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RETHINKING BARBARIAN INVASIONS THROUGH GENOMIC HISTORY

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Few topics in European history are as controversial and disputed as the barbarian migrations into the Roman world at the end of Antiquity. What was the nature of these barbarian peoples that appear in the written sources of the period? Were they discrete ethnic groups whose arrival in the Empire was the end of long migrations of unified social and cultural groups or were they heterogeneous coalitions formed in the recent past? What relationship can be determined between the names of peoples in written sources and different material cultures found by archaeologists? How large and significant were these migrations? Did they replace local populations, simply dominate them, or rapidly merge with them? An international and interdisciplinary team is attempting to employ new approaches developed in genomics to help resolve these questions.[2]

Given the paucity of written evidence and the ambiguity of archaeological evidence traditionally used to answer the above questions, scholars are increasingly teaming up with geneticists to attempt to exploit the genealogical patterns contained in the genomes of contemporary and ancient populations in order to estimate the demographic impact of these events. Many of these projects have used modern DNA collected from contemporary inhabitants and attempted to project backward in time the population structures of the past. In regions of significant population flux with potentially many distinct migration or colonization events prior to modern times however, such approaches are very problematic. A team of Hungarian, Czech, Italian, German, Austrian, British, and American historians, geneticists, and archaeologists have developed an innovative approach to circumvent this issue. We will study ancient DNA extracted from over 1,100 graves identified as characteristically Longobard or Lombards, a people who presumably emigrated from the region between present-day Vienna and Budapest in the 560s into Italy where they established the Lombard kingdom that existed until its destruction in 774, as a first step toward a deeper understanding of the demographics underlying migration period Europe.

Our project attempts to decouple identity as defined culturally or politically, from population demographics. It seeks to understand shifts in populations between the frontiers and the heartlands of the Roman Empire without essentializing or reducing the complexity of human relations to a single genetic identity such as a haplogroup let alone a race or people, and without relying on written accounts of migration by medieval authors. It also seeks to integrate genomic research into careful cultural archaeology, physical anthropology, and historical studies.

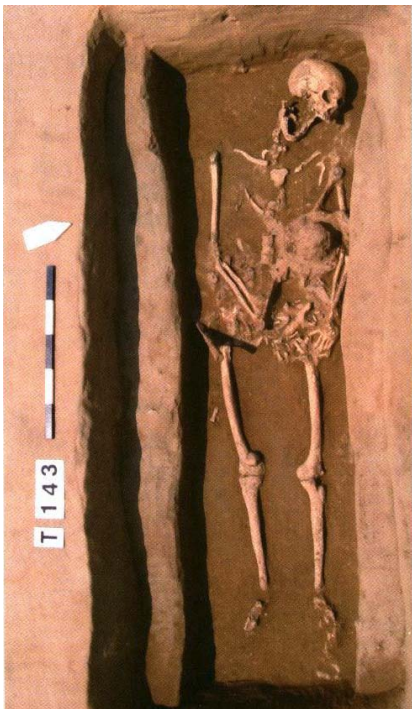

Fig. 1: Collegno (Torino), Longobard cemetery: grave of a man with weaponry and a glass chalice (after: Luisella Pejrani Baricco: Il Piemonte tra Ostrogoti e Longobardi. In: I Longobardi. Dalla caduta dell'impero all'alba dell'Italia, catalogo della mostra (Torino 2007), ed. Brogiolo, Gian Pietro – Chavarria Arnau, Alexandra. Milano: Silvana Editoriale Spa, Cinisello Balsamo, 2007, 264, Fig. 6.)

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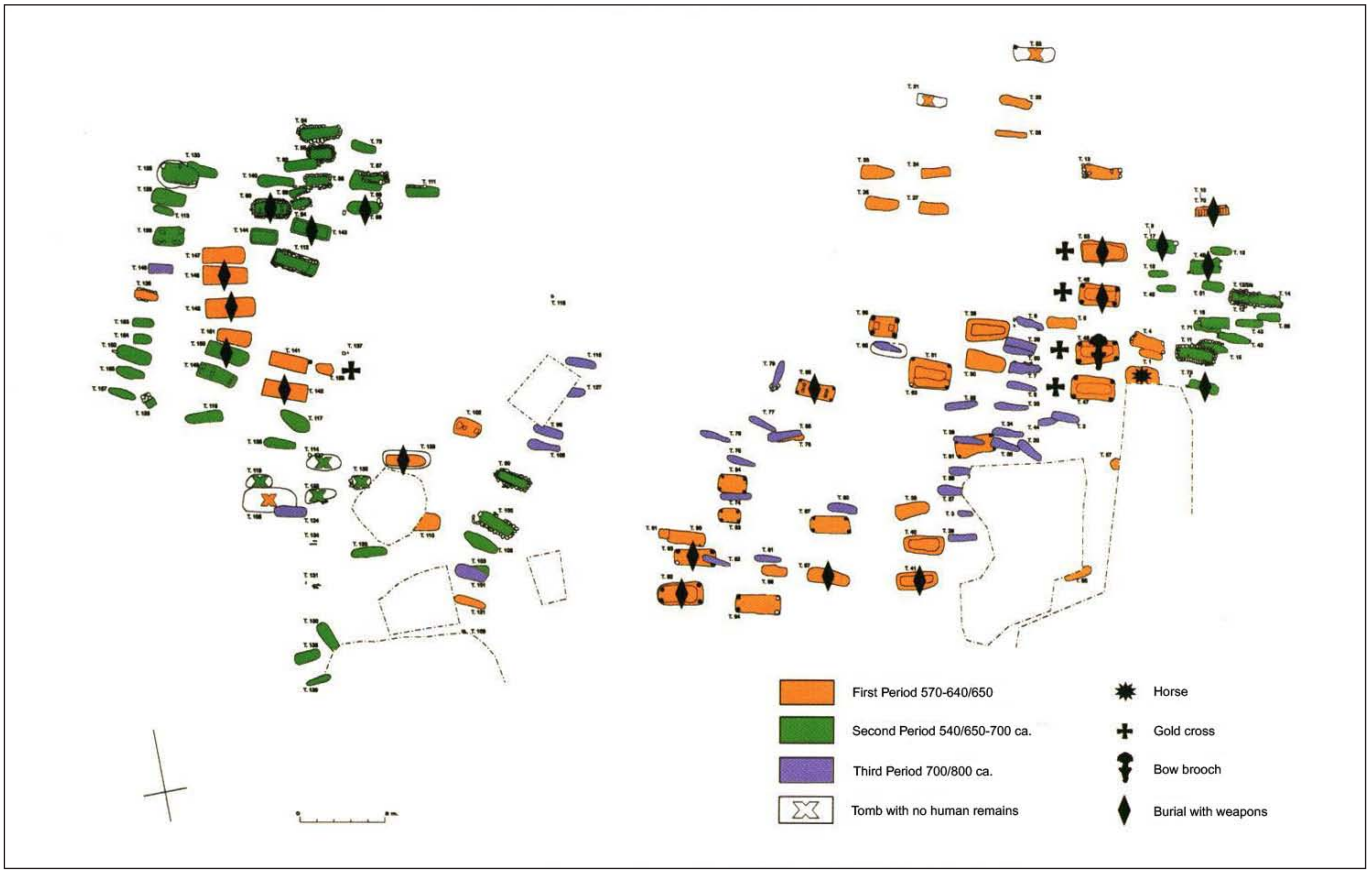

Fig. 2: Collegno (Torino): map of the Longobard cemetery at the end of the excavation (2006) (after: Luisella Pejrani Baricco: Il Piemonte tra Ostrogoti e Longobardi. In: I Longobardi. Dalla caduta dell'impero all'alba dell'Italia, catalogo della mostra (Torino 2007), ed. Brogiolo, Gian Pietro – Chavarria Arnau, Alexandra. Milano: Silvana Editoriale Spa, Cinisello Balsamo, 2007, 263, Fig. 5.)

We plan to examine many sites from the Czech Republic, Austria, Hungary, and Italy, and as such the total cost of the project will be considerable. Therefore we are currently conducting a much smaller pilot project to test the validity of our approach. For this project we have selected two cemeteries that appear characteristically Longobard, Szólád in Hungary and Collegno in Italy.[3] These have the advantage of having been recently and carefully excavated, we have detailed information on each tomb, and we have been able to obtain stable isotopic data from both sites that provide additional information on the short-term population demography and lifestyle. Currently we are in the process of extracting and sequencing ancient DNA from twenty samples from each site in the laboratory of the Department of Evolutionary Biology at the University of Florence and in the Institute of Archaeological Science in Tübingen. We will also sequence samples from near-by closely contemporary sites that have different cultural characteristics and are thus considered non-Longobard.

As a first step we began by sequencing the mtDNA from our samples. However mtDNA only provides information about a single genealogy of mothers. We want to know much more about the ancestry of our samples and thus we are proceeding to the next step, which is sequencing the recombinant autosomal DNA in our samples in order to obtain a much more fine-grained and intricate insight into the genealogical

[3] On Szólád, see Uta von Freeden – Tivadar Vida: Ausgrabung des langobardenzeitlichen Gräberfeldes von Szólád Komitat Somogy, Ungarn. Vorbericht und Überblick über langobardenzeitliche Besiedlung am Plattensee. *Germania: Anzeiger der Römisch-Germanischen Kommission des Deutschen Archäologischen Instituts* 85/2 (2007), 359–384. On Collegno, see Caterina Giostra: La necropoli di Collegno. In: *I Longobardi. Dalla caduta dell'impero all'alba dell'Italia, catalogo della mostra*, ed. Gian Pietro Brogiolo – Alexandra Chavarria Arnau (Milano: Silvana Editoriale Spa, Cinisello Balsamo, 2007), 268–273.

relationships between our populations. Until about five years ago, obtaining such data from ancient specimens would have been virtually impossible, but thanks to rapid advances in what is often termed 2nd Generation Sequencing, we have a reasonable expectation of obtaining meaningful nuclear DNA from these samples

Even for these forty samples, our budget, which comes from the German Humboldt Foundation and the Swedish Riksbankens Jubieleumfond, does not allow for whole genome sequencing of all samples. Thus we will concentrate on certain parts of the genome that we know from other studies are likely to provide us with information about populations and their inter-relationships. First we will interrogate roughly ca. 350,000 single nucleotide sites (SNPs) in each individual, allowing us to infer subtle differences in genome-wide allele frequencies and thus discriminate between individuals from different regions and even villages within Europe and accurately infer kinship within individual cemeteries to the level of at least 2nd cousins.

Second, we will target 5,000 independent 1kb regions of contiguous sequence from putatively neutral (i.e. not affected by natural selection) regions of the genome. These will allow us to apply population genetic theory to test competing models that describe the potential demographic histories of the region.

Finally, we will also sequence candidate sites in genes that have relevance to phenotypic variation. These will primarily be loci thought to be involved in disease susceptibility and resistant such as bubonic plague and will be of interest to a wide number of researchers and historians.

The questions we will be seeking to answer do not include identifying Longobards and separating them from non-Longobards. To attempt to do so would be to essentialize genetically what is rather a cultural category. However we can ask a variety of questions about population structures, relationships, and movements that can contribute to a greater understanding of European demographics in the sixth century. We would like to know how the cemeteries designated by archaeologists as "Longobard" and "non-Longobard" are structured. Are locations in cemeteries and quantity and quality of grave goods evidence of kinship ties, or might they indicate, as has been suggested by many archaeologists, evidence of age or social status? What is the biological relationship between individuals buried in neighboring cemeteries or cemeteries that are chronologically successive but that archaeologists see as representing distinct cultural traditions? Are these populations significantly distinct biological groups or has there been substantial gene flow between groups even if their material culture suggests cultural differentiation? Moreover, if there

Fig. 3: Szólád: gilded bronze buckle and two shield-shaped applique on the belt, S-shaped gielded silver brooch with almandin inlay (after Uta von Freeden, Daniel Peters, Tivadar Vida)

Fig. 4: Szólád: burnished jug and handmade vessel (after Uta von Freeden, Daniel Peters, Tivadar Vida)

was gene flow between these groups, is there evidence via mtDNA, X chromosome and Y-chromosomes of this process being sex-biased, with, for example, men constituting a tighter genealogical network while women are more heterogeneous? Is there genetic continuity between Pannonian and Italian cemeteries that archaeologists see as Longobard?

In order to attempt to answer these questions our analysis will focus both on uniparental markers, that is mtDNA and Y-Chromosomes, which track only individual lines of genetic inheritance (e.g. matriline and patriline), as well as on autosomal DNA, which preserves the DNA of a network of many ancestors. Some of this analysis is what is termed "unsupervised," meaning that we examine the data for patterns that may help generate hypotheses. Given this information, the next step is to perform supervised, or quantitative model-based analysis of our data in which we can test many models or hypotheses against each other to see which ones best fit our real data (and estimate any associated parameters), as in our preliminary examination of possible continuities between our Longobard mtDNA data and that of contemporary sites in the Piedmont. Our best models can then be compared with existing models previously proposed by cultural archaeologists, physical anthropologists, and historians, with the ultimate aim of finding a model or set of models that can accommodate all of the data from all disciplines.

We will avoid asking such questions as whether there is a specific genetic profile for Longobards or even if the cemeteries we are examining are in some meaningful sense Longobard at all. We anticipate producing a complex image of a deeply asymmetric, hybrid, unstable, and complex society uniting Pannonia and Italy in the so-called Migration Age. We can imagine gene flow, like transcultural flow, moving in both directions (though perhaps at different rates) rather than a simple migration from north to south, and we can imagine finding significant subgroups obscured by the cultural archaeological record. We can also imagine a world in which men and women have very different migration dynamics and kinship histories. Our hope is that genomic research, when properly contextualized with data from archaeology and history, provide us with new evidence for ultimately redirecting how we think about the complexity of Europe's population at the end of Antiquity and thus, perhaps, how we understand complexity in our own age.

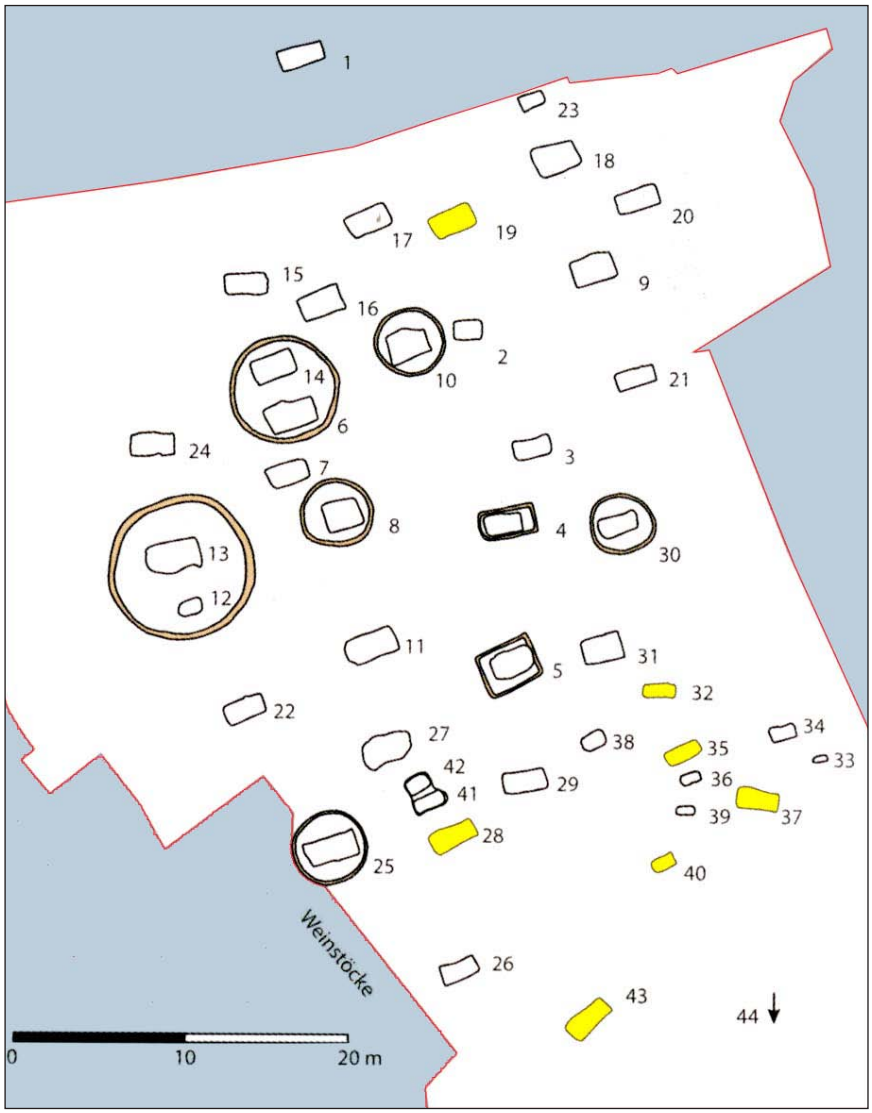

Fig. 5: Map of the cemetery at Szólád (after Uta von Freeden, Daniel Peters, Tivadar Vida)

Participants of the project

The project, tentatively called *Tracing Early Medieval Population Movement through ancient DNA*, is currently supported by the Anneliese Maier Research Award of the Alexander von Humboldt Foundation, the German Federal Ministry for Education and Research, and the Swedish Riksbankens Jubieleumfond.

There is no formal affiliation or rigid membership in the project and Stefania Vai,[4] a postdoctoral fellow, is the only individual directly supported by the project. The following list includes individuals who continue to provide guidance and assistance to various aspects of it. Csanád Bálint[5] was instrumental in the formulation of the original plan. John Novembre[6] and Robert Wayne[7] helped devise the original genetic research plan and continue to advise us on the project. The actual collection of the samples and the mtDNA sequencing is being done by Stefania Vai in David Caramelli's[8] lab in Florence; preliminary statistical analysis has been

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done in Guido Barbujani's[9] lab in Ferrara by Silvia Ghirotto;[10] the 2nd generation sequencing will be done in Johannes Krause's[11] lab by Stefania Vai with the assistance of Cosimo Posth;[12] Francesca Conselvan[13] is preparing a data base of all of the archaeological materials and relevant publications and is supervised by Walter Pohl[14] who consults on the historical data; Caterina Giostra[15] and Maria Cristina Larocca[16] provide us with information and access to archaeological materials in Italy; István Koncz,[17] Tivadar Vida,[18] and Balázs Mende[19] do the same in Hungary, as does Zuzana Loskotova[20] in the Czech Republic; Daniel Peters[21] and Susanne Hakenbeck[22] are both involved in obtaining isotopic data with which to compare our genetic data; Kurt Alt[23] assisted in obtaining samples from Szólád; Joachim Burger[24] has advised our principal geneticist, Krishna Veeramah,[25] on the selection of the continuous sequences to use in our 2nd generation sequencing.

Glossary

Autosomal DNA: In humans, the 22 pairs of chromosomes found in the nucleus that recombine in each generation and thus preserve the DNA of a network of many ancestors.

Haplogroup: Specific lineages of either mitochondrial DNA or non-recombining portion of the Y chromosome that are defined by a genealogically concordant combination of alleles (that is, haplotypes) at slowly evolving binary markers.

mtDNA: A circular piece of non-recombining DNA of ~16,000 bp that is found in the mitochondrion and that is inherited exclusively from the maternal parent.

Y-chromosome: The chromosome or single piece of coiled DNA, whose presence determines male sex. The middle ~95% of the Y chromosome is passed directly from father to son and does not undergo recombination during meiosis, thereby allowing inheritance of genetic ancestry to be traced exclusively down the paternal line.

Nuclear DNA: the genetic material found within the nucleus of a cell which includes the 22 autosomes, the X chromosome and Y chromosome. Other than 95% of the latter this DNA undergoes recombination during meiosis when producing gametes (sperm and egg), thus results in the transmission of DNA that is a combination of both parent's DNA.

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2ND GENERATION SEQUENCING: DNA sequencing is a process of determining the exact order of nucleotides within a DNA molecule. Next Generation Sequencing is an innovation that allows for massive, high-throughput sequencing, producing millions of sequences in a single experiment.

SNP: A Single Nucleotide Polymorphisms are DNA sequence variations that occur when a single nucleotide (A, T, C or G) in the genome differs between members of a biological species or paired chromosomes in an individual. Under some criteria the rarer of the two nucleotides must be at a frequency of at least 1% to be considered a SNP.

PHENOTYPIC VARIATION: Variation in the traits or characteristics of an organism that exist within a population above that of changes in the underlying DNA sequence.

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