEM and LEM), two T1 variants different to those seen earlier and including SNPs 16050 and 16113 appear at two different sites (Lausen LSB8 and Reinach MG12), together with T3 (Figure 2, Table S3).

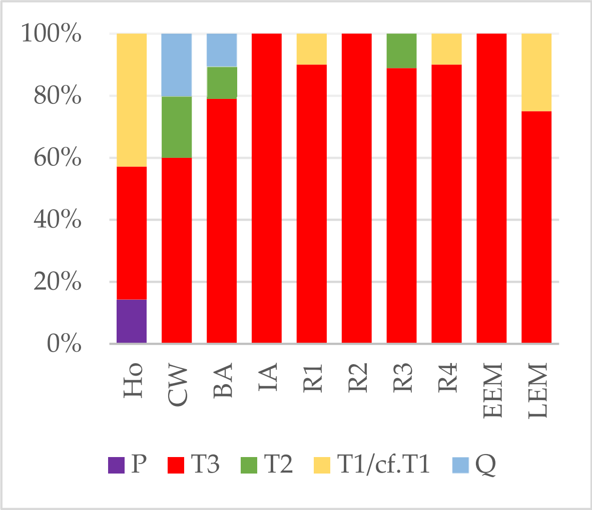

**Figure 2.** Representation of mtDNA haplogroups during the cultural periods from Neolithic to Late Early Medieval time in Switzerland. Included is a Horgen time domestic cow from Twann (upper Horgen, OH) with a P haplotype [58]. Ho = Horgen, *n* = 7; CW = Corded Ware, *n* = 5; BA = Bronze Age, *n* = 19; IA = Late Iron Age, *n* = 5; R1 = 1st half of 1st century CE, *n* = 10; R2 = 2nd half of 1st century CE, *n* = 10; R3 = 2nd century CE, *n* = 9; R4 = 3rd to 4th century CE, *n* = 10, EEM = Early Early Medieval, 5th to 7th century CE, *n* = 16; and Late Early Medieval = LEM, 7th to 8th century CE, *n* = 8.

### *3.2. Genetic and Morphometric Diversity through Time*

Shorter sequence lengths were used for diversity and network calculations and for comparison with previously published data from the Bronze Age [57] (see methods), showing reduced diversity (Table S3). The data included in the calculations, however, cover the most variable region of the d-loop.

Both hd (haplotype diversity) and MNPD (mean number of pairwise differences) follow the same overall scheme: high diversity during the Neolithic period with the highest number in the Horgen period at Twann. Diversity measures decreased slightly during the Corded Ware period and the Bronze Age, and then dropped sharply during the Late Iron Age in Basel. With the first Roman contacts in the region in the first half of the first century CE, diversity increased strongly and further until the end of the first century CE (R2). From the second century AD (R3), diversity decreased continuously until the Early Early Medieval period, which is represented by cattle from three sites: Kaiseraugst, Reinach and Lausen. An abrupt rise in diversity during the Late Early Medieval period (LEM) was found in cattle from Lausen and Reinach (Figure 3); yet, in the second century CE (R3), one cf. T1 cattle was detected.

Morphological changes mirror changes in genetic diversity with few exceptions: during the Late Iron Age, cattle seemed to show an increase in size, whereas diversity was quite low, and during the Late Early Medieval period, the converse was true, with cattle showing a decrease in size, but diversity was rising. During the Roman period, the pattern was slightly offset, with genetic diversity dropping off after R2 and the corresponding size decrease not seen until R4. It should be noted that during all time periods, large and small cattle coexisted, although fewer small cattle were observed in R3 and R4.

### *3.3. Median-Joining Network*

A median-joining network approach was used to display the relationships between cattle rather than as a phylogenetic (evolutionary) or phylogeographic tool. The network shows the high diversity and star-like topology around the main T3 haplotype (Figure 4). Cattle belonging to T1/cf. T1 as well as to T2 and Q haplotypes are separated from the T3 types. The sample ZHV29 falls into the T2 branch due to the presence of SNP 16057. Although the main T3 haplotype is shared across all periods, few T3 haplotype variants are shared between or within periods. For example, six T3 variants are shared within the

Roman period, and one variant is shared between the Roman and Medieval times (B31). T2 variants are shared between the Bronze Age and Roman periods (B6). The network clearly shows a large number of private haplotypes during all time periods, particularly in R1 where few cattle belong to the main T3 type, resulting in the observed indication of high diversity (see above).

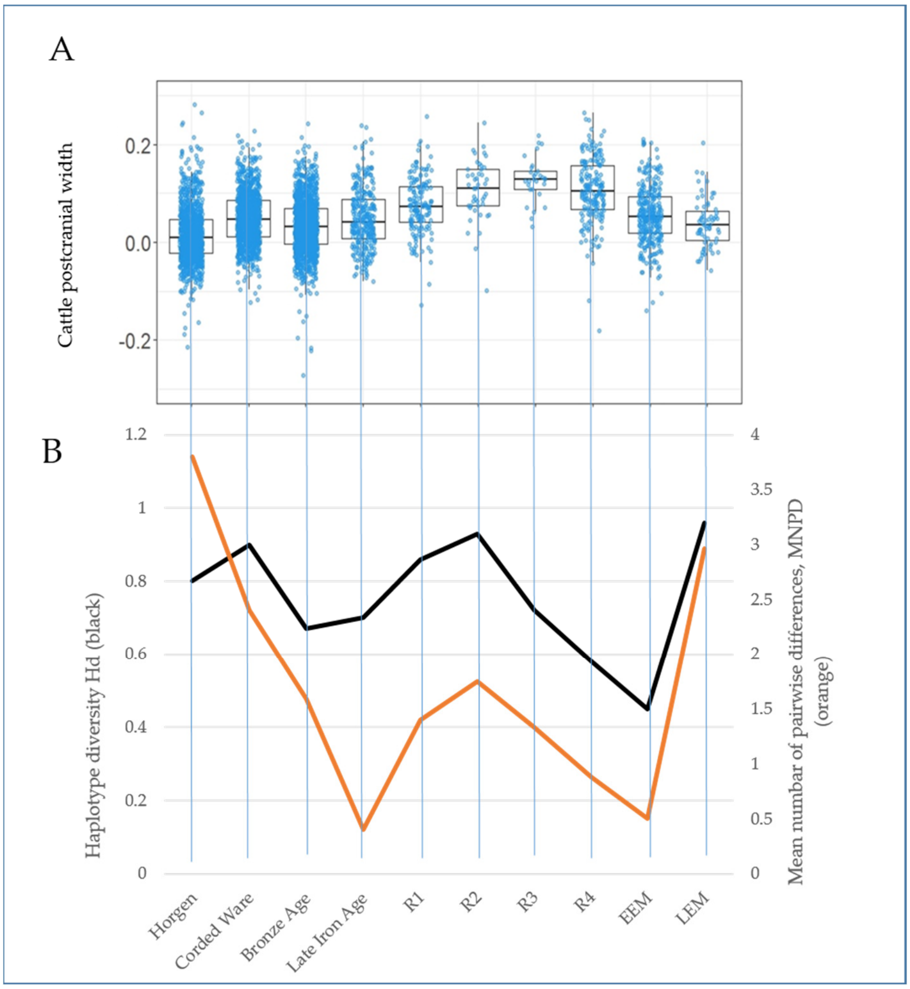

**Figure 3.** (**A**) Changes in size through time modified from [32,42,59]. R1 = 1st half of 1st century CE, R2 = 2nd half of 1st century CE, R3 = 2nd century CE, R4 = 3rd to 4th century CE, EEM = Early Early Medieval time from 5th to 7th century CE, and LEM = Late Early Medieval time from 7th to 8th century CE [57,60]. The chronological classifications are according to Table S1. (**B**) Fluctuations of mtDNA d-loop diversity through time. The time slots are the same as in Figure 3A.

### *3.4. Relationships between the Archaeological Cattle "Populations"*

The results from the AMOVA (analysis of molecular variance [72]) revealed a significant differentiation of cattle from the Horgen and EEM periods compared to most other groups at a 5% level, whereas Late Iron Age cattle are similar to all other groups (Table S4).

Linearised Slatkin's $F_{ST}$ calculation and visualisation with MDS (multidimensional scaling) was used to reveal the relationships between the populations [73]. We used this approach to address the relationship between archaeological cattle "populations" from different time periods. The analysis shows that Neolithic cattle from the Horgen and Corded Ware periods are separated on the x-axis and positioned away from all other "populations". Those groups cluster close together, regardless of time period, and respective cultural period (Figure 5). The Horgen and Corded Ware periods, in addition to the LEM period, are also separated on the *y*-axis. The quality of the plot is significant as the stress factor is below 0.1 (stress 0.058, Figure 5).

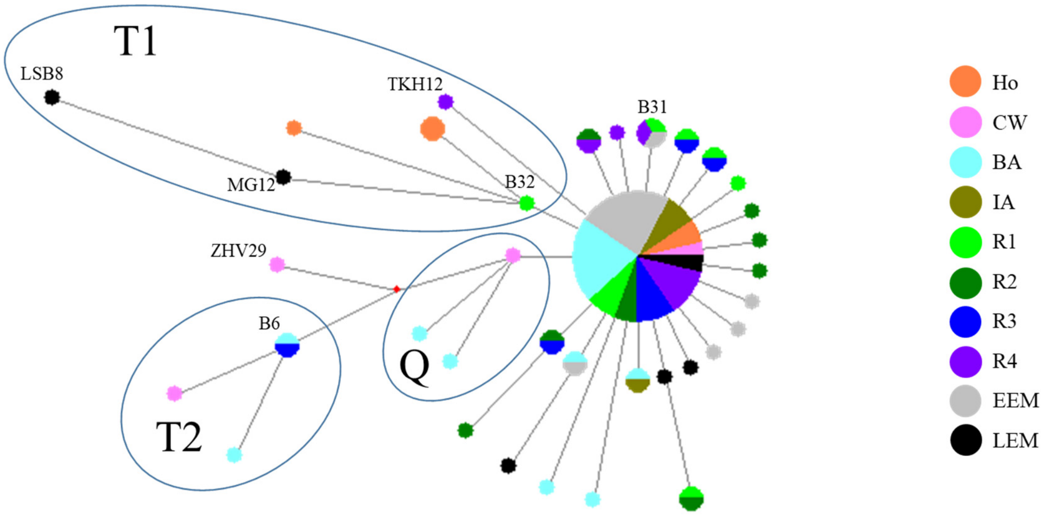

**Figure 4.** Median-joining network of 98 archaeological cattle from Switzerland, comprising 42 SNPs and 36 haplotypes (189 bp). Circles are proportional to the number of samples, and branch length is proportional to number of mutations separating the samples. Ho = Horgen, CW = Corded Ware, BA = Bronze Age, IA = Late Iron Age, R1 = 1st half of 1st century CE, R2 = 2nd half of 1st century CE, R3 = 2nd century CE, R4 = 3rd to 4th century CE, EEM = Early Early Medieval time from 5th to 7th century CE, and LEM = Late Early Medieval time from 7th to 8th century CE [57,60]. The chronological classifications are according to Table S1.

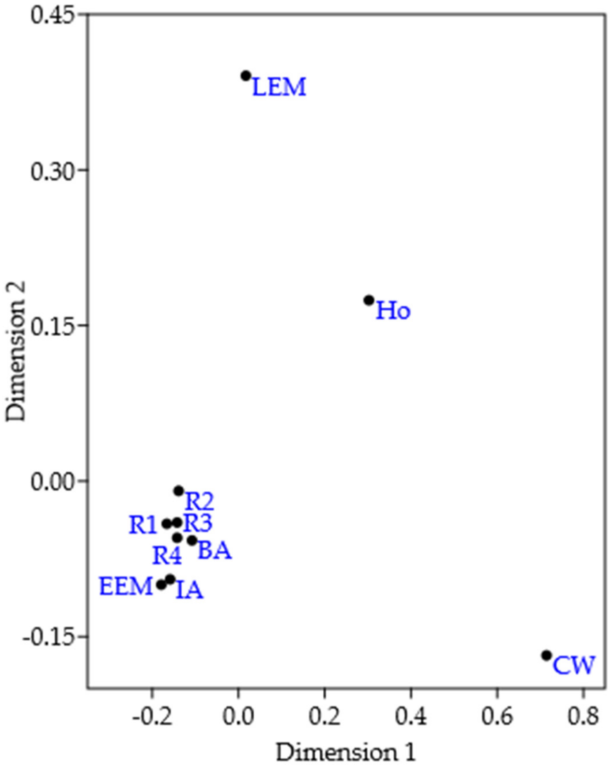

**Figure 5.** Non-metric multidimensional scaling plot of linearised Slatkin's $F_{ST}$ based on pairwise distances between archaeological "populations" (189 bp). Ho = Horgen, CW = Corded Ware, BA = Bronze Age, IA = Late Iron Age, R1 = 1st half of 1st century CE, R2 = 2nd half of 1st century CE, R3 = 2nd century CE, R4 = 3rd to 4th centuries CE, EEM = Early Early Medieval time from 5th to 7th century CE, and LEM = Late Early Medieval time from 7th to 8th century CE. Stress 0.058, $R^2$ axis 1: 0.83, and $R^2$ axis 2: 0.095.

## 4. Discussion

We present a diachronic view of mtDNA and size diversity in cattle in Switzerland from the Neolithic (Horgen and Corded Ware) to Medieval periods (eighth century CE).

T3 variants are the most common haplotypes in this study and have been documented all over Europe based on both ancient and modern DNA [3,4,74]. Cattle carrying Q, cf. T1/T1 and T2 genomes are rare, but both T1 and T2 are consistently present through time. T1 cattle are common in Africa but are also found in Iberia, Italy, the Balkans and Southeast Europe [3,4,7,10,75]. The presence of T1, T2 and Q at both Twann and Zurich, north of the alps, at the very end of the fourth century/early in the third millennium BC (3093–3072 cal BCE at Twann and 2720–2690 cal BCE at Zurich) is surprising and is a new insight into early cattle haplogroup distributions. T1 cattle have also been reported in both Iberia for the Neolithic period and Austria in the Iron Age [17,18]. Cattle belonging to haplogroup T2 were extremely rare in ancient times [74]; they are today mainly found across the Balkans and Southeast Europe, with rare occurrences in Switzerland, Italy and Southern France [3,60,74]. Cattle belonging to Haplogroup Q are descendants of another domestication event in the Near East from wild Q aurochs and are today found in low numbers in Italy, the Balkans and Egypt [4,11,13]. The geographical distribution and frequencies of haplogroups in modern cattle have often been used to hypothesise about cattle spread and trade connections in the past [10,17,18]; however, we are cautious about conflating the ancient movement of people with cattle based on current geographical haplogroup distribution, as distribution in the past might have been different to today's distribution (as has been demonstrated for T1, T2 and Q) [17,18,76,77]. Diversity might have been less diluted than expected from modern cattle mtDNA d-loop data [3,78]. Unfortunately, cattle aDNA data from major regions with an expected cultural impact on Swiss sites (namely from Germany, Italy, France or the Balkans) are currently missing, thus hampering our ability to discuss cattle trade.

The high diversity seen during the Neolithic period, based on haplogroup and haplotype diversity as well as MNDP measures, is best explained by the—expected—initial arrival of early farmers. Interestingly, the haplogroup representation and MNPD values differ between Horgen Twann (presence of cf. T1) in the West and Corded Ware Zürich in central Switzerland (presence of Q and T2). It should be noted that at Horgen Twann, a small biometrically domestic cow with a highly divergent haplogroup P was also found, which was interpreted as evidence of the local introgression of aurochs [58]. The differences seen between these two Neolithic sites could be explained by geography, time or a combination of the two. Twann is located in Western Switzerland, which during the Neolithic period, and indeed beyond, was largely influenced by cultures in the west and south, via the Rhone valley (see, e.g., [26]). The presence of T1 at Twann could, therefore, be related to a Mediterranean influence, as we know that T1 cattle have been present in Iberia since the Neolithic period [17,79]. The presence of Q and T2 at Zurich might relate to the more eastern influence seen at sites in central and eastern Switzerland at the time; however, it might not be a coincidence that these haplogroups were also appearing at around the same time as a larger form of cattle, which might have links to the introduction of Corded Ware in the region [32]. Further work on this time period is clearly needed to investigate this further.

Interestingly, the two Neolithic cattle populations differ from all later populations based on the AMOVA and $F_{ST}$ values (MDS plot), indicating a discontinuity in cattle husbandry and trading from the Bronze Age onwards.

During the Bronze Age, new socio-cultural influences came into play, such as mining activities, the arrival of pastoralists from the Pontic steppe region around 2860–2460 cal BCE [80] and a higher female mobility [81]. The AMOVA and MDS ordination of $F_{ST}$ values support the indication that cattle from the Bronze Age onwards are very similar to cattle from later periods, although they still carry the T3, T2 and Q genomes. During this period, trade routes across the Alps were known, including one that passed through the hill-top site of Savognin Padnal. This meant that an influx of cattle from the Balkans and from Italy might have taken place [18,36,57,82,83]. The presence of cattle belonging to different size groups has led to the suggestion that new cattle "breeds" might have arrived in this region from northern Italy [84].

During the Late Iron Age, members of the haplogroup Q disappeared in Switzerland and are not known in modern cattle from the area. The cattle from the large Late Iron Age proto-urban settlement, Basel-Gasfabrik, show a genetic bottleneck, and only the T3 haplotypes with low diversity were identified. A possible scenario is that the reduction in diversity is due to a small tight-knit cattle population in the catchment area of the settlement, since a low genetic diversity is observed despite the likelihood of incoming cattle through trade and exchange [85,86]. We know, for example, that the Celts of the Raurici tribe, settling in Basel, had trade networks that stretched to the Mediterranean regions [87]. In this context, the results of our study indicate that it is possible that these networks did not involve the movement of cattle as no animals with anything other than the T3 haplotypes were detected.

A synchronous increase in cattle size and in genetic diversity was observed at around the time of the beginning of Roman influence in the northern alpine foreland (in the first century CE—R1 and R2). Genetically, this is predominantly based on the presence of diverse haplotypes belonging to the haplogroup T3, although one cf. T1 is also present. One potential explanation is the import or trade of large cattle from the Roman motherland to the flourishing trade center of Augusta Raurica on the Rhine River. This would be in keeping with a more widespread scenario that has previously been suggested for other sites across Europe [48].

During the second century CE (R3), the impact of the so-called "Romanization" continued. Farming intensified to supply a growing human population, and cattle played a major role as working animals (ploughing), producers of manure [45] and, in cities, as a source of raw material for crafting [88,89]. By modelling the number of cattle needed for this type of intensive farming, it was suggested that an increasing number of animals must have been present (e.g., at a *villa* at Biberist, Switzerland [90]). Yet, at this time, we observed a decrease in mtDNA d-loop diversity. One explanation is that our sample did not capture the diversity present at producer sites as all samples are from the *colonia* Augusta Raurica and found within a *taberna*-like building, where they were interpreted as being slaughter waste [91]. It is worth considering that, after the first century CE, local breeding with large cattle, which was "imported" earlier, might have played a crucial role in cattle husbandry, leading to the observed low genetic diversity and the continued presence of large cattle in the second century CE. Local breeding of large cattle is additionally supported by the rare but ongoing occurrences of small cattle [49] and the presence of perinatal cattle in *villae rusticae* [92].

In the late Roman period (R4), war-like disturbances and civil unrest might have interrupted livestock management strategies, leading to the further depletion in cattle diversity [55,93]. Yet, we know that cattle from Pratteln, the site from which most of our samples were taken, were kept in a *villa rustica* [94–96] and that larger cattle were abundant. One individual with a variant of the T1 haplogroup was also present. Consequently, despite the general economic and social upheaval experience at the time, local breeding of large cattle was apparently ongoing as large cattle were still recorded [42]. The AMOVA analyses support a tight continuity within Roman cattle populations, which include more shared haplotypes with the rest of the Roman time groups than with any other time periods.

The Early Early Medieval cattle herds from Reinach, Lausen and Kaiseraugst are even less diverse than the late Roman cattle, indicating that they experienced a severe bottleneck. They were also small sized. After the withdrawal of the Roman military and administration [97], the occupation by Frankish–Alemannic tribes in the region led to changing societal structures, a disruption of animal management systems due to an increase in self-supply [98] and shifting trade networks [55,99]. A low population and a small body size might also be due to other factors, such as diseases or food shortages in the wake of de-intensified farming [100].

In the Late Early Medieval period (eight century CE), cattle of a new T1 haplotype, which were not seen before, are either relics from the initial Neolithic expansion or a renewed import from the south/southwest region. One possible reason for this could be a more intensive long-distance relationship caused by the expansion of the Frankish Empire to the south, reaching Langobardian Italy in 774 CE [55,99,101]. The route along the river Birs and over the Jura Hauensteinmountain pass, which passes both Reinach and Lausen, was part of an important line of communication and trade between the Upper Rhine valley, the Rhone Valley and the Alpine passes [102]. Cattle belonging to the haplogroup T1 are no longer found in modern local breeds in Switzerland and northern Europe today [3,4].

As discussed above, periods of high diversity alternate with bottlenecks. Fluctuations in genetic diversity appear to coincide with past socio-cultural conditions and with size developments of cattle, which have previously been linked with these socio-cultural changes [32,42,59]. Body size is a complex genetic trait with high heritability [103]. It involves many genes in cattle [104] and is also strongly dependent on other factors, such as foddering and health [105,106]. In humans, for example, individual mtDNA variants are associated with disease or complex traits, such as height and body mass index [107], and in cattle, different variants have previously been linked with reproductive traits and milk production [108,109], with further associations likely to be detected in the future [110]. Here, we consider genetic cattle "populations" rather than individuals, and the corresponding developments of cattle size and mtDNA d-loop diversity are not necessarily causative but appear to follow the same cultural–social–economic forces.

Overall, this work is a good starting point for exploring the links between cattle genetics and socio-cultural change in Switzerland and highlights a number of interesting future avenues for research. In the future, new sequencing technologies will be able to inform us further about which genes might have been involved in the size developments of cattle in the past. Ideally, samples also need to be selected from sites with a similar background, geography, climate and temporal coverage in order to compare contemporary cattle populations [79], although this is generally difficult to achieve with archaeological materials.

## 5. Conclusions

Ancient cattle from Switzerland belonged to a number of haplogroups, mainly to T3, but with low abundances of T2, T1, Q and P, which were particularly abundant during the Neolithic and Bronze Age periods. The presence of cf. T1 variants as early as ca 3000 BCE, as well as Q and T2, corroborates the suggestion that ancient geographic distribution of haplogroups did not reflect modern distributions. Interestingly, T1 variants, although rare, continue to appear throughout all time periods, suggesting an initial introduction with potential for later new introductions.

The diversity measures indicate an alternation between periods of high diversity, indicating intensified trade/incoming cattle and exchange networks, and bottlenecks in the Late Iron Age, the Late Roman and the earliest Early Medieval centuries, with the last among the three periods related to civil unrest and changing social structures. There are few shared haplotypes through time, with the exception of the main T3 type, indicating there is little evidence for genetic continuity across the timescale included in this work.

Fluctuation in diversity correlates roughly with size variation: high and low diversity measures correspond to large- and small-sized values, respectively, which in turn reflect broad socio-economic changes.

Although the dataset presented here reflects the situation at individual sites and within small regions, the patterns identified fit with an archaeological narrative backed up by other archaeological sources, and there is a general indication that changes in cattle diversity can, therefore, be linked to socio-cultural changes. The exact way in which this link is established, however, is complicated and will vary according to individual circumstances. It is particularly interesting that the Roman sample, which is focused on a particular region, seems to reflect social-cultural changes that took place over a wide geographical area;

clearly regional circumstances were heavily impacted by the rise and fall of the empire and the trade networks within it.

**Supplementary Materials:** The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/d15050687/s1. Table S1: Archaeological, archaeozoological and genetic details of cattle samples investigated in this study. Period classifications are Ho = Horgen, CW = Corded Ware, BA = Bronze Age, IA = Late Iron Age, R1 = 1st half of 1st century CE, R2 = 2nd half of 1st century CE, R3 = 2nd century CE, R4 = 3rd to 4th centuries CE, EEM = Early Early Medieval from 5th to 7th century CE, LEM = Late Early Medieval from 7th to 8th century CE. Sites are sorted according to chronology. Imdas = local database Augusta Raurica. ** slightly different chronologies exist [111]; Table S2: Primer list and amplification of mitochondrial d-loop. Positions are according to V00654 (Anderson et al. 1982) [66]; Table S3: SNPs in mtDNA d-loop, pos. 15903–16338 and 33–198 (V00654). Haplogroup identification following Achilli et al. (2009) [8] and Bonfiglio et al. (2012) [7]; SNPs underlain with grey are not included in the Arlequin, Network and MDS analyses (16042–16271); * results from the 2nd extract target positions 16185–16220 not reproducible; Table S4: AMOVA output calculated using Arlequin vers. 3.5.2.2 for the ten archaeological populations of this study; Supplemental Text S1: The sites; Supplemental Text S2: Citations in supplementary tables.

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