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MISSING LACTASE PERSISTENCE IN LATE IRON AGE CENTRAL EUROPE

Mammalian milk contains everything that is necessary to nourish newborns during the first phase of their lives and is produced by the mothers only during this specific time and for this specific purpose. After the period of weaning, the offsprings' diet switches to the food sources exploited by the adults of the species. The enzyme lactose-phlorizin hydrolase (LPH, commonly called lactase), necessary for digesting the milk sugar lactose in the small intestine, becomes obsolete and its production eventually ceases (Swallow 2003). This change results in lactose intolerance, which is characterised by a diverse set of symptoms caused by intake of milk sugar by the intolerant organism, including diarrhoea, colicky stomach pains and flatulence. The milk sugar lactose (β-galactose-1,4-glucose) is a disaccharide present in the milk of most mammals (Matthews et al. 2005). One glass of milk (200 ml) contains on average 10 g of lactose (Swaggerty/Walling/Klein 2002). In humans, LPH catalyses the reaction in which lactose is hydrolysed into D-galactose and D-glucose, which can then be absorbed through the intestinal walls and into the bloodstream. Even though a topic of intensive research, the regulation of the decline of the LPH production is not fully understood (Swallow 2003). In vivo testing in different animals suggests that the interaction of various transcriptional factors influences and regulates the activation of the LPH promoter and seems to be responsible for the natural decline of the lactase production during childhood (Lloyd et al. 1992; Rossi et al. 1997; Troelsen/Mitchelmore/Olsen 2003; Wang et al. 1995). Without sufficient levels of LPH in the small intestine, lactose is able to enter the colon where it can no longer be digested. Instead, the high electrochemical gradient of sugar in comparison to the bloodstream leads on to osmotic pressure and, as a result, approximately three times the normal amount of liquid is absorbed into the intestine. In addition, fermentation by the local bacterial flora is triggered and large amounts of hydrogen, methane and carbon dioxide are produced. By-products of this anaerobic fermentation are short-chain fatty acids and potentially toxic metabolites like acetaldehyde, acetoin, ethanol and formiate (Harrington/Mayberry 2008). Within 30 to 120 min after the consumption of fresh milk, its accelerated passage along the gastrointestinal tract ensues along with the symptoms mentioned above. As a result, the organism not only dehydrates, but also loses parts of its sustenance, which is excreted undigested, thus resulting in potential nutrient deficiency and malnutrition.

Worldwide, about a third of the human population preserves the ability to digest lactose beyond infancy, but there is considerable variation among and within populations (Liebert et al. 2017; Pribila et al. 2000). While the overall frequency of lactase persistence is very low in Asia and Africa, some African pastoralists like the Tutsi exhibit 90 % persistence (Tishkoff et al. 2007; Wang et al. 2021; Segurel et al. 2020). In Europe, the distribution follows a north-south gradient with up to 89-96 % lactase persistent individuals in Scandinavia, Britain and Ireland, 62-86 % in Central Europe, and decreasing to 15-45 % in Eastern and Southern Europe (Sahi 1994; Bersaglieri et al. 2004; Mulcare et al. 2004; Ingram et al. 2009). However, the specific dispersion of a trait does not necessarily imply its origin or underlying evolutionary mechanisms (Witas et al. 2015).

Genetically, lactase persistence in Europeans is associated with two alleles: A C to T SNP, i. e., a single-nucleotide polymorphism (SNP) exhibiting the exchange of a cytosine base for a thymine base in the DNA molecule, in intron (non-coding gene section) 13 (-13910C/T, rs4988235), and a G to A SNP, i. e., the exchange of a guanine base for an adenine base in intron 9 (-22018G/A, rs182549) of the minichromosome maintenance type 6 gene (MCM6, essential for genome replication) located upstream of the lactase gene (LCT) on the longer arm of chromosome 2 (Enattah et al. 2002; Kuokkanen et al. 2003). The former shows a strong, near-complete association of phenotype and genotype. The homozygous wild types (C/C and G/G, respectively) result in phenotypic lactose intolerance, while the T and A variants represent the dominant mutations responsible for lactase persistence in heterozygotes (Sahi et al. 1973). Heterozygosity imparts either complete or partial lactose tolerance, the latter possibly indicating incomplete genetic dominance or environmental modification (Kelly 2013). As in vitro studies suggest, the variants function as Cis-regulatory elements, capable of enhancing differential transcriptional activation of the LCT promoter. Such differential regulation is consistent with a causative role in the mechanism specifying lactose (in-)tolerance phenotypes (Olds/Sibley 2003; Lewinsky et al. 2005). In populations beyond Europe, other lactase persistence SNPs have been identified and analogous mechanisms proposed. While the -13910C/T mutation is also associated with lactase persistence in Central Asia (Heyer et al. 2011) and India (Babu et al. 2009; Romero et al. 2011), the ability to digest lactose probably originates from different polymorphisms in African populations (Tishkoff et al. 2007; Ingram et al. 2007; Imtiaz et al. 2007; Enattah et al. 2008; Peng et al. 2012; Raz et al. 2013; Jones et al. 2015; Hassan et al. 2016; Gerbault et al. 2013).

The age of the two European lactose tolerance SNPs has been calculated twice. Bersaglieri et al. (2004) estimated it to be between 2,188 and 20,650 years old, using a method of long-range haplotype conservation. Coelho et al. (2005) determined an age between 7,450 and 12,300 years, analysing the variation in closely linked micro-satellites. This is consistent with the estimated beginnings of farming in Europe ~7,500 years BP and indicates that -13910T and -22018A might already have been present at the onset of the Neolithic, when milk became available as a foodstuff with the domestication of cows, sheep and goats (Simoons 1969; Kretchmer 1971; Scrimshaw/Murray 1988; Bollongino et al. 2006; Isern/Fort/Vander Linden 2012). The pattern of a co-evolution of dairy farming and lactase persistence resulting in a selective advantage based on the additional nutrients available through dairy products seems conclusive (Simoons 1969; Kretchmer 1971; McCracken 1970). More recent studies support this theory by approximate Bayesian computation and DAnc (*Differentiation with Ancestral*) statistic, incorporating ancient and recent genomes (Enattah et al. 2002; Itan et al. 2009; Key et al. 2016), and genome-wide scans for selection (Mathieson et al. 2015). Molecular genetic studies on ancient individuals, on the other hand, struggle to spot the mutant alleles with increasing timescale. A number of studies on individuals from the Mesolithic (Burger et al. 2007; Malmström et al. 2009), the Neolithic (Burger et al. 2007; Malmström et al. 2009; Lacan et al. 2011; Plantinga et al. 2012) and the Bronze Age (Allentoft et al. 2015; Burger et al. 2020; Saag 2020; Jeong et al. 2018) found mostly homozygous wild types. Only Malmström et al. (2009) report 5 % T allele in 4,800-4,200 BP Neolithic individuals from Gotland, while Mathieson et al. (2015) and Olalde et al. (2018) detect it in their Central European Bell Beaker sample (4,750-4,200 BP) in very low frequencies. The numbers of lactase persistent individuals increase subsequently and reach almost recent values in the Middle Ages (Burger et al. 2007; Nagy et al. 2011; Krüttli et al. 2014; Margaryan et al. 2020). As shown in the diachronic investigation carried out by Witas et al. (2015) in central Poland, the frequency of the -13910T allele begins to rise in the Roman period (1,800-1,700 BP) but there is already one homozygous individual in their Hallstatt period sample (2,800-2,600 BP). The numbers they record for the Middle Ages are somewhat higher than in modern-day Poland.

The early use of domestic animal milk, on the other hand, has been traced in various studies, starting with the first evidence of milk herding in the Euphrates Valley (10,700-10,500 BP; Vigne 2011), indications for

the preference of female calves since 10,500 BP (Gerbault et al. 2013), cattle mortality profiles revealing mixed dairy and meat husbandry throughout the early Neolithic *Linearbandkeramik* (Gillis et al. 2017) and evidence of dairying by lipid identification on ceramic by $\delta^{13}C$ isotopic data of milk fat or proteins. Such biochemical evidence is available for the Neolithic in the Levant (9,000 BP) and Romania (7,900-7,150 BP; Evershed et al. 2008), Poland (7,150-6,750 BP; Salque et al. 2013), England (6,100 BP; Copley et al. 2003), Hungary (5,900-5,500 BP; Craig et al. 2000), Germany (5,871-5,851 BP; Spangenberg et al. 2008), Switzerland (5,333-5,319 BP; Spangenberg/Jacomet/Schibler 2006), and Denmark (5,000 BP; Craig et al. 2011), as well as for Iron Age Scotland (2,500 BP; Craig et al. 2000) and Switzerland (3,000-2,500 BP; Carrer et al. 2016). Also, specific types of ceramic (sieve vessels) have long been associated with cheese production (Salque et al. 2013; Virchow 1882). Only recently has the advance of laboratory technology provided direct evidence of human dairy consumption via the analysis of dietary proteins in ancient dental calculus for Neolithic individuals from Britain (Charlton et al. 2019) and northeast Africa (Bleasdale et al. 2021). Animal bones in Iron Age settlements give ample evidence of cattle raising (Benecke 1994), and the reconstruction of herd structures by slaughter age analysis shows that cattle were systematically kept both as draught and dairy animals (Schibler/Stopp/Studer 1999). Outlining a high-input, high-output, high-risk operation, dairying requires an elaborate economy with sophisticated land-use patterns (Craig et al. 2000; Halstead 1998; Ebersbach 2002; Knipper 2011; Gerling et al. 2017).

Recent genomic data has corroborated earlier results on the substantial time lapse between the exploitation of domestic animal milk and the positive selection of the lactase persistence trait in European populations (Liebert et al. 2017; Mathieson et al. 2015). In this study, we address the question whether the ability to digest milk sugar was already present in Central Europe during the La Tène period, and if so, how frequent the trait was. For this, human tooth samples from seven Late Iron Age sites in Central Europe assigned to the La Tène culture were analysed. The La Tène culture (ca. 450-0 BCE) extended from France to the Carpathian Basin and from the Alps to the German Central Uplands. We analyse mitochondrial haplogroup variability within the investigated sites in order to assess how heterogeneous the local populations were (Warnberg et al. in prep.). Autosomal DNA is analysed and provides data on the status of the SNPs -13910 and -22018 to determine to what extent lactase persistence is already present in this period. Thereby the timeframe when the mutation was established is narrowed down and light is shed on the genetic and social processes underlying its dissemination.

MATERIAL AND METHODS

Sampling Procedures

Sample material was gathered from seven sites in Central Europe (**fig. 1**). Individuals were selected for a good state of surface preservation of teeth and bones and sampled in local labs and storage facilities. Samples that had undergone remedial conservation or restoration were rejected. Appropriate measures were taken to avoid contamination, such as the use of protective clothing (disposable gloves, caps, lab masks etc.) and bleach cleaning of all surfaces and tools before and in between use. Two independent tooth samples were taken from each individual. When possible, a first and third lower molar were chosen in order to investigate both aDNA and stable isotopes from dental enamel on the same teeth, minimising destructive sampling. In cases where the lower jaw offered no suitable material, maxillary teeth were selected. The samples were individually packed and transported to the aDNA laboratory.

Fig. 1 Location of the seven La Tène period sites in Austria, France, Hungary and Switzerland analysed in the present study. – (Map ABBS, P. von Holzen).

Sites

All sites sampled date to the Late Iron Age La Tène period. The individuals included in this study were inhumation burials from cemeteries, except at the Swiss Basel-Gasfabrik site, where both cemetery and settlement burials were sampled. A more detailed description of the archaeological sites is found in the Catalogue below the main text.

Austria – Pottenbrunn, Oberndorf in der Ebene, Ossarn (all three distr. St. Pölten/A): The three neighbouring sites are located between Krems and St. Pölten (Lower Austria) in the Lower Traisen valley (Ramsl 2012b; 2002). In total, 37 individuals were sampled from the three cemeteries and 33 of them typed.

France – Bobigny (dép. Seine-Saint-Denis/F): The vast cemetery of Bobigny »Hôpital Avicenne« is situated some kilometres north of Paris (Marion/Métrot/Le Bechennec 2005; Marion/Le Bechennec/Le Forestier 2006/2007). In total, 31 individuals were sampled. The two lactose tolerance SNPs were typed on the best 25.

Hungary – Nyíregyháza, Tiszavasvári (both Kom. Szabolcs-Szatmár-Bereg/H): The two neighbouring sites are situated in the Northern Great Plain region of Hungary (Szathmáry 1984-1986; Almássy 1997-1998; Almássy et al. 2005). In total, 20 individuals were sampled from the two cemeteries, of which 7 were typed.

Switzerland – Basel-Gasfabrik (Ct. Basel-Stadt/CH): The site is located within the modern city of Basel and comprises a settlement and two largely contemporaneous cemeteries (Hecht/Niederhäuser 2011; Blöck et al. 2014). In total, 42 individuals were sampled from both the settlement and cemeteries A and B. These included both complete skeletons and disarticulated skulls/jaws belonging to separate individuals (Pichler in print). The two lactose tolerance SNPs were typed on the best nine specimens, all of which come from settlement contexts.

Laboratory Methods

Sample preparations for aDNA analysis followed the standardised protocol described in Brandt et al. (2013). With minor alterations, extraction was carried out using the protocol introduced by Brotherton et al. (2013). The analysis was implemented in two steps. First, 0.2-0.25 g of sample powder was rotated for 20-23 h at 37 °C in buffer, containing 3320 µl EDTA and 40 µl proteinase K. In a second step, a further 40 µl proteinase K was added and rotated for 2 h at 56 °C as described in Fehren-Schmitz et al. (2011) to utilise the enzymes'

temperature optimum for a maximum aDNA yield. Also, the amount of medium-sized silica suspension was reduced to 100 µl. PCR products for mitochondrial DNA sequencing were processed following Brandt et al. (2013). Products of the PCR and the Sanger sequencing PCR (Sanger/Nicklen/Coulson 1977) were additionally cleaned with 0.2 µl Exonuclease 1 and/or 0.33 µl FastAP Thermosensitive Alkaline Phosphatase plus buffer (Thermo Fisher), respectively. Also, 22 mitochondrial coding region SNPs were typed, using the single base extension technique (ABIPrism 2000) and the primer system developed by Haak et al. (2010). In cases where individuals were successfully typed as haplogroups H or U, sub-groups were determined using the two SBE systems with 16 and 7 SNPs, respectively, designed by Martínez-Cruz et al. (2012) and Keerl (2014), to provide an unambiguous classification of the mitochondrial haplogroup to the lowest level the respective systems allow. Sequencing and SBE products were cleaned both mechanically by MultiScreen$_{HTS}$ Vacuum Manifold (Millipore) and enzymatically, again using 0.33 µl Alkaline Phosphatase.

A primer system was developed to type the two SNPs 13910C/T and 22018G/A. The primers to generate amplicons of 97 and 105 base pairs length around the SNPs and the SBE Primers were created and blasted using PrimerSelect (DNASTAR Inc., Madison, USA) and NCBI Primer Blast (Ye et al. 2012). By applying the single-base extension technique, a small number of distinct SNPs can be investigated in a quick and cost-efficient manner and therefore represents a viable option for laboratories with limited resources. Due to its straightforward design, the method is able to generate reliable results even from sample material with poor preservation, provided measures for authentication are in place. However, like other PCR based methods, it is sensitive to contamination and unspecific products, which might produce errors. Also, the utilised polymerases may potentially cause mutations, which can accumulate during the cycling process. High throughput next-generation sequencing methods offer a greater coverage and thus make it possible to investigate a range of polymorphisms simultaneously. They also require less template DNA to analyse. It is, however, more costly, so that method and means are to be considered in each specific case.

Prior to SBE testing, the amplicons were sequenced and aligned to verify that the correct targets were amplified. The PCR and the SBE PCR were carried out using the parameters listed in the Supplement below the main text and the Catalogue (**tab. S1a-d**). Primer sequences are also shown in the Supplement (**tab. S2a-b**). To avoid unspecific products, a Touchdown PCR setup was applied (Don et al. 1991). The primers were first evaluated by voluntary testing on laboratory staff, who gave anonymous samples providing information on their lactose tolerance status. All volunteers are Europeans of Dutch, French, German or Swedish origin and reported levels of high tolerance to severe intolerance to lactose. In a blind study, the tolerance status of the tested individuals was predicted correctly in each case. All possible combinations of SNPs were reported. All lactose intolerant controls featured the homozygous wild type allele in both analysed SNPs. At least 5 % no-template-controls were carried along in each PCR. In every second PCR, a positive control from the prior tests was included. Recent human DNA extract was only added after the test tubes containing ancient samples or NTCs had been properly sealed.

All sequencing products to determine the mitochondrial haplotype were replicated from at least two independent DNA extracts at least three times, using a system of overlapping amplicons. Fragments containing uncertainties were cloned as stated in Brandt et al. (2013). After successful authentication of the sequencing products, all SNP typing results were replicated at least once for each of the two independent extracts. Inconsistent results from samples lead to their discard from further analysis, dropouts are listed as such. Mitochondrial haplogroup assignments made from the HVR1 sequences and the assignments made from coding region SNPs had to be congruent. Characteristic postmortem DNA degenerations were observed in 13.9 % of amplicons (Gilbert et al. 2003b; 2003a). These polymorphisms could usually be identified and neglected, since they are neither reproducible nor consistent. All obtained data was manually verified and aligned using the DNASTAR software package version 9.04 (DNASTAR Inc., Madison, USA) and assigned to

site		Bobigny	Basel-Gasfabrik	Potten-brunn	Obern-dorf	Ossarn	Nyíregy-háza	Tisza-vasvári	total
reproduction success									
no. of sampled individuals		31	42	12	12	13	8	12	130
no. of tested individuals		25	9	12	8	13	4	3	74
no. of reproduced results		12	5	9	5	6	1	1	39
allele frequencies									
-13910C/T	homozygous	5	5	5	5	4	1	1	26
	heterozygous	0	0	0	0	0	0	0	0
-22018G/A	homozygous	10	5	6	4	6	1	0	32
	heterozygous	1	0	3	0	0	1	0	5

Tab. 1 Number of sampled and tested individuals from the La Tène period sites of Bobigny (France), Basel-Gasfabrik (Switzerland), Pottenbrunn, Oberndorf, Ossarn (Austria), Nyíregyháza and Tiszavasvári (Hungary) and allele frequencies for lactase persistence from successfully typed samples.

haplogroups using HaploGrep (Kloss-Brandstätter et al. 2011) according to the polymorphisms from HVRI and all coding region SNPs based on the mitochondrial haplogroup phylogeny of Phylotree (build 16; van Oven/Kayser 2009). Sequence polymorphisms were reported relative to the Reconstructed Sapiens Reference Sequence (RSRS) by using the FASTmtDNA 1.3 software (Behar et al. 2012).

Results

In total, 74 individuals were tested, 39 of whom (52.2 %) provided reproducible results for at least one of the two autosomal lactose tolerance polymorphisms (**tab. 1**). Reproducibility was site-dependent. From the sites of Nyíregyháza and Tiszavasvári, of a total of 20 individuals only 7 were typed for their status of two diagnostic SNPs. 2 of these 7 generated reproducible results (28.5 %) and were thus successfully typed, while typing was unsuccessful in the other 5. Basel-Gasfabrik is another site with poor aDNA preservation. Here, 9 of 42 sampled individuals seemed promising and of these 9, 5 yielded enough autosomal DNA for reproducible results from both markers (55.5 %). Bobigny and especially Pottenbrunn, Oberndorf and Ossarn returned better numbers. At Ossarn (n=13) and Pottenbrunn (n=12), the HVRI results looked promising enough to investigate all 25 individuals. This produced 9 results from Pottenbrunn (75 %) and 6 from Ossarn (46.1 %). Of the 8 Oberndorf individuals tested, 5 (62.5 %) were successfully typed, as were 12 of 25 (48 %) from Bobigny. Throughout the study, negative extraction and negative PCR controls consistently showed negative results.

Across all analysed sites, subgroups of the haplogroups H, HV, J, K, N, T, U and V were identified. The majority of these represent groups which are also present in recent Central European populations, while the frequencies differ from their modern-day occurrence as well as from site to site. Within the sites, the diversity of mitochondrial haplogroups is high. Only the individuals OF18-II and OF28-I of the Oberndorf site and the individuals PB4 and PB6/1 from Pottenbrunn share identical U5a1 and K types, respectively. Since the density of Iron Age DNA data is sparse up to the present day, it is not possible to determine how common specific haplotypes are in their timeframe. However, both these types are fairly common today.

The results of the analysis of the two diagnostic SNPs for lactose (in-)tolerance are rather one-sided. All 26 individuals providing data for the -13910 SNP show the homozygous wild type C allele. The mutant T allele was not detected. Of the 32 individuals providing results on the -22018 SNP, 4 (12.5 %) show a het-

erozygous allele, the remaining also homozygous wild types. The highest concentration of heterozygotes is detected at Pottenbrunn with 3 individuals (PB6/2, PB54, and PB1003), but neither their mitochondrial haplotypes nor their mortuary contexts provide any evidence of shared genetic kinship. Individual PB1003 rather appears to be interred according to a different ritual and is suspected to be a non-local individual, who, judging from costume elements, possibly originated from Bohemia/Moravia or the northern Alpine region (Ramsl 2002; Novotny/Ramsl/Teschler-Nicola 2012). Allele counts for each site are summed up in table 1. The results for all successfully typed individuals are listed in table 2.

DISCUSSION

The high mitochondrial diversity within the sites shows that the proportion of individuals genetically related on the maternal line is low, suggesting a highly diverse population structure. Only one pair of individuals from the Oberndorf site and one pair from the Pottenbrunn site share identical U5a1 and K types, respectively. Genetic kinship among these pairs is conceivable, but not necessarily existent, as both haplotypes are fairly common in recent European populations (0.32 % and 2.56 %, respectively: exact matches within the investigated sequencing range in 31,282 recent European datasets, as used by Brandt et al. (2013). Based on strontium and oxygen isotope analyses as well as on material culture, a number of studies were able to show that residential mobility constitutes a decisive factor in the make-up of La Tène period communities (Knipper et al. 2018; Scheeres et al. 2014; Müller-Scheeßel/Grupe/Tütken 2015; Fernández-Götz/Ralston 2017; Knipper et al. 2014). This high rate of mobility, together with a frequently short settlement duration, most likely contributed to the observed mitochondrial diversity at the sites.

The unequal reproducibility of results for individuals from different sites underscores the fact that soil or sedimentary conditions rather than the time elapsed since deposition determine the preservation of human remains and ancient DNA alike (Burger et al. 1999). The Austrian and the French sites provided a higher number of reproducible results than the sites in Switzerland and Hungary. In particular, the Basel site is adjacent to the Rhine river. The two cemeteries were located in the acidic and weathered gravel of the river's lower terrace, resulting in good drainage and a low ph-value, both associated with poor DNA preservation. Determination of the mitochondrial haplogroups of the individuals from the cemeteries proved more difficult than of those found in the settlement, as these were deposited in pits or features filled with loamy, more calcareous sediments (Pichler et al. 2013). As a consequence, all results regarding the two diagnostic SNPs for lactose (in-)tolerance come from individuals found in the settlement. Furthermore, sectors of the excavation site were chemically contaminated by industry formerly located at the site, which potentially damaged the remaining DNA even more. In contrast, the French site of Bobigny was located on calcareous sediments mixed with sand and alluvium of the former Seine terrace, which is associated with a rather good preservation of human remains. This apparently also applies to the soil conditions at the three Austrian sites.

The reproduction success of the study of more than 50 % appears to be rather satisfying, taking into account that it was conducted on autosomal aDNA. The sample size of 39 individuals from seven different sites is still small and does not represent the complete Central European population of the timeframe. Therefore, a sampling effect cannot be wholly ruled out.

In any way, the two alleles -13910T and -22018A represent a rare example for the strong recent selection and co-evolution of genes and culture (Gerbault et al. 2009; Greenfield 2010; Laland/Matthews/Feldman 2016). Different studies suggest that the appearance of the mutant alleles coincides with the introduction of farming into Europe (Bersaglieri et al. 2004; Coelho et al. 2005; Bollongino et al. 2006). There is ample archaeological, zooarchaeological and archaeometric evidence of dairying during the Neolithic and thus for the regular

site/ lab number / burial or individual number	-13910 rs4988235	-22018 rs182549	HVR RSRS	CR RSRS	Hg HVR1	sequencing range
Bobigny						
AVI73 Bobigny 73	CC	CC	16129G 16187C 16223C 16230A 16278C 16311T 16356C	2758G 3010A 7028G 10873T 11719G 12705C 14766C	H1b	16046-16406
AVI132 Bobigny 132	n. d.	CC	16129G 16187C 16189T 16223C 16230A 16278C 16298C 16311T	2758G 4580A 10873T 11719G 12705C 14766C	V	16046-16407
AVI148 Bobigny 148	n. d.	CC	16069T 16126C 16129G 16187C 16189T 16193T 16230A 16311T	2758G 10873T 12612G 12705C	J	16046-16408
AVI195 Bobigny 195	CC	CT	16051G 16129c 16187C 16223C 16230A 16278C 16311T 16318G 16362C	2758G 11467G 12705C 16051G	U2e	16046-16409
AVI308 Bobigny 308	n. d.	CC	16129G 16187C 16189T 16192T 16223C 16230A 16256T 16278C 16291T 16311T 16399G	2758G 3197C 10873T 11467G 12705C 14793G	U5a	16046-16410
AVI321 Bobigny 321	CC	CC	16126C 16129G 16187C 16189T 16223C 16230A 16278C 16294T 16296T 16304C 16311T	2758G 10873T 12705C 13368A	T2b	16046-16411
AVI410 Bobigny 410	n. d.	CC	16129G 16187C 16223C 16230A 16278C 16311T	2758G 3010A 7028G 10873T 11719G 12705C 14766C	H1	16046-16412
AVI452 Bobigny 452	CC	CC	16092C 16147a 16154C 16172C 16187C 16189T 16230A 16248T 16278C 16311T 16320T 16355T	2758G 10238C 10873T	N1a	16046-16413
AVI478B Bobigny 478B	n. d.	CC	16129G 16187C 16223C 16230A 16278C 16311T 16356C	2758G 3010A 7028G 10873T 11719G 12705C 14766C	H1b	16046-16417
AVI491 Bobigny 491	n. d.	CC	16129G 16187C 16189T 16193T 16213A 16223C 16230A 16256T 16270T 16278C 16311T 16399G	2758G 3197C 10873T 11467G 12705C 14793G	U5a1	16046-16414
AVI494 Bobigny 494	CC	n. d.	16129G 16187C 16189T 16223C 16230A 16278C 16311T	2758G 6776C 7028G 10873T 11719G 12705C 14766C	H3	16046-16415
AVI523 Bobigny 523	n. d.	CC	16129G 16187C 16189T 16209C 16223C 16230A 16278C 16311T	2758G 6776C 7028G 10873T 11719G 12705C 14766C	H3	16046-16416
Basel Gasfabrik						
BGS1 individual in well no. 1941/4.1568	CC	CC	16129G 16184a 16187C 16189T 16223C 16230A 16278C 16311T	2758G 7028G 10873T 12705C 11719G 14766C	H	15997-16408

Tab. 2 Results of all successfully typed individuals from the La Tène period sites of Bobigny (Marion/Métrot/Le Bechennec 2005; Marion/Le Bechennec/Le Forestier 2006/2007), Basel-Gasfabrik (Hecht/Niederhäuser 2011; Pichler et al. 2013), Pottenbrunn (Neugebauer 1992; Ramsl 2002), Oberndorf (Blesl/Gattringer 2004; Neugebauer/Gattringer 1984; Ramsl 2012a; 2014), Ossarn (Neugebauer 1992; Neugebauer/Gattringer 1984), Nyíregyháza (Almássy et al. 2005) and Tiszavasvári (Almássy 1997/1998). – n. d. = no data. – HVR RSRS = Hyper Variable Region of the Reconstructed Sapiens Reference Sequence. – CR = Coding Region.

site/ lab number / burial or individual number	-13910 rs4988235	-22018 rs182549	HVR RSRS	CR RSRS	Hg HVR1	sequencing range
BGS7 isolated mandible in ditch no. 2000/20.1463	CC	CC	16129G 16187C 16189T 16223C 16224C 16230A 16278C	2758G 10550G 10873T 11467G 12705C	K	15998-16408
BGS13 isolated mandible in ditch no. 2004/18.66	CC	CC	16129G 16187C 16189T 16223C 16230A 16278C 16298C	2758G 10873T 11719G 12705C 14766C	HV	15997-16408
BGS14 isolated mandible in pit no. 2004/36.63	CC	CC	16129G 16187C 16189T 16213A 16223C 16230A 16278C 16311T	2758G 4793G 7028G 10873T 11719G 12705C 14766C	H7	16001-16404
BGS15 isolated skull in pit no. 2004/37.130	CC	CC	16069T 16126C 16129G 16145A 16187C 16189T 16222T 16223C 16230A 16261T 16278C	2758G 10873T 12612G 12705C	J1b	16001-16405
Oberndorf						
OF4 burial 4	CC	CC	16129G 16187C 16189T 16192T 16223C 16230A 16256T 16270T 16278C 16291T 16311T 16399G	2758G 3197C 10873T 11467G 12705C 14793G	U5a1	16046-16418
OF18-II burial 18	CC	CC	16129G 16187C 16189T 16223C 16230A 16256T 16270T 16278C 16311T 16399G	2758G 3197C 10873T 11467G 12705C 14793G	U5a1	16046-16421
OF28-I burial 28	CC	CC	16129G 16187C 16189T 16223C 16230A 16256T 16270T 16278C 16311T 16399G	2758G 3197C 10873T 11467G 12705C 14793G	U5a1	16046-16422
OF102 burial 102	CC	CC	16129G 16187C 16189T 16223C 16230A 16256T 16270T 16278C 16311T	2758G 3197C 10873T 11467G 12705C 14793G	U5a	16046-16419
OF118 burial 118	CC	CC	16129G 16187C 16189T 16223C 16230A 16278C	2758G 3992T 7028G 10873T 11719G 12705C 14766C	H4	16046-16420
Ossarn						
ON7/1984 burial 7	CC	CC	16129G 16187C 16223C 16230A 16234T 16278C 16290T 16311T 16324C 16327a 16399G	2758G 9698C 10873T 11467G 12705C	U8	16046-16427
ON13 burial 13	CC	CC	16129G 16187C 16189T 16192T 16223C 16230A 16256T 16270T 16278C 16311T	2758G 3197C 10873T 11467G 12705C 14793G	U5a	16046-16423
ON18-II burial 18	CC	CC	16129G 16187C 16189T 16223C 16230A 16278C 16311T	2758G 3010A 7028G 10873T 11719G 12705C 14766C	H1	16046-16426

Tab. 2 (continued)

site/ lab number / burial or individual number	-13910 rs4988235	-22018 rs182549	HVR RSRS	CR RSRS	Hg HVR1	sequencing range
ON19 burial 19	CC	CC	16126C 16129G 16187C 16189T 16223C 16230A 16278C 16292T 16294T 16311T	2758G 10873T 12705C 13368A	T2	16046-16424
ON22 burial 22	CC	CC	16129G 16187C 16189T 16223C 16230A 16278C 16311T	2758G 3010A 7028G 10873T 11719G 12705C 14766C	H1	16046-16426
ON23 burial 23	n. d.	CC	16129G 16187C 16189T 16223C 16230A 16278C 16298C	n.D.	H	16046-16425
Pottenbrunn						
PB3 burial 3	CC	CC	16129G 16187C 16189T 16223C 16230A 16278C 16292T 16311T	2758G 3010A 7028G 10873T 11719G 12705C 14766C	H1	16046-16428
PB4 burial 4	CC	CC	16126C 16129G 16187C 16189T 16223C 16230A 16278C 16298C 16311T	2758G 4580A 10873T 11719G 12705C 14766C	V	16046-16429
PB5/1 burial 5	n. d.	CC	16129G 16187C 16189T 16223C 16224C 16230A 16278C	2758G 10550G 10873T 11467G 12705C	K	16046-16430
PB5/2 burial 5	CC	CC	16126C 16129G 16163G 16186T 16187C 16223C 16230A 16278C 16294T 16311T 16325C	2758G 10873T 12705C 13368A	T1a	16046-16431
PB6/1 burial 6	CC	CC	16129G 16187C 16189T 16223C 16224C 16230A 16278C	2758G 10550G 10873T 11467G 12705C	K	16046-16433
PB6/2 burial 6	n. d.	CT	16129G 16187C 16189T 16223C 16230A 16278C 16311T	2758G 10873T 11467G 12705C	U8	16046-16434
PB54 burial 54	CC	CT	16129G 16187C 16189T 16223C 16230A 16256T 16278C 16311T 16352C	2758G 7028G 7645C 10873T 11719G 12705C 14766C	H14	16046-16432
PB99 burial 99	n. d.	CC	16126C 16129G 16187C 16189T 16223C 16230A 16278C 16294T 16296T 16311T 16354T 16365T	2758G 10873T 12705C 13368A	T	16046-16435
PB1003 burial 1003	n. d.	CT	16051G 16129c 16187C 16223C 16230A 16278C 16311T 16325C 16362C	2758G 11467G 10873T 12705C 16051G	U2	16046-16436
Nyíregyháza						
NH*	CC	CC	16069T 16126C 16129G 16187C 16189T 16193T 16223C 16230A 16278C 16311T	2758G 10873T 12612G 12705C	Jb2	16024-16408
Tiszavasvári						
TV3 Tiszavasvári 3	CC	n. d.	16129G 16187C 16189T 16223C 16230A 16278C	2758G 10873T 11719G 12705C 14766C	HV	15997-16408

Tab. 2 (continued)

use of milk by former European communities (Salque et al. 2013; Spangenberg et al. 2008; Greenfield 2010; Marciniak 2011). A growing number of molecular studies focussing on the mutant alleles that enable grown-ups to digest milk sugar have, however, succeeded in identifying only low proportions of individuals carrying the lactose tolerance genes during the Neolithic and the Bronze Age (Mathieson et al. 2015; Malmström et al. 2009; Allentoft et al. 2015; Burger et al. 2020; Olalde et al. 2018). Several studies have, however, revealed increased numbers of lactose-tolerant individuals in the Middle Ages (Krüttli et al. 2014; Witas et al. 2015; Margaryan et al. 2020). From these results, it was clear that the spread of lactase persistence must have occurred at some time during the roughly three millennia between the Bronze Age and medieval times. Our investigation of seven La Tène period sites shows that the mutant variant is still uncommon in 2,300-2,000 BP. None of the 39 successfully typed individuals shows the mutant allele in -13910, and only 5 individuals (13 %) are heterozygous at -22018. This halves the timeframe for the spread of the prevalence of lactase persistence in Europe to approximately 1.3 millennia: somewhere between 2,000 BP and the year 1200 CE.

In view of the rapidity with which this process must thus have proceeded, it was conceivably linked to a major population shift, like the one accompanying the Migration Period, or in the wake of some Pan-European cataclysmic event. One such event is recorded, for instance, in the plague epidemic that swept Europe in 1346-1353 CE, killing at least one-third of the overall population (Alfani/Murphy 2017). Whether this or some other change in the composition of European populations is also responsible for the sudden rise in lactase persistence alleles must be a topic of future research.

Yet even while the majority of the La Tène period population could not digest fresh milk, there is ample evidence for dairying throughout prehistory. Even though domestic animals were kept for multiple purposes in the past rather than the specialised milk or meat breeds of the present, zooarchaeological data clearly demonstrates the existence of dairy herds in the Late Iron Age (Schibler/Stopp/Studer 1999). Artefactual evidence (e. g. sieve vessels) and organic residue analysis suggests that the milk of cows, sheep and goats frequently went into making cheese or other dairy products. The presence of dairy farming and consumption of milk and milk products in the La Tène Iron Age are, of course, not mutually exclusive. Processing milk into cheese not only extends its »shelf life«, but it also preserves its nutritional value while reducing lactose content, with mature cheese being practically lactose-free. The production of cheese during the Iron Age was clearly demonstrated by organic residue analysis for Scotland and Switzerland (Craig et al. 2000; Carrer et al. 2016). While yoghurt contains more lactose than cheese, this steadily decreases due to it being digested by the living bacterial cultures while these also supply the gut with lactase enzymes (Marette/Picard-Deland 2014).

As a further consideration, the amount of consumed lactose can be taken into account, as gastrointestinal symptoms are partly dose-dependent (Wahlqvist 2015). As evidence suggests that most of the 1.5-2.5 l of cows' milk available per day per animal (Ebersbach 2002; Gross/Jacomet/Schibler 1990; Ebersbach 2010) was being processed, little fresh milk was actually available for consumption, thus reducing the need for possessing the mutant alleles. Moreover, unlike modern breeds, prehistoric cattle was probably not reproductively active throughout the year, thus setting seasonal limitations on the availability of milk as well as increasing the desirability of producing storable dairy products to supplement diets over extended parts of the year (Balasse et al. 2021). Iron Age populations, therefore, could still benefit from the positive nutritional effects of dairy consumption.

CONCLUSION

Even though the antiquity of the mutant alleles has been estimated from genetic data, it is not entirely clear yet when and why the frequencies of the genetic trait that enables humans to consume lactose

throughout their lifetime start rising to recent numbers. The evolution of the trait seems linked to the introduction of farming in Europe as well as other parts of the world. It apparently co-evolved as a selective advantage, even if Asian or African pastoralists have not acquired lactase persistence to the same degree as European populations. Lactase persistence thus represents a rare yet no less remarkable example of culture-driven genetic evolution. Previous studies found that alleles for lactase persistence were absent in almost all Neolithic Europeans but present in many medieval ones. Our study on individuals from seven La Tène period sites from Central Europe shows that the trait was present in heterozygous expression and low frequency only even during the Iron Age. The time window of when lactase persistence allele frequencies rose has thus unexpectedly narrowed to the 1300-year interval preceding the modern era. As dairying has been practised since the Neolithic, other factors must have promoted the recent rapid spread of the mutation. The shortness of the time in which such a dramatic shift occurred is further evidence of how deeply the interplay between cultural practices and historic developments affected the genetic makeup of human populations.

CATALOGUE OF SITES

The Sites of Basel, Switzerland, and Bobigny, France

Basel-Gasfabrik (Ct. Basel-Stadt/CH)

The Basel-Gasfabrik site, located in an industrial area of the modern city, comprises a settlement dating to the Middle and Late La Tène period (LT C2-D1; ca. 170/150/100 BCE) and two cemeteries. The unfortified, proto-urban settlement has been under investigation since 1911. It covered an area of about 150,000 m^2 that was purposefully subdivided into lots containing houses with associated yards, garden plots, animal pens or work areas and specialised crafts zones. There were also numerous pits of varying functions and sizes, large grain silos and deep wells (Hecht/Niederhäuser 2011). After serving their primary functions, these pits etc. were intentionally and rapidly filled with sediments containing various types of (settlement) waste (Brönnimann/Rissanen 2018). Complete or partial human skeletons were encountered in 12 of these pits and wells, while newborns and a large number of isolated human bones come from a variety of archaeological features (Pichler et al. 2013).

Although settlement and cemeteries alike are much affected by modern building activities, over 200 inhumations and 2 cremations were recovered from the settlement's two cemeteries A and B. Overall, few burials had grave goods like fibulas, bracelets, pendants, iron tools, and ceramic; weapons are lacking entirely. Children were more often furnished with grave goods than adults (Rissanen et al. 2013). While the demographic structure of the individuals from the cemeteries seemingly include representative sections of the former population, the human remains from the settlement appear skewed with regard to both age (with too few juveniles) and sex (with males outnumbering females; Knipper et al. 2017). In spite of these apparent differences, osteologic and bioarchaeometric analyses uncovered no obvious dissimilarities between the individuals from the cemeteries and the settlement regarding both diets and regions of origin or patterns of mobility respectively (Knipper et al. 2017; 2018). At Basel-Gasfabrik, only individuals from the settlement were successfully typed. These had been deposited in well 114 (BGS 1), in two ditches (BGS 7, BGS 13), in feature FK 103917 in an unnumbered pit (BGS 14) and in pit 493 (BGS 15).

Bobigny »Hôpital Avicenne« (dép. Seine-Saint-Denis/F)

The cemetery of Bobigny »Hôpital Avicenne« is situated on a former terrace of the Seine valley, some kilometres north of Paris (Marion/Métrot/Le Bechennec 2005; Marion/Le Bechennec/Le Forestier 2006/2007). The upper layers, in which the graves were dug, are geologically very heterogeneous and varied: lime sludge mixed with sand and alluvium from older terraces. These sediments generally provide good conditions for bone preservation, but may vary from one grave to another. The cemetery was in use for a little over a century, from about 2,300 BP (LT B2) to 2,200 BP (LT C1/C2 transition). It is composed of more than 500 funerary units, including the unexcavated parts of the cemetery; it can therefore be expected to comprise more than 700 graves. Inhumations predominate, complemented by about 20 cremations. The density of the graves is exceptional in Europe for the 3rd century BCE: nearly two-thirds of the graves

show stratigraphic interrelations – graves being superimposed, or graves cutting the pits of other graves. The population seems to be, following preliminary observations, of good health and the large number of juveniles indicate a natural population, in which only the perinatal individuals are missing (Le Forestier 2009). However, the relative lack of children too is rather typical for cemeteries of the Iron Age.

The overwhelming number of graves have only a small number of grave goods. Three-quarters of the graves have no grave goods or are only furnished with brooches. A few have metal objects consisting of belts or jewellery, e. g., neck rings (torques), bracelets or finger rings of iron, bronze or lignite; most of the individuals with grave goods are women or children. Additionally, a few men can be distinguished by their warrior's equipment (sword, lance, shield). All these observations indicate that the burials at Bobigny »Hôpital Avicenne« are among the few sites where a representative segment of a larger population including also the poorer classes was interred, to which some privileged individuals were added. These observations are in contrast with other cemeteries of the region and of the same period, which show a rather restricted range of burials (Marion 2012). These cemeteries, like Roissy-en-France or Le Plessis-Gassot (both dép. Val d'Oise/F; Olivier 2001; Lejars 2005; Ginoux 2009), are composed of small numbers of graves, dominated by warriors, and where the rare aristocratic funerals are equipped with chariots and objects of art.

The site of Bobigny is a key site of the Iron Age not only for northern France but also for Western Europe in general: nowhere else is there such a large number of graves with such good bone preservation. The composition of graves, which seems representative of a complete living population, make it one of the best cases for population and DNA studies.

The Sites of Pottenbrunn, Oberndorf and Ossarn, Austria

Individuals from three sites (Pottenbrunn, Oberndorf in der Ebene and Ossarn) situated in the Lower Traisen valley located between Krems and St. Pölten (Lower Austria) were examined. The area was densely populated during the La Tène period (Ramsl 2012b).

Pottenbrunn, Flur Steinfeld (distr. St. Pölten/A)

The necropolis of Pottenbrunn is located at the southwestern outskirts of the local community of Pottenbrunn, within the urban area of St. Pölten. It is situated on the right bank of the Traisen river on a slight gravel bank. Adding to the first discoveries in 1930, 12 cremations and 31 inhumations were discovered in 1981/1982 by the Federal Antiquities and Monuments Office (Neugebauer 1992, 48. 52). This cemetery, although numerically small, harbours burials of the social elite of the time, who were buried with grave goods such as weapons, jewellery of precious metals and even surgical instruments. The analysis of the extraordinary material was realised in a project funded by the Austrian Science Fund (FWF) Project P12531 (Ramsl 2002).

Among the 31 investigated inhumations are 7 juveniles below the age of 20 (2 infans I, 3 infans II, 2 juveniles) and 24 adult individuals (13 adultus, 6 maturus, 3 senilis and 2 of undetermined age). 12 of the adults were female, 10 male and 2 of undetermined sex. Inflammations like stomatitis (66.6 %), sinusitis frontalis (73.3 %) and unspecific stress markers like porotic hyperostosis (32 %) and cribra orbitalia (19 %) could be observed. Evidence of intracranial inflammatory changes (meningitis) was diagnosed in 19.2 % of the individuals (Gerold 2002).

Oberndorf in der Ebene, motorway exit Herzogenburg-South (distr. St. Pölten/A)

The cemetery of Oberndorf in der Ebene, located at the motorway exit south of Herzogenburg, was excavated in the years 1982 (Neugebauer/Gattringer 1984, 66-67 figs 17-20) and 2004 (Blesl/Gattringer 2004, 29 fig. 25) by the Department of Historic Preservation (now Department of Archaeology) of the Federal Antiquities and Monuments Office. 6 cremations and 34 inhumations were uncovered and analysed by P. C. Ramsl within the FWF-Project P23517-G19 (Ramsl 2012a; in print). The site dates from the Ha D3 to the LT A2 periods. Square- as well as round-shaped grave enclosures were observed. Grave 37 of the excavation in 2004 is of particular interest. It contained a woman (sex determined anthropologically) with weapons and multifunctional tools made of antler (Ramsl 2014, pls 2-3).

18 individuals of the Oberndorf cemetery (41 % of the population) died before reaching adulthood and 25 (58 %) were older than 20 years. The age-specific investigation showed 5 infans I, 7 infans II, 4 juveniles, 12 adult and 9 mature individuals. 4 individuals can only be assessed as full-grown. Among the over-20-year-olds are 8 females, 13 males and 4 individuals of undetermined sex. Regarding pathological features, 87.7 % of the assessable individuals show changes of the palate caused by inflammation (stomatitis), 14.3 % porotic hyperostosis and 16.7 % cribra orbitalia. Sinusitis frontalis was observed in 15 % of the individuals, sinusitis maxillaris in 10 %, and meningitic inflammatory changes on the inner cranium were diagnosed in 27.6 % of the assessable individuals (Novotny/Ramsl/Teschler-Nicola 2012).

Ossarn, Flur Langwiesfeld (distr. St. Pölten/A)
For the cemetery of Ossarn, Flur Langwiesfeld, some burials dating to the Early Bronze Age and La Tène Iron Age have been discovered during excavations in 1966 and 1969. An extensive excavation took place in 1984 (Neugebauer/Gattringer 1984, 97. 100 figs 21-24). However, this did not cover the entire area as only segments of the original extent of the cemetery were investigated. The graves date from the Ha D3 to the LT A2 periods (Ramsl in print). Grave 17 (1984) is of particular interest. It contained the skeleton of a 15-year-old girl with a figural bronze fibula in the shape of a sphinx, a belt buckle with elaborate incisions and plastically decorated hooks as well as a torqued necklace. This characteristically shaped necklace is commonly found in the Champagne region of France and represents a unique find in eastern Austria (Neugebauer 1992, fig. 12).
The analysis of the age at death shows eight individuals who died before reaching adulthood, while 22 died after the age of 20. An age-specific examination identified 3 as infans I, 5 as juveniles, 14 as adult and 8 as mature. Among the over-20-year-olds are 9 females, 10 males and 3 individuals of undetermined sex. Regarding pathological features, porotic changes of the palate (stomatitis) were identified in 66.7 % of the assessable individuals were affected, while porotic alterations of the calvarium (porotic hyperostosis) were found in 46.2 %. Sinusitis frontalis was diagnosed in 18.2 %, sinusitis maxillaris in 22.3 %, and meningitic lesions were observed in 35.5 % of the assessable individuals (Novotny/Ramsl/Teschler-Nicola 2012).

The Sites of Tiszavasvári and Nyíregyháza, Hungary

Tiszavasvári, Városföldje, Jegyző-tag (Kom. Szabolcs-Szatmár-Bereg/H)
In 1983-1989, 35 graves were excavated by E. Istvánovits and the Jósa András Museum near Tiszavasvári in the sand quarry of Jegyző-tag. The graves belong to the following culture periods: 2 cremation burials from the Nyírség culture (Bronze Age), 16 graves of a biritual cemetery from the Late Iron Age (LT C period), 8 graves from the Sarmatian period (1,800-1,700 BP), 2 from the Hun period (1,500 BP), and further 7 graves that were not datable.
The Celtic cemetery is not excavated completely, the related La Tène period settlement has not yet been found. The graves were dated to the beginning of the LT C period (late 3rd century BCE), based on the flattened, long-bodied iron fibulas and other tied-foot bronze fibulas or fibulas with a big knob on their foot. Anklets of five to six pieces, and eight-formed belt chains were also typical in the cemetery. Anthropological remains were analysed by L. Szathmáry (Almássy 1997/1998; Szathmáry 1984-1986).

Nyíregyháza-Császárszállás, Vasútállomástól Nyugatra (Butyka), site 137 (Kom. Szabolcs-Szatmár-Bereg/H)
In 2005, a rescue excavation led by K. Almássy took place along road no. 4 that was connected to the M5 motorway construction. On a total of 2.77 ha, beside a Celtic cemetery, a Roman period settlement and a small cemetery, a Late Bronze Age settlement and an Árpád age settlement were uncovered. The 43 graves from the Celtic period were found in the southern and eastern part of a reused prehistoric kurgan. The biritual Celtic cemetery was dated to the LT C1 period based on glass bracelets, bronze belt chains, anklets, and *filettato* fibulas. The archaeological finds are curated at the Jósa András Museum (Nyíregyháza). The La Tène period cemetery is unpublished, only a preliminary report is available (Almássy et al. 2005).

SUPPLEMENT

mix	volume
	per sample [µl]
buffer	2,4
$MgCL_2$ (2mM)	4
dNTP (200µM]	1
primer FWD	3,8
primer REV	3,8
BSA	1
Taq polymerase (2.5 U)	0,25
ddH_2O (2nM)	6,75
target DNA extract	6
total	29

Tab. S1a Volumes for PCR.

programme	DigePlex55	time
initial denaturation	94 °C	11 min
1. touchdown	-0,5 °C steps	
denaturation	94 °C	30 sec
annealing	64 °C-55 °C	30 sec
elongation	72 °C	30 sec
steps	18	
2. generic		
denaturate	94 °C	30 sec
annealing	55 °C	30 sec
elongation	72 °C	30 sec
adenylylation	60 °C	5 min
control	block	
cycles	30	

Tab. S1b Cycling parameters for PCR.

mix	volume
	per sample [µl]
RR mix	2,5
primer	0,74
ddH_2O	0,76
PCR product	1
total	6

Tab. S1c PCR parameters for SBE PCR.

programme	SBE	time
denaturation	96 °C	10 sec
annealing	55 °C	5 sec
elongation	60 °C	30 sec
	4 °C	∞
control	block	
cycles	35	
		rapid ramp

Tab. S1d Cycling parameters for SBE PCR.

SNP	orien-tation	wild type forward	mutant forward	PCR primer sequence 5'->3'	primer length [bp]	product length [bp]	concen-tration [µM]
-13910	reverse	C	T	CGCTGGCAATACAGATAAGATA	22		0,12
rs4988235				AGGGCTCAAAGAACAATCTAAA	22	105	0,12
-22018	reverse	G	A	AAAGTACTGGGACAAAGGTGTGA	23		0,12
rs182549				CTATCAGTAAAGGCCTATAAGTTACC	26	97	0,12

Tab. S2a Specifics of the used PCR primers to amplify the relevant DNA fragments, containing the SNPs as listed in the left column.

SNP	PCR primer sequence 5'->3'	primer length [bp]	product length [bp]	concentration [µM]
-13910	TTCCTTTGAGGCCAGGG	17	28	0,13
rs4988235				
-22018	4CT+CAGCATTCTCAGCTGGGC	18+8	19+8	0,08
rs182549				

Tab. S2b Specifics of the used SBE PCR primers to detect the relevant diagnostic SNPs for lactose (in-)tolerance.

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Zusammenfassung / Summary / Résumé

Fehlende Laktasepersistenz im Mitteleuropa der Jüngeren Eisenzeit
Die Fähigkeit, auch nach der Säuglingszeit Milchzucker zu verdauen, ist ein relativ neues Merkmal beim Menschen. Das errechnete Alter der verantwortlichen Mutation stimmt weitgehend mit der Einführung der Milchwirtschaft überein. Moderne europäische Bevölkerungen zeigen ein Gefälle für die Laktosetoleranz, mit hohen Werten im Norden und niedrigeren im Süden des Kontinents. Die Laktasepersistenz soll als selektiver Vorteil zusammen mit der Landwirtschaft bzw. Viehhaltung entstanden sein. Allerdings fehlen bislang paläogenetische Daten prähistorischer Individuen dafür, dass die Ausbreitung der Mutation für Laktasepersistenz bereits vor der römischen Epoche eintrat, während sie im Mittelalter ständig zunahm. Im Gegensatz dazu reichen die Belege für eine Milchverarbeitung bis zur Einführung der Landwirtschaft im Neolithikum zurück. In der vorliegenden Studie wird die Laktasepersistenz während der Latènezeit der europäischen Eisenzeit untersucht. Dazu wurde der Genotyp von 39 Individuen aus Österreich, Frankreich, Ungarn und der Schweiz erfolgreich auf die zwei mit Laktosetoleranz assoziierten SNPs 13910C/T und 22018G/A analysiert. Bei keinem der Individuen fand sich eine homozygote Variante eines der beiden SNPs, dagegen tragen vier Individuen heterozygot das Allel 22018G/A. Dies deutet darauf hin, dass während der Eisenzeit verarbeitete Milchprodukte wie Käse oder Joghurt noch immer die Hauptquelle milchbasierter Nährstoffe darstellten, während Frischmilch in den hier untersuchten Regionen wohl nur eine untergeordnete Rolle spielte. Die bevölkerungsübergreifende Verbreitung der Laktosetoleranz fand demnach erst nach der Eisenzeit statt.

Missing Lactase Persistence in Late Iron Age Central Europe
Being able to digest milk sugar beyond the age of weaning is a rather new trait in humans. The calculated age of the responsible mutations largely coincides with the introduction of dairy farming. Recent European populations exhibit a gradient of high levels of lactose tolerance in the north and lower numbers in the south. Lactase persistence is believed to have co-evolved with farming or livestock keeping as a selective advantage. Palaeogenetic data of prehistoric individuals, however, have so far not provided any clear evidence that the spread of the lactase persistence mutation predates the Roman period, while persistence increases throughout the Middle Ages. In contrast, evidence of dairy processing reaches back to the introduction of farming in the Neolithic. In this paper, we investigate lactase persistence in the La Tène period of the European Iron Age. 39 individuals from Austria, France, Hungary and Switzerland have been successfully genotyped for the two single nucleotide polymorphisms (SNPs) 13910C/T and 22018G/A, which are associated with lactose tolerance. None of those individuals carries the homozygous variant of either of the two SNPs, while four individuals are heterozygous at 22018G/A. This implies that during the Iron Age processed dairy products like cheese and yoghurt still represented the common supply of milk-derived nutrients while fresh milk played only a minor role in the regions studied here. The population-wide spread of the lactose tolerance trait in Europe therefore clearly post-dates the Iron Age.

Pas de persistance de la lactase en Europe centrale au second Âge du Fer
La capacité de digérer le lactose, même après la période d'allaitement, est une propriété relativement récente chez les humains. L'âge calculé pour la mutation déterminante correspond en grande partie à l'introduction de l'économie laitière. Les populations européennes actuelles présentent un gradient dans leur tolérance au lactose, avec des valeurs élevées dans le Nord et faibles dans le Sud du continent. La persistance de la lactase serait apparue comme avantage sélectif avec l'agriculture et l'élevage. Pourtant, nous ne disposons toujours pas de données paléogénétiques d'individus préhistoriques établissant que la mutation de la persistance de la lactase se serait diffusée déjà avant l'époque romaine, alors qu'elle ne cesse de croître au Moyen Âge. Par contre, les preuves d'une transformation laitière remontent à l'introduction de l'agriculture au Néolithique. Cette étude traite de la persistance de la lactase durant la période La Tène de l'Âge du Fer européen. On a analysé avec succès le génotype de 39 individus originaires de l'Autriche, de la France, de l'Hongrie et de la Suisse quant à la présence de deux PNS 13910C/T et 22018G/A associés à la tolérance au lactose. Aucun de ces individus ne présentait une variante homozygote de l'un des deux PNS, tandis que quatre individus se révèlent hétérozygotes pour 22018G/A. Ceci semble indiquer que des produits laitiers transformés, comme le fromage ou le yoghourt, représentaient encore l'essentiel des aliments à base de lait durant l'Âge du Fer, alors que le lait frais ne jouait qu'un faible rôle dans les régions étudiées. La diffusion de la tolérance au lactose à travers les populations s'est donc déroulée après l'Âge du Fer.

Schlüsselwörter / Keywords / Mots-clés

Europa / Jüngere Eisenzeit / aDNA / Laktoseintoleranz / Laktasepersistenz / Paläogenetik
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