THE TRANSFORMATION OF EUROPE IN THE THIRD MILLENNIUM BC

PART I

PROCEEDINGS OF THE INTERNATIONAL CONFERENCE
RIVA DEL GARDA, TRENTO, ITALY, 25–28 OCTOBER 2023

Edited by
Franco Nicolis, Gabriella Kulcsár,
and Volker Heyd

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THE YAMNAYA IMPACT ON PREHISTORIC EUROPE

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ERZSÉBET JEREM and WOLFGANG MEID

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The Maritime Bell Beaker from Ensisheim
(Reguisheimer Feld, obj. #8347, Haut-Rhin, France)
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Detail of the decorated bottom of the Bell Beaker from Santa Cristina di Fiesse (Brescia, Italy)
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Tracing the Bell Beaker phenomenon through ancient DNA studies

ALISSA MITTNIK – IÑIGO OLALDE – CLAUDIO CAVAZZUTI – WOLFGANG HAAK

Abstract

The period of the Bell Beaker phenomenon (BBP) falls amidst a time of major cultural and genomic transformations in Europe spanning the 3rd millennium BC. Preluded by the arrival of 'steppe-related' ancestry mediated through Corded Ware and Yamnaya-associated pastoralist groups, individuals associated with the BBP show - in addition - an increase in early European farmer-related (EEF) ancestry, which attests to a certain extent of local admixture. At the same time, BBP groups were the carriers of a further westward spread of 'steppe-related' ancestry. This is accompanied by distinct shifts in genomic ancestries and Y haplogroup profiles, resulting in nearly complete turnovers of Y haplogroup profiles in Central Europe, the Iberian Peninsula, Britain and Ireland, the reasons for which are not well understood. Critically, these genetic changes contrast with the proposed western origin and chronological developments of the material cultural elements within the BBP itself.

Here, we present and discuss the currently available archaeogenomic data associated with the BBP and compare it with preceding Late Neolithic and Copper Age groups as well as contemporaneous and subsequent Early Bronze Age (EBA) groups. Our synthesis ranges from broader population genetic affinities to recent methodological advances that can elucidate cross-regional connections via identity-by-descent analyses and parental background relatedness that informs on effective population sizes, and also includes the first insights into kinship structures and social organisation. We showcase the new insights the archaeogenomic data offer by focusing on specific regions (Iberia, Northern Italy, Central Europe-Bohemia), but also address the ensuing complexities and challenges for the interpretation at a broader scale. The finer characterization of the main trends in changes of genomic ancestry are as important as the integrated regional aspects, involving the analyses of various 'outlier' individuals or individual life histories, all of which contribute to a more nuanced picture of the major transformations in prehistoric Europe.

Keywords: *Bell Beaker phenomenon, ancient DNA, genomic transformation, archaeogenomics, Y haplogroups*

1. Introduction

More than 20 years ago, the conference "Bell Beaker today" showed the extraordinary progress of archaeological research and highlighted the complexity of the Bell Beaker phenomenon (hereafter shortened to BBP or just BB where more appropriate) across Europe. As stated by Franco Nicolis in the introduction of the proceedings, the primary scope was to interrelate different cultural features from the more tangible, such as technology, economy or settlement structures, to the more immaterial ones, such as ideology, beliefs and symbols (Nicolis, 2001, 31). However, the biological aspects of European populations of the 3rd millennium BC acted as a sort of "stone guest": bioanthropology was mainly applied as a variable to investigate gender differentiations in burial rites (Müller 2001; Turek – Černý 2001), but many crucial issues raised at that time, particularly those concerning the origins and the degree of relatedness among and between the different geographical BB groups, remained suspended. In our paper we will address these fundamental questions, by integrating results from established as well as newly developed methods of archaeogenomic research.

First, on the matter of the cradle of the BBP: a long historiography in brief, the BBP has been postulated to have originated in the lower Tagus valley in today's Portugal (the "Iberian hypothesis" (Sangmeister 1976; 1984; Harrison 1977; 1980; *contra* Jeunesse 2015), or in the Low countries (the "Dutch model"; Lanting – Van der Waals 1976; Van der Waals 1984), mostly on the basis of chrono-typological methods and available radiocarbon dates. Volker Heyd's recent proposal integrates archaeological evidence with the recent aDNA results and sets the Lower Rhine River valley as the original core of the All Over Corded/All Over Ornamented (AOC/AOO) Beakers, and the Upper Rhine as the hotspot for the development and diffusion of the Maritime style after ca. 2600 BC (Heyd 2021, 398–403).

Second, on the question of connectivity: the detection of shared haplotypes between individuals that are identical-by-descent (IBD), which we will apply in the following, represents a useful tool for exploring this subject, and which will occupy a special place in the current theories on the BB network. Despite the different terminologies used to define the complex (e.g. "metastructure", "metapopulation", etc. Vander Linden 2024; Heyd 2013), the various explanatory models now converge towards the idea of a mosaic of interrelated cultures, although "cultures" do not interact, people or cultural groups do. People organise themselves in societies, often founded on ethnic bases (to a large extent artificially constructed), and manage physical territories, as well as external relations. Therefore, it would be more realistic to speak of socio-political units, although their identification might be complicated by the elusive evidence for the BB settlement pattern.

The question remains "what level of connectivity" and "what type of interaction" underlies the entire complex (Vander Linden 2024, 24). Acknowledging the relevance of this topic, we will highlight distant biological relations between individuals labelled as "Copper Age", "Corded Ware", "Bell Beaker" and "EBA" in the archaeogenomic dataset up to around fifteen degrees of relatedness. By using this 3rd millennium BC time transect, it is possible to visualise corridors of preferential interaction/ migration, which may be integrated with data from the material analysis.

After a critical evaluation of the archaeological evidence from each single context, a total of 234 individuals (of which 128 were radiocarbon dated) were selected for combined analysis. These include individuals associated with BB vessels and/or typical BB grave goods, as well as single inhumations coming from BB burial contexts but without typical grave goods. By contrast, we excluded those cases in which the association with the BB grave goods is uncertain, i.e. the presence of artefacts in collective burials with a long occupation time. As with all other kinds of analysis in archaeology, the resolution of the resulting picture is largely dependent on the sample size and its distribution, which is still uneven across the various regions of Europe. We will nonetheless propose general explanations in the concluding chapter and raise further questions and challenges emerging from the analysis of the currently available dataset.

2. Archaeogenomic background

In this chapter we will summarise the relevant findings from recent archaeogenomic studies which provide the necessary background for the time before, during and after the BBP. Even though genetic ancestry is never linked to just singular moments in time and can have a lasting effect, we will restrict the characterisation of the genetic legacy of the BB era to the period of the EBA in this overview paper.

In brief, the genomic history of Holocene Europe is characterised by two major genetic transformations which are crucial to understand the genomic landscape at the time of the Bell Beaker phenomenon.

The Meso-Neolithic transition in Europe's prehistory

The Mesolithic-Neolithic transition in Europe, which broadly describes the transition from a foraging lifestyle to a new subsistence strategy linked to agriculture and animal husbandry is an ideal test case and proof-of-principle for archaeogenomic research based on a long-lasting scholarly debate. While the archaeological record on the basis of radiocarbon-dated assemblages and typological features left little doubt that the material culture associated with farming practices and a sedentary way of life spread from the earliest occurrences in the Near East, it remained long unclear as to whether this dispersal was facilitated by a transfer of ideas only (cultural diffusion) or – alternatively – carried by expanding early farmers from the Levant and the Fertile Crescent (demic diffusion) (WHITTLE, 1996; PRICE 2000; BOCQUET-APPEL – BAR-YOSEF 2008; JOBLING *et al.* 2013).

Earlier aDNA studies based on maternally inherited mitochondrial DNA already found convincing evidence for genetic discontinuity between late hunter-gatherer individuals and the earliest European farmers (BRAMANTI *et al.* 2009; BOLLONGINO *et al.* 2013; BRANDT *et al.* 2013), and an increased affinity of the latter to modern-day population of the Near East (HAAK *et al.* 2010). Recent genome-wide nuclear data from prehistoric individuals directly associated with autochthonous European hunter-gatherers as well as early European farmers confirmed that both groups were genetically different from each other (GAMBA *et al.* 2014; LAZARIDIS *et al.* 2014; SKOGLUND *et al.* 2014; HAAK *et al.* 2015; FU *et al.* 2016). Improvements in sample selection and sampling techniques (GAMBA *et al.* 2014; PINHASI *et al.* 2015) also opened up hot and humid regions that were not favourable for aDNA preservation due to their climatic conditions. Genomic data from early farmers in Western Anatolia, the Levant, and the Fertile Crescent, showed that early European farmers resembled the early Near Eastern/Anatolian farmers (MATHIESON *et al.* 2015; BROUSHAKI *et al.* 2016; KILINÇ *et al.* 2016; LAZARIDIS *et al.* 2016). The fact that the Near Eastern farmers and their associated material cultural package predate the early Neolithic Central Europeans provides a temporal succession and directionality that has been complemented with a continuously growing body of ancient genome data. In sum, these observations are in strong support of the demic diffusion model, in which farming had spread with expanding groups from the Near East, Anatolia and south-eastern Europe and thus reject the alternative model of an autochthonous development of farming in Europe. In parallel, the close genetic similarity between late and transitional hunter-gatherers and early farmers around the Fertile Crescent argues for local genetic continuity and a gradual change of subsistence, such as the local development of farming practices in the region itself (BROUSHAKI *et al.* 2016; LAZARIDIS *et al.* 2016; FELDMAN *et al.* 2019). Genome-wide data directly contributed to settling a long-lasting debate.

However, European hunter-gatherers were not completely replaced by incoming farmers. Genome-wide data show that Early European farmers harboured low proportions of European hunter-gatherer ancestry, acquired through admixture with local hunter-gatherers as they expanded from the Near East into the European continent (LAZARIDIS *et al.* 2014; MATHIESON *et al.* 2015; 2018; LIPSON *et al.* 2017; RIVOLLAT *et al.* 2020; YU *et al.* 2022). Interestingly, ancestry from these Mesolithic hunter-gatherers increased during the Middle Neolithic, when Neolithic individuals carried a higher European hunter-gatherer ancestry than Early Neolithic groups. This pattern became known as "hunter-gatherer resurgence" and has been observed in Iberia, central/northern Europe, the Carpathian Basin and the Balkans. It points to further pulse(s) of admixture with groups rich in European hunter-gatherer ancestry several centuries after the initial period of contact and suggests a prolonged period of parallel societies, even though hunter-gatherer burials are exceptionally rare in the archaeological record after the arrival of early farmers. On the basis of genetic differentiation, it is thus possible to investigate potential mixture events between late foragers and early farmers directly, e.g. in regions where both overlap temporally and geographically, and also the extent and mode of interactions.

The spread of steppe-related ancestry during the Bronze Age

Archaeogenomic studies have also described a large-scale contribution of a new form of ancestry from the North Pontic steppes to late farming groups in central Europe (Allentoft *et al.* 2015; Haak *et al.* 2015). This so-called 'steppe-related ancestry' (or in short 'steppe ancestry' in what follows) was formed by a preceding mixture of Eastern and Caucasian/Iranian hunter-gatherer ancestries (Jones *et al.* 2015) and was already present in Eneolithic individuals from the Eurasian steppe dating to the late 5th millennium BC (Wang *et al.* 2019; Penske *et al.* 2023). The arrival of 'steppe ancestry' has substantially further transformed the prehistoric European gene pool during the 3rd millennium BC and was primarily attributed to individuals associated with the Yamnaya cultural complex and the Corded Ware (CW)/ Single Grave/Battle Axe cultural complex in eastern and central/north-eastern Europe. The magnitude of this steppe ancestry contribution was substantial and stood in stark contrast to late Neolithic groups, very similar to the Mesolithic-Neolithic transition a few millennia earlier. This observation came almost as a shock to many scholars who had not or no longer considered scenarios of migration and expansions of such an extent during this time period (Furholt, 2017; Heyd, 2017). It also rang the alarm bells, as it was the CW complex in particular that had been used in Kossinna's *Siedlungsarchäologie* (settlement archaeology) as a prime example of 'pots equal people'. The fear was that linking a substantial turnover of genetic ancestry with a cultural phenomenon would evoke old theories of steppe incursions and invasions of Indo-Europeans (e.g. Gimbutas, 1993). However, aDNA data could also show that the continuous spread of steppe ancestry across Europe might appear to have occurred swiftly at regional scale but was a process that had lasted several centuries at least, if one considers the proposed core region of e.g. the Yamnaya complex and the attested arrival of steppe ancestry in the south- and north-western corners of Europe after ca. 2400 BC. It has to be stated that this demographic process could only be detected after the fact and involved individuals, which are associated (also in hindsight) with many archaeological Late Neolithic/Eneolithic/Chalcolithic/Copper Age and EBA cultures. If anything, archaeogenomic data can help describe a transient state as in the case of individuals who are associated with the BBP who appear genetically heterogeneous, while some contemporaneous individuals do not carry steppe ancestry (Olalde *et al.* 2018; 2019; Villalba-Mouco *et al.* 2021). Also, in all likelihood no single individual carrying steppe ancestry travelled or migrated from the Samara region in Russia all the way to the Atlantic coast, and it is equally unlikely that early farmers migrated with a clear intention from Western Anatolia directly to the fertile loess plains of central Europe. In both cases, where migration, or better, range expansion, is genetically attested, many archaeological cultures and groups are involved. What becomes apparent from the reconciliation of genetic and archaeological data is that the resolution needs to be adjusted to maximise compatibility.

It is warranted to advise against the designation of a single culture/phenomenon to a single distinct ancestry profile. Quite the contrary is true. Despite substantial demographic changes in prehistory attested by aDNA studies as a result of migration/range expansions, both were ultimately processes overarching the resolution of archaeologically defined cultures. The spread of genetic 'steppe ancestry' involves over the course of 1000 years of prehistory many archaeological periods and/or cultures, such as CW, BB and numerous EBA groups in the West, and amongst many others, Yamnaya, Catacomb, Afanasievo, Srubnaya, and Andronovo in the East. While likely originating somewhere in the North-

Pontic steppe region, individuals contributing to the formation of 'steppe ancestry' are in turn associated with a number of Eneolithic complexes emerging from the 5th to 4th millennium BC, which highlights the perpetual kaleidoscope of genetic ancestries, which is rather fluid and ephemeral than tied to a defined point in space and time.

Further archaeogenomic findings have shed new light onto the transformative nature of the 3rd millennium BC from yet another angle. Initially surprised by the magnitude of genetic change visible in genomes from this time period, researchers began to screen for evidence of pathogens in the sequence data obtained from prehistoric individuals and were indeed successful (Rasmussen *et al.* 2015). Upon further investigation, genome data of the pathogen *Yersinia pestis*, the causative agent of the Medieval Plague, could be identified positively in a handful of individuals of the same dataset (Allentoft *et al.* 2015). Applying targeted capture techniques or deep shotgun sequencing, the number of positive individuals could soon be increased to several dozen (Andrades Valtueña *et al.* 2017; 2022; Rascovan *et al.* 2019; Susat *et al.* 2021) and also included a BB-associated individual from the site of Hostivice-Palouky in today's Czech Republic. Nearly all strains dating to the time range ca. 5000–3000 BC belong to a single, now extinct lineage that was widely and rapidly dispersed. This lineage was non-flea-adapted, but the first evidence for the fully flea-adapted lineage was soon also discovered in regions of today's Ukraine and Spain, dating to after 4000 BC. Key questions revolving around the transmission modes and pathogenicity and lethality of these early forms still need further investigation. However, the specific case of *Y. pestis* but also other diseases such as Hepatitis B (HBV) or zoonosis such as *Salmonella enterica* show that early outbreaks of emerging diseases might have played a critical role in the demographic fluctuations of early agropastoral societies in Western Eurasia (Key *et al.* 2020; Kocher *et al.* 2021). In this framework, the increase in mobility and connectivity might have incremented the probability of disease diffusion. In several cemeteries from Bohemia, Moravia, Germany, Hungary and Northern Italy, e.g. (Turek 2006a; 2008; Patay 2013; Czene 2017; Marchi *et al.* 2021; Salzani *et al.* 2021), the presence of cremated individuals associated with Bell Beaker pottery and other grave goods could be interpreted not only as the adoption of a different funerary ritual, but also as a response to the frequent occurrence of virulent pathogens, among which *Y. pestis* is likely the most relevant.

3. Methods and concepts

What can ancient DNA contribute to questions about migration in prehistory?

The time stamp of ancient DNA samples, i.e. the clear link of genetic information with a certain period in prehistory, is the key element of archaeogenomic investigations into the past. As such, aDNA research operates along a time-axis, which allows the detection of changes (discontinuities) or lack thereof (continuity) in genetic data through time. On the basis of this principle, one can deduce processes such as migration or range expansion of a group (or individual mobility) by evaluating local discontinuities, i.e. genetic changes over time. For instance, in the absence of sufficient time for evolution, a significant difference in genetic profiles between two groups from the same geographical location but different time periods may suggest that the newer group underwent a range expansion or migrated from someplace else to replace (completely or in parts) the previous genetic signal: the experimental framework to verify/falsify the null hypothesis (cultural diffusion) would require ideally two sampling points in time (for example before and after the arrival of farming) from two geographical regions (the source and the sink, i.e. the proposed origin and the destination). As a prerequisite, we assume genetic differentiation between the

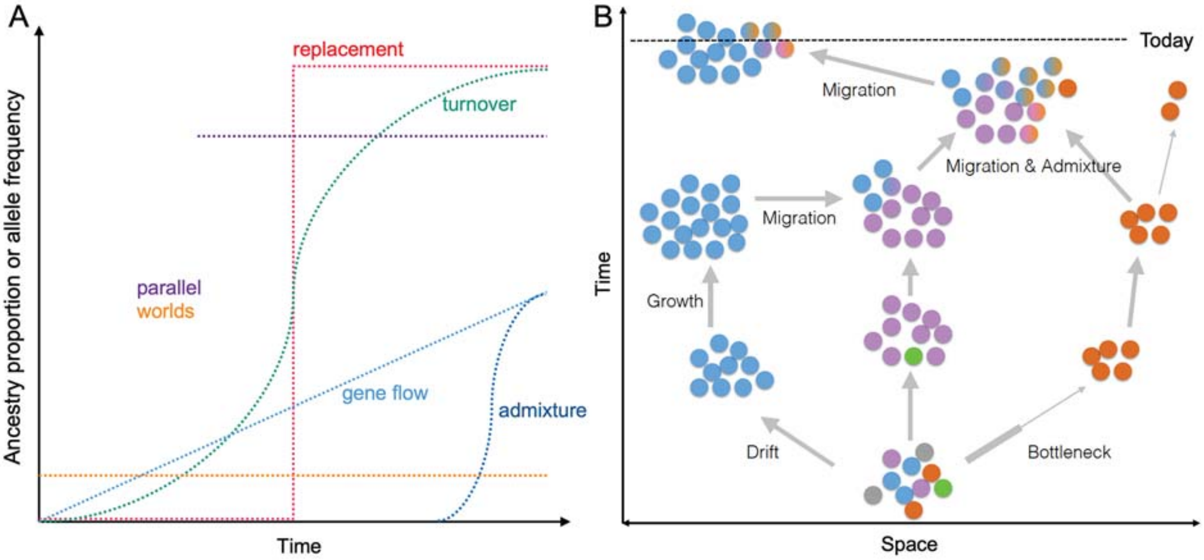

Fig. 1. Schematic overview of the various forms of interaction and the ability to detect these across space and time. Panel A distinguishes as per changing quantities on the y-axis and the speed at which such can be measured over time (x-axis), while panel B also includes effects that can lead to population differentiation and changes in effective population size across both space and time. (Image by W. Haak)

two geographic regions, or else we would lack any resolution to contribute to this question. If the genetic profile remained largely stable (continuous) over time in either region, i.e. before and after the arrival/establishment of farming, we would deduce cultural diffusion from the region where it occurred first to the other. In turn, if the region of origin remained genetically stable, but the sink region showed a genetic discontinuity, we would infer a spread or range expansion of one group (the source deme) into the other. For the sake of completing this line of thought, if there was genetic discontinuity in both regions before and after, one would have to infer a movement from a third, unknown region to both regions tested.

This is an extreme example that illustrates the principle, and many prior expectations must be met to infer migration and replacement from genetic data on a time axis. However, with growing data in a virtual three-dimensional matrix, we are in principle able to detect genetic discontinuity across space and time, as well as address questions revolving around expansion, and as such individual mobility or group migration (Pickrell – Reich 2014). Dense sampling across space – but more so over time – is a natural prerequisite(s) for this work and it allows not only the identification of various forms of population interactions but also demographic processes, such as bottlenecks. Figure 1 summarises the potential of genomic time series data to illustrate extreme effects, such as replacement and turnover, described above, but also more subtle effects such as admixture and gene flow (*Fig. 1*). Using sophisticated methods and modelling approaches, it is possible to leverage high-resolution genome data to explore demographic factors such as differences in effective population sizes, migration rates, levels of homozygosity or inbreeding, while the contextualisation of archaeological and anthropological meta-data can provide insights into social organisation (patrilineality vs. matrilineality), and lastly family and/or kinship structures.

BOX 1: How to approach and interpret genetic data

Two main properties of DNA make it an excellent means of studying the history of humans, and in fact, of any organism. The first one is that DNA accumulates changes at known rates through the process of mutation. When two individuals or populations diverge from a common ancestor for sufficient time without significant gene-flow, the number of accumulated genetic changes enables their differentiation and allows for the estimation of the time since divergence. The second one is the fact that DNA is transmitted from one generation to the next. A child necessarily derives all his/her DNA from his/her parents and in the same vein, if a population at a given point in time directly descends from an earlier population, it will inherit all its DNA from this population (Jobling *et al.* 2013). The commonalities and differences between the individual genomes of various organisms define the variable degree of biological relationships. For example, at a coarse level of resolution, the placement of humans within the tree of life can be defined. Scalability and increasing resolution further allow distinguishing between groups of people at continental, regional and local levels, ultimately reaching the level of individual identification. While further resolution to tissue types and/or single cells forms an integral part of molecular biological research at a primarily epigenetic level, the focus of aDNA studies remains at the individual level, where it is central to the reconstruction of close degrees of biological relatedness, and widely applied in pedigree analyses and kinship studies (Novembre – Ramachandran 2011; Jobling *et al.* 2013). Genetic resolution at the individual level is also widely used in forensics and commercial parental testing. Through the analysis of aDNA from prehistoric individuals with reliably dated archaeological meta-data with a geographic reference point (latitude and longitude) the genetic information of prehistoric individuals or groups thereof receives a temporal dimension (Pickrell – Reich 2014), and with this a contextualisation that exceeds the perception of a DNA molecule that is simply subject to evolution.

BOX 2: Terminological issues

The simple attribution of a lifestyle/culture to a cluster of genetic profile appears straightforward, but is considered haphazard. Indeed, applying labels and bins to biological clusters is a crucial point of concern in archaeogenomic studies. The pre-filtering or post-hoc labelling of prehistoric individuals according to their associated archaeological cultures is based on a pre-emptive view that material culture equals people (hence, pots = people), a concept which could in theory be corroborated by genetic studies. This idea was not new and understandably raised red flags as it evoked demons of the archaeological past, such as Gustav Kossinna's law of settlement archaeology (German "*Siedlungsarchäologie*"), which proposed in quite a dogmatic manner that archaeologically defined cultures at all times correspond to peoples (a biological entity) who spoke a common language (hence, pots = people = language) (Kossinna 1911). From a genetics perspective, there are two main caveats, which illustrate that this simple equation does not hold. Firstly, biological clusters, provided they can be detected, are a priori assumption-free and independent of any pre- or post-hoc sorting and labelling. At the same time, genetic group labels are subjective, non-permanent, flexible with respect to in/exclusivity and can be adjusted freely. Importantly, these labels can be lumped or split and refined according to additional data or the need for further sub-structuring. Following Eisenmann and colleagues (2018), labels should be considered a merely pragmatic solution to add geographical, archaeological and/or chronological attributes as informative, and meaningful descriptors that any user, reader and the public can relate to. Secondly, given the inherent imprecision of category labels and the non-alignment of scales, biological clusters never fully correspond to distributions of archaeologically defined cultures or phenomena nor to labels that are applied to modern-day groups. The structure of genomic data is also rarely uniquely cluster-like. In fact, the emerging patterns from reduced data dimensions or clustering algorithms are often clines or clouds with considerable overlap, and often include outliers, see e.g. (de Barros Damgaard *et al.* 2018; Mathieson *et al.* 2018; Narasimhan *et al.* 2019). However, within some of these clouds, the (momentary) correspondence between a genetic ancestry profile and the archaeological cultural background can be striking, and can potentially be explained by converging, eco-geographic and/or geo-political factors.

BOX 3: Methods for analysing archaeogenomic data

A wide range of theoretical frameworks, methods and analytical tools exist that allow the qualitative and quantitative exploration of autosomal genetic data. Prime examples include multivariate statistics to reduce data dimensionality such as principal components analysis (PCA), multidimensional scaling of distance or similarity matrices, or heuristic clustering algorithms, such as *ADMIXTURE*, or *NGSadmix* (e.g., Patterson –Price – Reich 2006; Novembre *et al.* 2008; Alexander *et al.* 2009; Patterson *et al.* 2012; Skotte – Korneliussen – Albrechtsen 2013). More strictly quantitative methods, such as *f*- and *D*-statistics (Reich *et al.* 2009; Patterson *et al.* 2012) are used to test the coherence of the genetic clusters of individuals and/or the existence of statistical outliers.

PCA and ADMIXTURE

Principal component analysis (PCA) was one of the earliest statistical approaches to be used for the analysis of genome-wide data and has become an extremely popular tool in the field of archaeogenomics (Patterson –Price – Reich 2006). The objective of this method is to extract the most important information from multivariate data and reduce the high dimensionality to a number of vectors that can be visualised. Specifically, PCA transforms a series of correlated variables (in our case genetic variants across thousands of loci) into a smaller number of linearly uncorrelated variables called principal components that represent the relatedness between individuals. This method has several advantages: the projection of samples onto the principal components reveals population structure in a visual manner, it does not assume any specific genetic model, and it is computationally fast. Another popular tool for analysing population structure is the model-based clustering method ADMIXTURE (Alexander *et al.* 2009). In the model underlying this approach, individuals are assumed to have inherited part of their ancestry from two or more hypothetical ancestral populations (k) that instantly diverge, characterised by a set of allele frequencies at each locus. The goal is to estimate for each individual the proportion of the different ancestral components and the allele frequencies of each ancestral population. The genetic information is explored on the basis of scalable degrees of dis/similarity, and then transposed into the ancestry components of k-ancestral populations. By iterating through an increasing number of k it is possible to achieve scales of resolution that range from continental to regional groups, and in theory to the individual level. Both PCA and ADMIXTURE are powerful tools for detecting genetic structure and admixture and can be used to formulate hypotheses. However, both methods are sensitive to the sampling scheme and do not directly reveal the actual history that produced the observed patterns. In fact, the observed patterns could be compatible with multiple population histories, and do not provide any formal tests of admixture between populations (Engelhardt – Stephens 2010; Patterson *et al.* 2012).

F-statistics

This set of statistics examines allele frequency correlation patterns across populations and provides formal tests for whether admixture occurred (Patterson *et al.* 2012). *F*-statistics have been extensively used in archaeogenomic studies over the past decade. A drawback of these methods is that individuals must be first classified into populations, which is not assumption-free and thus can be subjective to a certain extent. The general intuition behind these methods is the fact that if population X is a mix of populations A and B, the frequencies of the possible variants (alleles) of a given genetic marker in X will tend to be intermediate between allele frequencies in A and B of the same marker. Of course, when looking at one or a few genetic markers, these patterns can appear by chance, but when observed at hundreds of thousands of genetic markers these tests provide powerful statistical means to test for admixture and also permit the quantification of ancestry proportions.

Detection of identical-by-descent (IBD) segments

Using the *F*-statistics framework we can determine ancestry proportions for a given individual. For instance, when we state that a BB-associated individual or group harbours ancestry related to EBA Steppe populations associated with the Yamnaya culture, it means that either the Yamnaya population from which DNA has been recovered, or a population very close to the sampled Yamnaya (i.e. diverging from it in their very recent past) are among the ancestors of the Bell Beaker group. However, with this framework we cannot establish direct genealogical link between individuals. Very recently, a new analytical method for detecting such links has been adapted for ancient DNA data (Ringbauer *et al.* 2024). When two individuals share a common ancestor in the recent past, they share long stretches of DNA of millions of base pairs (Mb) that we refer to as segments that are identical-by-descent (IBD). Of note, the length of DNA sequences is often also measured in centimorgans (cM), in which 1cM roughly corresponds to 1 million base pairs. When DNA is transmitted to the next generation, recombination between the maternal and paternal chromosomes breaks up these IBD segments randomly into smaller chunks. The more generations separate two individuals, the shorter these IBD segments will become. The number of shared IBD segments also decreases over time, as each individual carries only two copies of a certain region which only reflects a fraction of nominal ancestors. As an example, first cousins, who share a pair of ancestors two generations back, tend to share between 10–30 long IBD segments (some as long as 60–70 Mb) which translates into ca. ¼ of their genome (ca. 800 Mb). Third cousins

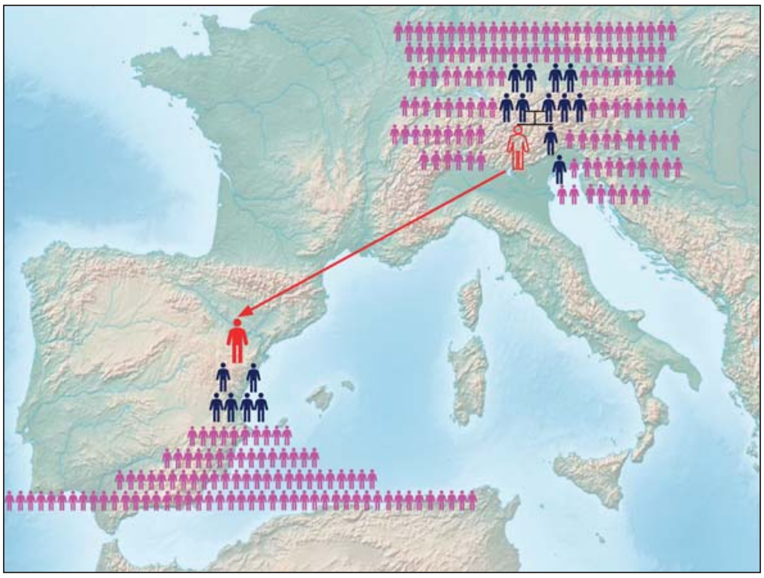

Fig. 2. Identifying individual cases of mobility with IBD detection. With traditional methods for detecting biological relatedness in aDNA data, the movement of the red individual from his place of birth near the Alps to Iberia can only be identified if one of his few close relatives (or himself) in Iberia and one of his few close relatives at his place of birth (both represented in dark blue) made it into in the archaeological record and yield well-preserved DNA. With the ability to detect more distant relatives, this connection can be identified by sampling one of the red individual's more distant relatives in Iberia and one of his more distant relatives in his place of birth (both represented in pink), a far more likely scenario given that distant relatives are much more numerous than close relatives. (Image by I. Olalde)

instead share a pair of ancestors 4 generations back and tend to share only a handful of shorter IBD segments totalling ca. 50 Mb. The importance of detecting these more distant biological relationships, as compared to only close relatives to first cousins with traditional methods, is highlighted by the fact that we often have a few first cousins but thousands of more distant cousins (*Fig. 2*). An important point of consideration is that while ancestry signals persist in the genomes over thousands of years (e.g. we can still detect steppe-related ancestry in present-day Europeans) as a lasting legacy, long IBD segments eventually disappear due to recombination (i.e. no long IBD segment between a present-day European and his/her steppe Bronze Age ancestors is detectable anymore). Note that from about the 10th degree on and higher (e.g. 5th cousin), it is equally likely that two individuals do not share any IBD even though they are genealogically linked (Caballero *et al.* 2019).

Runs of homozygosity (ROH)

Recently developed algorithms (Ringbauer – Novembre – Steinrücken 2021) allow us to detect not only IBD segments between individuals, but also between two copies of an ancient individual's genome. These segments, referred to as runs of homozygosity (ROH), are inherited from the same ancestor through both the maternal and the paternal lines and inform us about the degree of relatedness between the parents. They can be used to study endogamic practices in the past but also to infer population sizes, because as the populations decrease in size, the rates of mating between relatives tend to increase.

4. State of the art: Broad overview

At the time of writing of the manuscript genomic data from 226 individuals associated with the Bell Beaker phenomenon were available from many regions across central and western Europe (*Fig. 3* and see *Table 1*). The data was complemented with 57 individuals who date to the same time period, but where a direct association is less clear from the archaeological context, e.g. when found in collective burials where BB-style artefacts are present alongside artefacts/features from other/contemporaneous groups. The latter are highlighted as orange symbols ('no Bell beaker grave goods') on the PCA plot.

When projected in PC space with commonly used West Eurasian population the BB-associated individuals form a large and heterogenous point cloud (*Fig. 4*) along PC2 ranging from individuals that

Table 1. List of published Bell Beaker individuals used in combined analyses and synthesis presented in this overview study

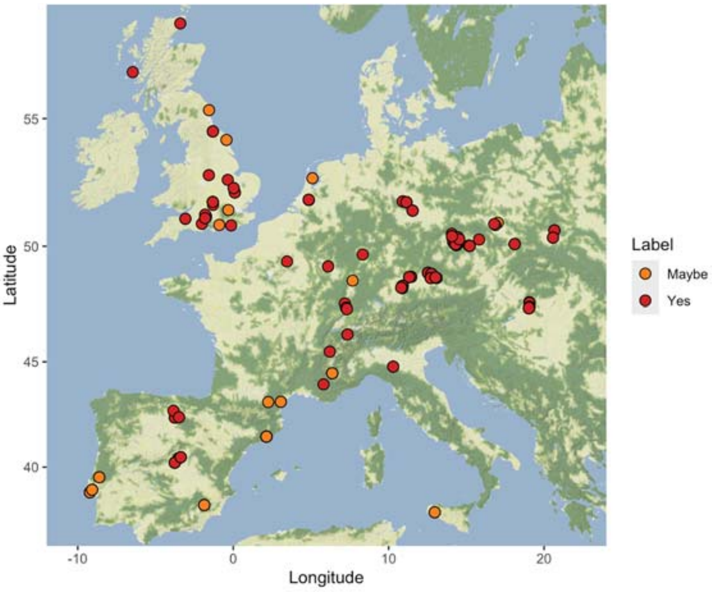

Fig. 3. Archaeological sites from which published genome-wide data associated with the Bell Beaker phenomenon are available and which were included in our synthesis. Red circles depict sites with a clear BBP association and orange circles show sites with no clear association (see also Fig. 4*). (Image by W. Haak)*

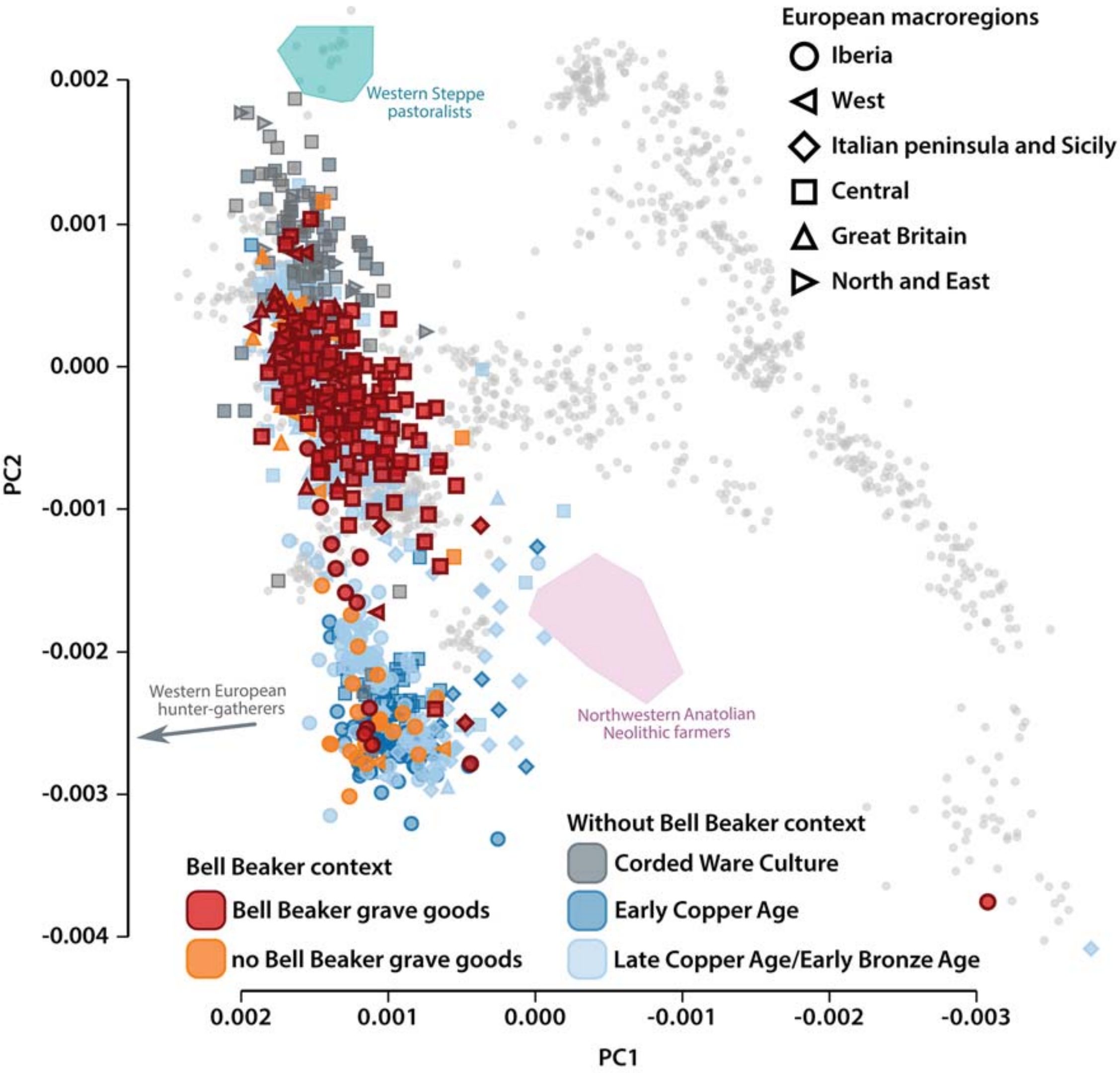

Fig. 4. Principal component analysis of BB-associated individuals (red and orange symbols) and relevant preceding and contemporaneous individuals (grey and blue symbols with darker outline) projected onto the genomic variation of 1196 individuals from 63 modern-day Western Eurasian populations (grey dots). Coloured polygons show the distribution of ancient individuals closely related to the three main genetic components contributing to Bronze Age European genetic variation, with the location of Western European hunter-gatherers falling outside of the pictured range. (Image by A. Mittnik)

are high in steppe ancestry, i.e. nearly overlap with preceding Corded Ware-associated individuals, to those with very low or no steppe ancestry overlapping with individuals from other Late Chalcolithic/ Neolithic archaeological contexts. In general, while nearly all BB-associated individuals carry steppe ancestry, they also carry a higher proportion (ca. 20% more) of EEF-related ancestry. By and large, the heterogeneity in ancestry, i.e., the distribution of BB-associated individuals in PC space from across all of central and western Europe indicates a dynamic time period of admixture that is ongoing at the time, and contrasts with Corded Ware and Yamnaya individuals who form tighter clusters in PCA with fewer outliers. The heterogeneity of the BB data is large and comparable to the range of early to late European farmers across Europe which range from 5% to 50% hunter-gatherer ancestry contribution. However, while the mixture of early farmer and hunter-gatherer-related ancestries reflects a process of assimilation and gene flow of 1500–2000 years, the BB-associated transformation covers a much smaller time scale of 200–300 years.

Despite the substantial number of individuals genotyped to date, ancestry gradients with respect to steppe- vs. EEF-related ancestries are only visible as broader geographic trends. For example, steppe ancestry is higher in the central, northern and eastern regions of the BB distribution and conversely lower in southern and southwestern Europe. However, this signal is not clear and confounded by the chronologically heterogeneous dataset that potentially pre-empts a robust correlation between ancestry vs. geography and/or ancestry vs. time. However, the observation that steppe ancestry is highest in regions where the BBP is preceded by a CW/Single Grave/Battle Axe cultural horizon is indicative of a broader trend in which steppe ancestry spreads roughly from East to West and from North to South. The spread from central to western and southwestern Europe appears to be associated with the BBP, but it is worth noting that ultimately steppe ancestry also arrives in the eastern Mediterranean and Mediterranean islands, sometimes many centuries later, and mediated by demographic changes that are no longer linked to the BBP.

The broad northeast to southwest trend is also confirmed by Y chromosomal data, through which the paternal history can be traced (*Fig. 5*). The overwhelming majority (ca. 95%; 110 out of 116) of male BB-associated individuals carry the Y chromosome lineage R1b-P312 (and derived lineages thereof). These are nested within and radiated with/from other ancestral R1b lineages, which were found also among CW- and Yamnaya-associated individuals and were absent in western, southern and central Europe before 3000 BC. The estimated divergence date of ca. 2800 BC (formation date) of R1b-P312 matches the radiation within the context of the spread of steppe ancestry from East to Central Europe. Several sublineages exist within R1b-P312, which suggest a phylogeographic pattern in the subsequent dispersal to the west and other regions. So is R1b-L2 more common in central Europe, while R1b-L21 is the predominant lineage of male BB individuals in Britain. R1b-Z195 became the most common lineage in the Iberian Peninsula during the EBA and thus must have derived regionally from an R1b-DF27 precursor or represent a separate pulse of immigrants (Villalba-Mouco *et al.* 2021).

Ultimately, R1 lineages have a long history and were first and foremost associated with hunter-gatherers of Eastern Europe and North Central Asia, including the 25,000-year-old Mal'ta boy from the Altai (Raghavan *et al.* 2014), but were also common among Mesolithic and Neolithic and Eneolithic individuals in the forest steppe and steppe regions who also contributed ancestry to the early and transitional pastoralist groups of the steppe. Several bottlenecks must have occurred, which resulted in

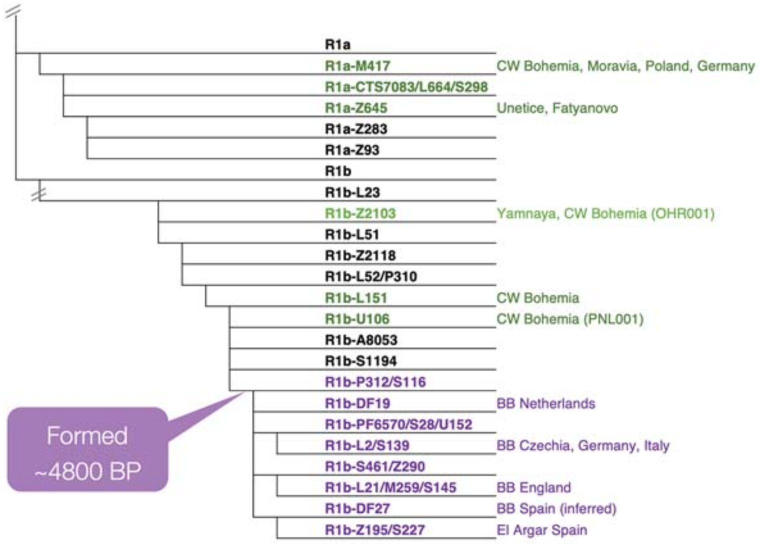

Fig. 5. Schematic and simplified overview of Y-chromosome haplogroup R1 in BB-associated male individuals and other relevant ancient groups. (Image by W. Haak)

some lineages becoming the predominant or near exclusive patrilines, such as R1b-Z2103 in Yamnaya- or R1a-M417 in CW-associated individuals, whereas R1b-P312 is clearly linked to the BBP and virtually absent in Yamnaya and CW male individuals. Such population bottlenecks would also have an effect on the genomic variability of the rest of the genome, but evidence for this is so far only seen in Yamnaya (Lazaridis *et al.* 2024; Ringbauer *et al.* 2024). Papac and colleagues (Papac *et al.* 2021) demonstrated that also particular forms of social organisation and kinship structures could have a similar effect, in which rare Y lineages are more prone to be lost, while other more common ones can randomly reach fixation. Indeed, the enhanced dataset from CW-associated individuals shows such a reduction from an initially more diverse pool to a near exclusive R1a-M417 during the classical phase of the CW. Such effects of isolated mating networks regulated by social norms could explain the random fixation of certain lineages in certain regions, including the R1b-P312 dominance among the BB-associated individuals.

Indeed, the first forays into elucidating the social organisation of two BB-associated communities have attested to a patrilineal and virilocal structure and practice of female exogamy (Sjögren *et al.* 2020), which can amplify the observed effects. At the Irlbach BB cemetery, an adult male individual was buried together with his son and his paternal uncle and aunt. At Alburg, three brothers were likely the founders of the cemetery and were buried together with two pairs of close relatives through the paternal line, highlighting men as the social bond that connects the consecutive generations at each site. The high diversity of mitochondrial lineages at both sites and the higher number of female isotopic outliers suggests the practice of female exogamy, although the available dataset also includes exceptions. Female 4 from Alburg was closely related to the founding brothers, possibly their niece, and was buried close to them and to her own daughter. This case shows that some women either stayed in the families they were born into or came back and were buried close to their biological family.

In other regions, such as in the Lech Valley of Bavaria, a model of patrilocality and female exogamy seemed to be more strictly adhered to, with a complete lack of buried adult daughters within any of the sampled multigenerational pedigrees, and a clear pattern of likely local origin for male and subadult individuals, whereas 60% of adult female individuals showed non-local origins according to strontium and oxygen isotopes (Mittnik *et al.* 2019). Women generally moved to the Lech Valley from afar only after adolescence, indicated by non-local strontium values in the late developing third molars. This practice persisted for several centuries into the EBA. Strontium measurements revealed another intriguing aspect of individual mobility: For a BB-associated family trio at the site Haunstetten–Hugo-Eckener-Straße 58–62 (*Fig. 6*), consisting of a father and mother in a double burial (Burial 8, feat. 68, Skeletons 1 and 2) and their adult son buried closely nearby (Burial 7, feat. 67), both the early and late developing molars exhibited local signatures for the mother and son. The father however had spent his childhood locally, moved away during adolescence and was again buried in the Lech Valley. This could indicate practices such as apprenticeship or fosterage which are attested in early historical societies of Europe, and also suggested by other isotope data from the BBP and Bronze Age contexts (Cavazzuti *et al.* 2019; Montgomery – Evans – Towers 2019).

A survey of ROH among BB-associated individuals, compared to preceding, contemporaneous and posterior groups (*Fig. 7*), reveals exogamous marital practices as the norm, with only few individuals showing evidence of being offspring of closely related parents. The sum of ROH segments longer than 20 cM only rarely exceeds the expected value for the offspring of 2nd cousins. The rarity of cousin-cousin marriage in Copper and EBA Europe stands in stark contrast to its high frequency in the contemporary Aegean (Skourtanioti *et al.* 2023). There, endogamous marriage practices have been hypothesised to be shaped by different social, economic, and ecological factors, such as geographic isolation, endemic pathogen stress, and agricultural and inheritance strategies.

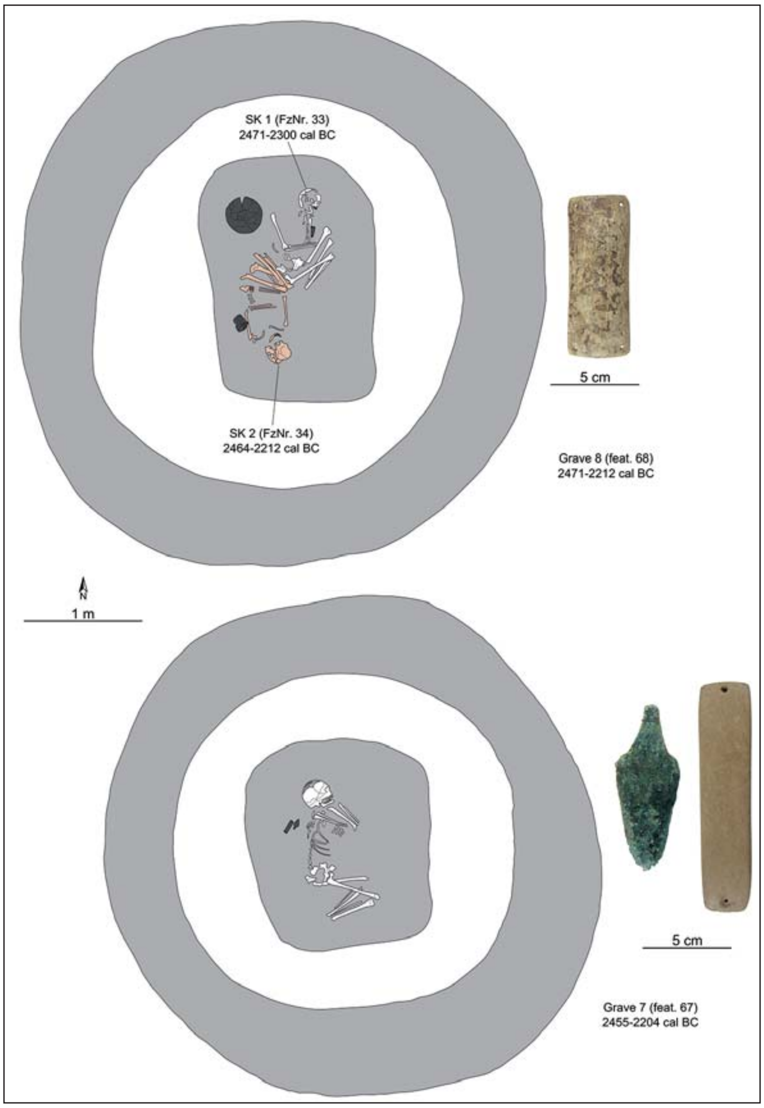

*Fig. 6. Burials 7 and 8 at Haunstetten–Hugo-Eckener-Straße 58–62, Germany (*Massy *et al. 2017)*

The amount and frequency of short ROH in a population, as captured by the mean sum of ROH segments 4–8 cM in length, can be used as a proxy for effective population size. This measure shows a significant decrease – from the earlier CW cultural complex to individuals of the BBP (*Fig. 7b*) – indicating an increase in effective population size, following an overall temporal trend. It is possible that the initial population bottleneck signal from the incoming steppe ancestry groups, who represented only a small fraction of the larger population of the steppes, was gradually diluted over time through intermarriage with the local EEF-rich groups.

Beyond the first insights on social organisation that can be obtained from the intra-site close familial relationships, the detection of long-distance relatedness between BB-associated individuals with high-quality genomic data (n=115) from different sites/regions sheds new light onto the expansion of the BBP. With only one exception, all 52 BB sites are connected to each other through long IBD segments (*Fig. 8*) between at least one pair of individuals. These links across the whole geographical range very often involve IBD segments longer than 20 cM, which are usually broken down rapidly beyond the 6th degree of relatedness (Caballero *et al.* 2019), meaning that the majority of BB-associated individuals share common ancestors with other BB individuals in the relatively recent past, or in other words, are distant cousins. Even in the regions with fewer available high quality data points such as Northern Italy and Iberia with one and three sites, respectively, all have at least one individual showing distant biological relationships with individuals hundreds of kilometres away. The region of Bohemia in today's Czech Republic seems to share the most IBD links with both Britain towards the west and Northern Italy/Southern France/Iberia towards the southwest, whereas Britain and the southern regions share fewer connections. However, results from IBD analyses are difficult to quantify and interpret. Although this could point to Bohemia as a hub from which BB groups expanded west and south, it could also be the result of this region being the one with the highest number of high-quality genome-wide data of BB-associated individuals, as the number of

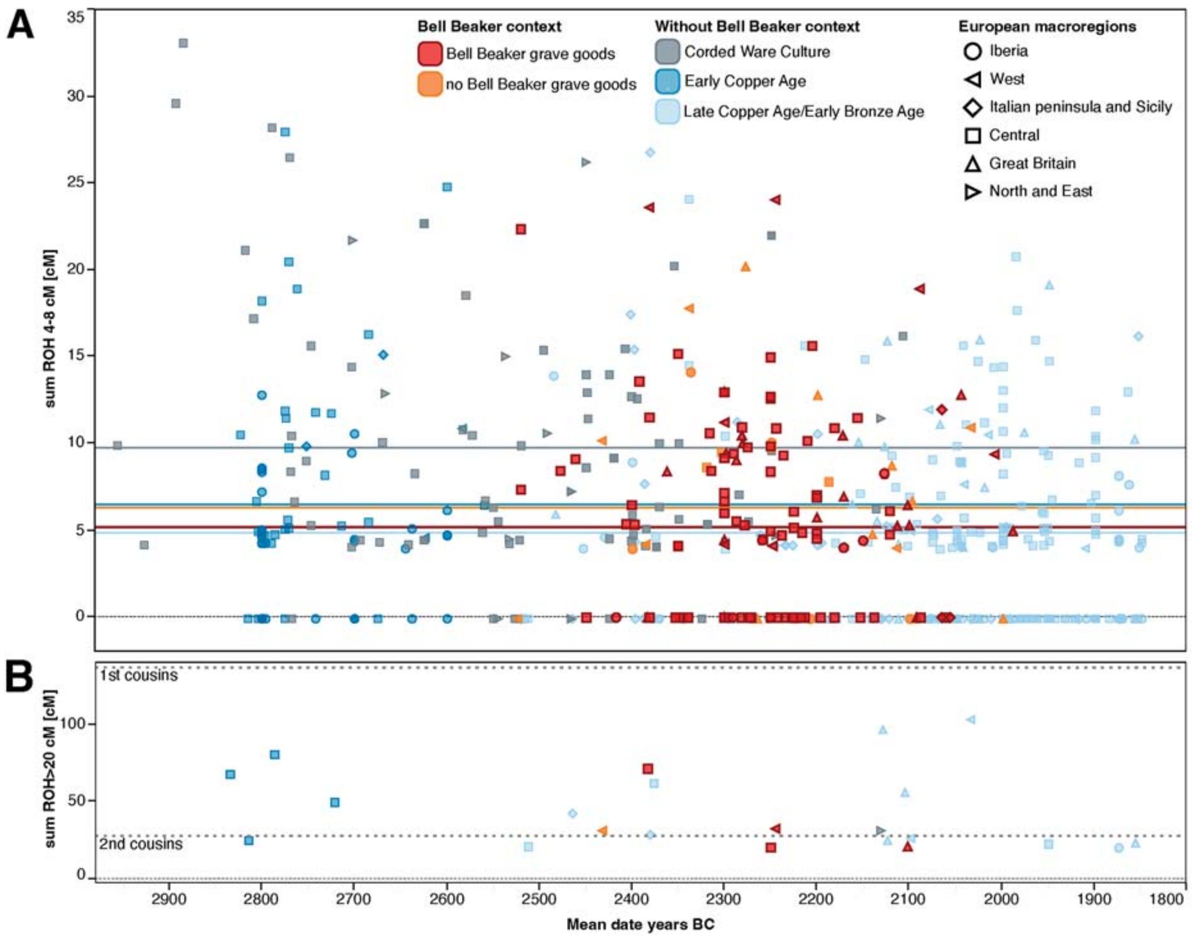

Fig. 7. Runs of homozygosity (ROH) among Copper Age to Early Bronze Age European individuals. BB-associated individuals are shown as red and orange symbols and other Copper Age and EBA individuals as grey and blue symbols. The sum of short ROH of 4-8 cM length carried in each individual, shown in a) indicates distant relatedness of the individual's parents. The solid-coloured lines show the mean sum of ROH of each corresponding group, excluding offspring of closely consanguineous parents where the sum ROH (>20 cM) >50cM. The presence of long ROH>20 cM, shown in b) indicates that the individual's parents were closely related. The dotted lines show the expected value for the offspring of 1st and 2nd cousins, respectively. (Image by A. Mittnik)

potential links scales up quadratically with the number of individuals analysed. It is also possible that the high number of links points to a more pronounced bottleneck in the respective meta-population, which would be consistent with the observed reduction in Y chromosome haplogroup diversity during the BB period.

The BB connections are framed by the general IBD network of the 3rd millennium BC (*Fig. 8*), which reflects the strong biological connections of the Pontic-Caspian steppe populations in the east all the way to the Kazakh steppe, and in the west to Central and Western Europe. Over the past decade, archaeogenomic studies have already uncovered Pontic-Caspian steppe ancestry moving east and west, and the IBD analysis now reveals directly the close genetic relations between individuals that underlie these ancestry patterns. The high rate of mobility within the BB network and more generally within the 3rd millennium BC can perhaps be best appreciated through a comparison with the same region during the preceding 4th millennium BC, that is before the arrival of steppe-related ancestry (*Fig. 8c*). In the BB

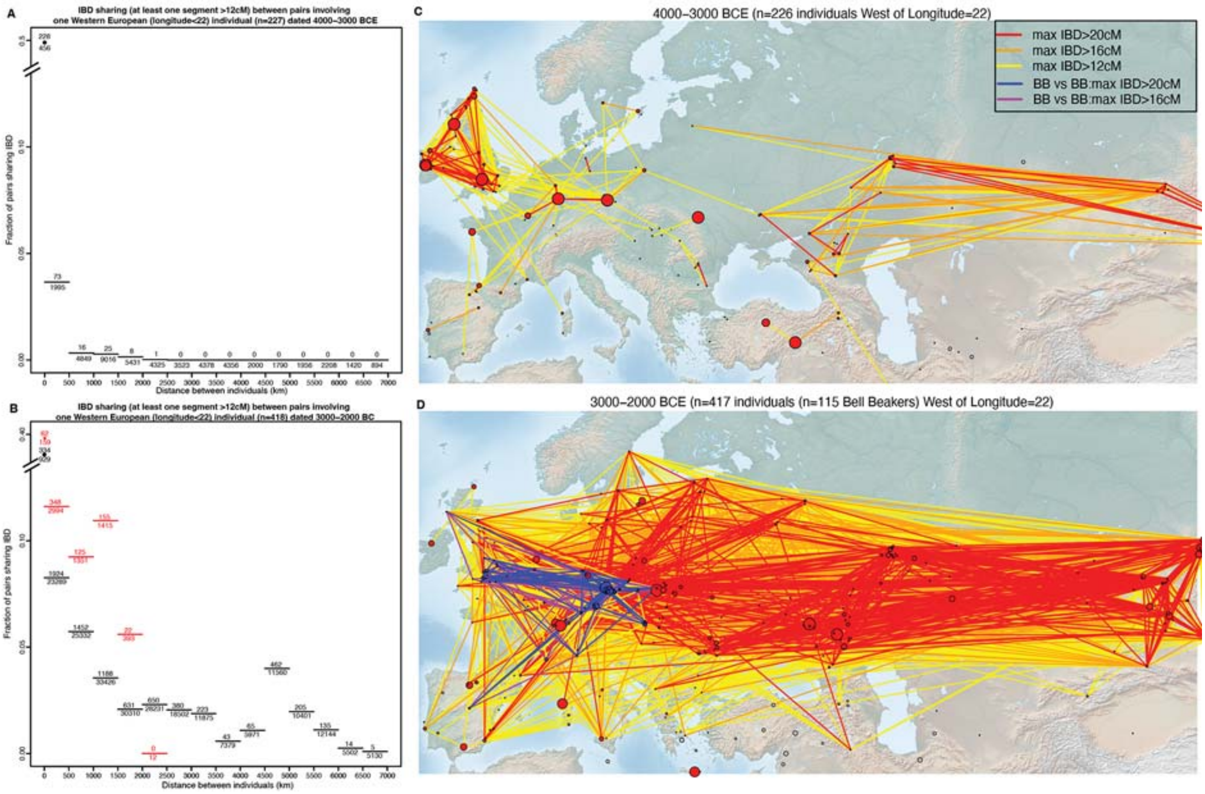

Fig. 8. Networks of close biological relatedness across West Eurasia between 4000–2000 BC as shown by IBD analysis. Fraction of pairs of individuals sharing at least one IBD segment during the a) 4th millennium BC and b) 3rd millennium BC (with rates obtained for pairs involving two BB individuals shown in red), depending on geographic distance. Only pairs involving one continental individual excavated west of 22 degrees longitude were considered. IBD connections between individuals during the c) 4th millennium BC and d) 3rd millennium BC. Lines are coloured according to the length of the longest IBD segment for a given pair. Connections between BB individuals are shown in different colours. (Image by I. Olalde)

network, the rate of IBD sharing remains relatively high even between pairs separated by 1000–1500 kilometres (rate of 11%) and 1500–2000 kilometres (rate of 6%) (*Fig. 8b*), while this figure was as low as 0.3% and 0.1%, respectively, during the 4th millennium BC (*Fig. 8a*). Visually, the lack of IBD segments >20cM between Bohemia and both Britain and Iberia (*Fig. 8c*) during the 4th millennium BC results in a lower rate of connectivity across regions that will later be strongly connected during the 3rd millennium BC and specifically through BB-associated individuals.

5. Regional studies

Iberian Peninsula

In Iberia, the earliest individuals with steppe ancestry in secure archaeological contexts are associated with elements of the BBP and found very close to the natural corridor connecting the northern plateau to the upper Ebro valley and the Cantabrian coast. At Arroyal I (Burgos, northern Spain), a young woman with ca. 37% steppe ancestry and dated to 2569–2344 cal BC (3950±26 BP, MAMS-25936; Jones *et al.* 2019) was buried inside a reused Megalithic structure with two BB pots (Olalde *et al.* 2018). Her

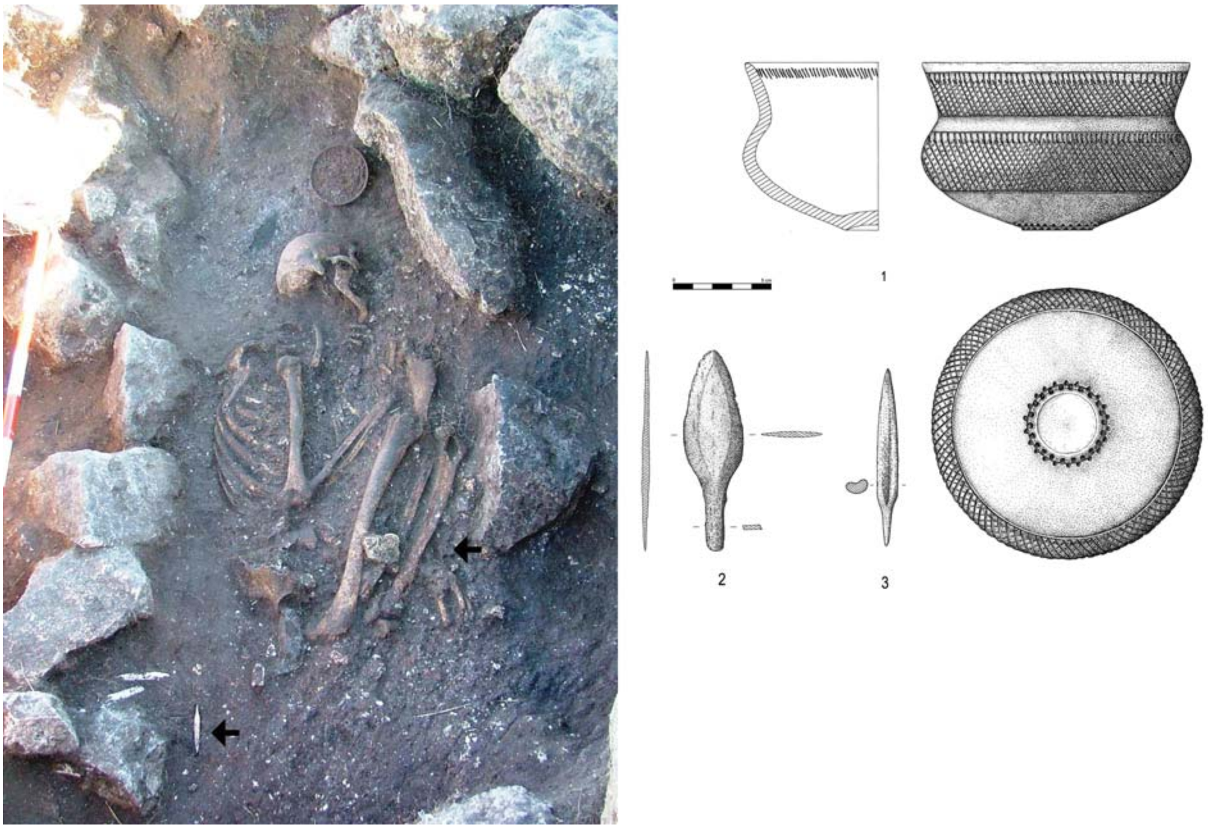

Fig. 9. Tomb 1 and associated grave goods at El Hundido (Monasterio de la Rodilla, Spain) (Alonso Fernández 2013)

body was surrounded by the long bones and skulls from previous burials, three of which yielded genome wide-data without steppe ancestry and included a father-son pair. At the site of El Hundido (Alonso Fernández 2013; 2015), 23 km from El Arroyal, two mature male individuals with steppe ancestry and a close kinship relationship (Olalde *et al.* 2019), the earliest dated to 2564–2299 cal BC (3933±32 BP, CSIC-1896), were buried again in a reused Megalithic structure with Ciempozuelos style beakers and Palmela points (*Fig. 9*). With the available data we can hypothesise that groups practising elements of the BBP arrived in Iberia ca. 2400 BC, possibly through the West Pyrenees, with a genetic make-up that strongly resembles that of the central European BB-associated individuals. These groups would have moved quickly throughout the central plateau, given that a man buried at the site of La Magdalena (Alcalá de Henares, central Spain; Heras y Martínez– Galera Olmo – Bastida Ramírez 2012) with Ciempozuelos type beaker, a Palmela point and a flint knife displays the highest levels of steppe ancestry in the entire peninsula (Olalde *et al.* 2018). He plots within the genetic variability of central European BB-associated individuals (*Fig. 4*), which points to little admixture with local Chalcolithic groups, even though other individuals without steppe ancestry are found in the same cemetery. The three cases mentioned above highlight that these incoming BB groups did not entirely break with previous funerary traditions, rather they repurpose them and were buried in close proximity to individuals with local ancestral origins.

From the central plateau these groups moved further south, reaching the southeast region by ca. 2200 BC (Villalba-Mouco *et al.* 2021), based on the earliest appearance of steppe ancestry in a double tomb from the site of Molinos de Papel (Caravaca, southeast Spain; Pujante Martínez 2005; Marín Muñoz *et al.* 2012) with grave goods related to the BBP, such as ivory buttons and copper

Palmela points. Steppe ancestry proportions tend to be lower in these and other Late Chalcolithic-EBA individuals from the south, implying substantial admixture as the incoming groups with steppe ancestry encountered local populations on their way south.

Northern Italy

Despite the small number of BB-associated individuals sequenced and published from Italy (Olalde *et al.* 2018; Fernandes *et al.* 2020; Saupe *et al.* 2021), the case of the Tomb 1 and 2 from Parma-via Guidorossi appear relevant to explore the dynamics of mobility, integration, and admixture in the southern regions of the BB world (*Fig. 10*). The two graves contain two and three individuals, respectively, and their quadrangular architecture resembles those of central European "houses of the dead", a feature that is known in other BB contexts in Northern Italy (such as Santa Cristina and Cà di Marco; Colini 1989–1902; Acanfora 1955; Tirabassi 2001) and also quite frequent among Bohemian, Moravian, and Austrian contexts (e.g. Turek 2006a).

In Tomb 1, a 30–40-year-old male individual (B) is positioned in left-side flexed position, N–S oriented, while a 30-year-old female individual (A) lays again crouched, but with opposite orientation

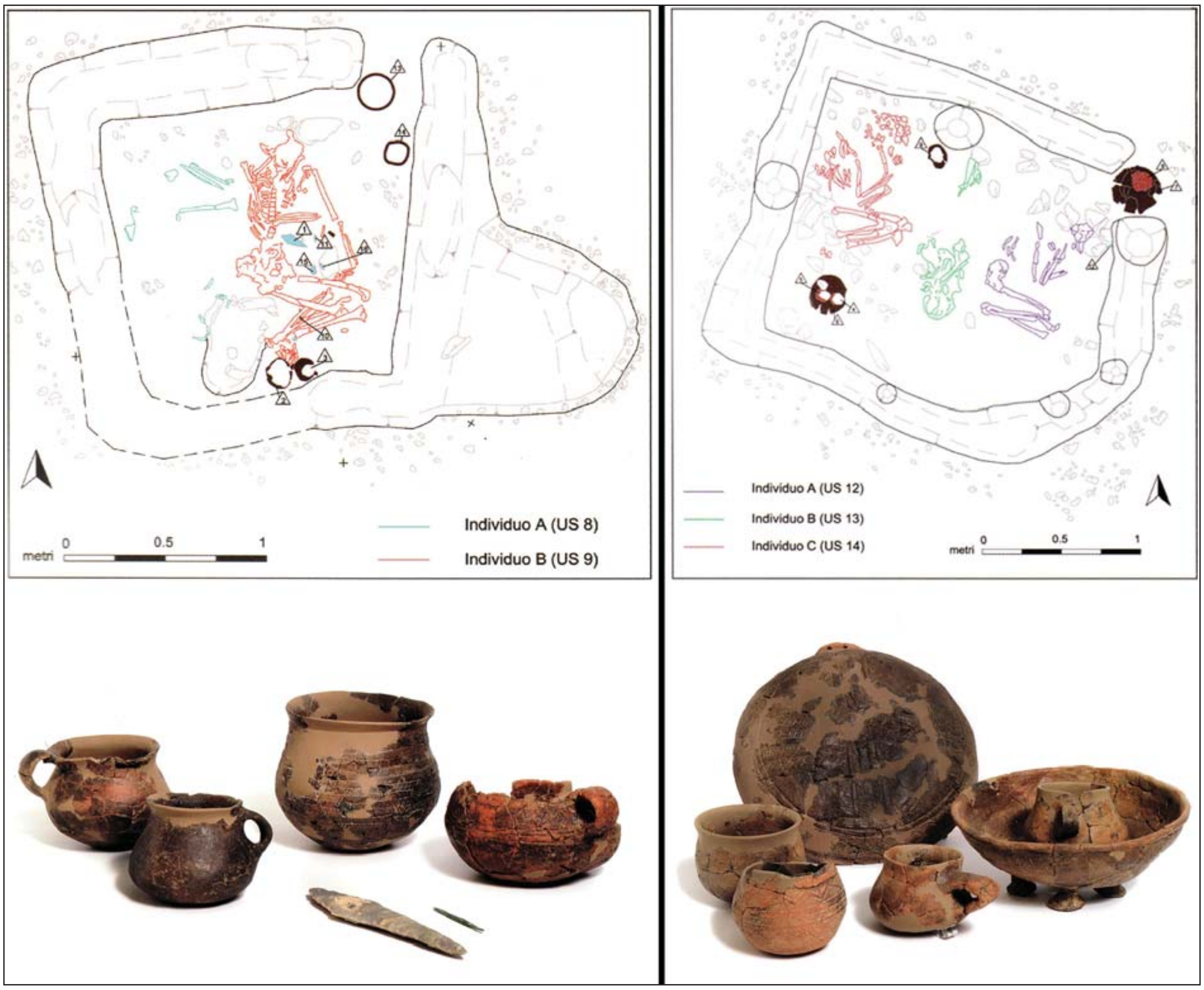

Fig. 10. Tomb 1 (left) and Tomb 2 (right) of Parma-via Guidorossi and the associated grave goods (mod. after Bernabò-Brea – Mazzieri 2013)

(the typical sex-differentiated "bipolar position") (Bernabò-Brea – Mazzieri 2013). The BB pottery, as well as a copper awl and a flint dagger seem associated with the adult male individual (and two vessels at the entrance of the tomb), who carries ca. 20% proportion of steppe ancestry, while this ancestry is nearly absent in the genome of the female individual (Olalde *et al.* 2018)[1]. Interestingly, his stature (170.8 cm) is around 7 cm higher than the average Copper Age Italian dataset and more than 10 cm higher than other Copper Age (pre-Bell Beaker) burials at via Guidorossi. His haplogroup is R1b-P312 and, looking at IBD connections, his closest relatives in the genetic dataset are at Prague 5-Malá Ohrada and Prague 5-Jinonice (Bohemia), Irlbach (Bavaria), Pełczyska (Southeastern Poland). The adult female has more distant connections with an adult male individual from grave 49 at Szigetszentmiklós, Felső Ürge-hegyi dűlő (Hungary), which include a BB, a bowl, a stone wristguard, a dagger and dates between 2460 and 2140 cal. BC (Patay 2013). The 15–18-year-old female individual B of Tomb 2 was deposed together with two mature male individuals, again with the typical BB taphonomic characteristics, and BB pottery, most notably a decorated polypod bowl (Bernabò-Brea – Mazzieri 2013). This individual carries ca. 25% steppe ancestry, but genetic data are not available for the other two individuals.

Although still quantitatively scarce, archaeological and archaeogenomic data converge in drawing a corridor of interaction that connects Central Europe, and particularly Bohemia, Bavaria and the Csepel Group in the middle-Danube area, with the Po plain in Northern Italy during the BB period. Coherently, strontium isotope data obtained from BB inhumations in Central Europe have shown an exceptional rate of migration: almost two thirds of the analysed samples revealed mobility through the lifetime (Price *et al.* 2004). This north-south corridor remains open during the subsequent phases, as testified by strong similarities in the material culture between these trans-Alpine and subalpine regions (e.g. *Brotlaibidole*, Únětice daggers, Gàta-Wieselburg pottery, etc.; Cardarelli *et al.* 2020, 233). Further genetic data of Italian BB and EBA individuals will likely reinforce this preliminary picture.

The two inhumations in tomb 1 also document a case of possible partnership between two individuals of different genetic ancestries: judging from the proportion of steppe ancestry, the male individual is unlikely a first-generation immigrant, but his biological relatedness with chronologically older Central European BB-associated individuals seems to indicate a possible origin of his lineage. Although we cannot generalise this model, such encounters and (free or forced) mixture with local populations may reflect the dynamic of expansion of the BB groups, at least in south and southwestern Europe where the steppe ancestry appears more diluted with those of the preceding groups. In our opinion, the possibility that BB-associated individuals in Italian contexts may lack the steppe ancestry or Y-chromosome R1b sub-lineages is also far from being unlikely. Pre-BB Eneolithic cemeteries (3000–2500 BC) in northern Italy are rather frequent, which suggests a relatively dense human presence, especially along the Adige River valley, in the lake Garda area and the Central Po plain. Such a presence is expected to be paralleled by relatively powerful socio-political structures. Similar to Iberia, the phenomenon of introgression of a significant amount of people from the regions north of the Alps, therefore, might result in a more articulated picture, in which BB-associated individuals are both part of the incoming lineage tradition, and at the same time, become adopted by local groups, strong enough not to be replaced/overcome and permeable to accept new ideas.

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[1] The individual B is dated to 2200–1930 cal. BC (Bernabò-Brea – Mazzieri 2013, 503). However, the date seems younger than expected, judging from the grave goods and the architectural similarities with Central European contexts which normally date 2500–2300 BC.

Central Europe – Bohemia

With genome-wide data available from ca. 60 individuals, Bohemia in today's Czech Republic is the most densely sampled region with regard to the BBP, followed by Germany (Mittelelbe-Saale and Bavaria) and England. Similar to other regions, mostly characteristic burials were sampled to determine the genomic profiles of the BB-associated individuals (Olalde *et al.* 2018; Papac *et al.* 2021) of the BB East Group (Heyd 2021). Papac and colleagues co-analysed the available genomic data, separated into a chronologically early BB phase (>2400 BC mean ^{14}C date, n=3) and late BB phase with mean ^{14}C dates younger than 2400 BC (n=56). Interestingly, the three female individuals, including female individual 77/99 from Tišice (TIS001; MAMS-30796; 3887±25 BP, 2464–2296 cal. BC; *Fig. 11*), from the earlier phase overlap in PC space with late Corded Ware individuals from the same region, whereas the later phase BB individuals carry on average 20% more EEF ancestry, which was modelled as being derived from local Middle Eneolithic farming groups. This and the observation of three female individuals with even higher proportions of EEF ancestry (HOP004, PRU001, I7283) suggests that individuals with high EEF or with Middle Eneolithic ancestry profile must have inhabited the region or nearby areas during the time and perhaps throughout the preceding centuries of the CW period but were less visible in the archaeological record. In general terms, the post-2400 BC BB phase represents both a period of assimilation, as seen from the individuals with higher and lower steppe ancestry, but also consolidation, which is particularly visible in the reduction of the Y chromosome lineage diversity to

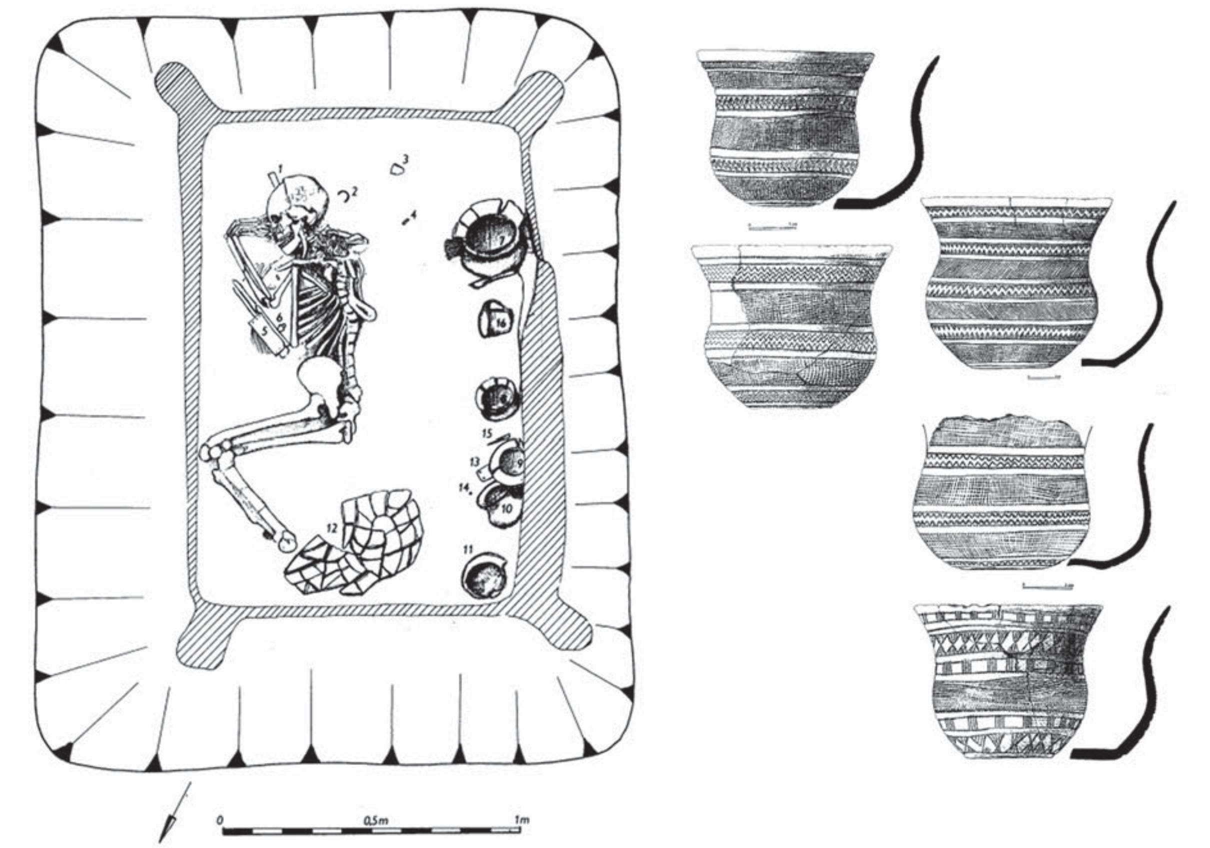

Fig. 11. Female individual 77/99 (TIS001; MAMS-30796 (3887±25 BP, 2464–2296 cal. BC)) from Tišice (Mělník district, Czech Republic), who was buried with five decorated Bell Beaker vessels (Turek 2006b; Papac et al. 2021)

nearly exclusively R1b-L2 lineages (see above). When combined with analogous to evidence from intra-site studies from other regions, this argues for a relatively strict patrilineally organised form of kinship, which was mutually exclusive from those of the preceding late CW groups in the region. Interestingly, the early CW phase in Bohemia was genetically more diverse and also includes male individuals with the Y chromosome lineage R1b-L151, which is the chronologically and geographically closest precursor of the central European Y lineage diversity.

6. Discussion

Twenty-five years after the seminal meeting at Riva del Garda, substantial progress was made on the topic of the BBP, in particular from isotope and archaeogenomic research. It is now clear how the genomic profiles of the individual buried in archetypal/characteristic BB burials look, how they compare with regards to the broader genetic transformations in prehistoric Europe. Moreover, it has also become clear how decisive the role the BB-associated individuals were in shaping the genomic profiles of central and western Europe at the time and their long-lasting genetic legacy in subsequent Bronze and Iron Age periods, in fact until today.

The first insights into the social organisation of BB communities are also available. However, more comparable studies from other regions covered by the BBP are needed to understand what the general trends, norms and exceptions were at the time. Importantly, recent studies that report on biological relatedness, kinship and social organisation in preceding Neolithic societies already show similar patterns with regards to exogamic practices, virilocality and patrilineality. In that sense, it still remains unclear as to what the exact differences in social organisation and community structure were between the Neolithic/Copper Age and BB groups that resulted in the observed differences in IBD networks or the drastic reduction in Y chromosome lineage diversity. Is it possible that the observed higher number of closer links is just the lasting effect of a recent bottleneck in the steppe-related ancestry that is shared by all BB-associated individuals? A related problem is that it is still largely unclear with whom we are dealing with. Are the BB-associated individuals studied thus far in the same way representative of the broader population at the time and thus truly comparable to the individuals from necropoles and collective graves of the preceding 4th millennium BC? The emerging emphasis on Single Grave Burial Rituals (SGBR) (see FURHOLT 2019) in many parts of Europe, with preceding, contemporaneous and subsequent forms, puts the BB burials into a different context, which also aligns with the reduced of the Y chromosome diversity and thus rather suggests a particular stratum of potentially hierarchical societies. If this holds true, an ensuing challenge will be to understand which factors contributed to this status, how it was maintained over generations and whether it held the same meaning in different communities and different regions of Europe.

Despite the seemingly large record of genomic data from BB contexts, the precise geographic origin and timing of the onset of the BBP are also still unclear. What became clear though is that the phenomenon is deeply connected to the spread of steppe-related ancestry and likely facilitated the continued spread to regions in western and southern Europe during the second half of the 3rd millennium BC. Here also, it is critical to acknowledge that the BBP forms part of the above-mentioned Single Grave Burial Ritual Complex and sits chronologically squarely amidst these pan-European developments. However, the real reason why it is so difficult to capture the origin and onset is that the large majority of archaeological and genomic data is coming from 'classical' BB period burials. These are relatively easy to assign from an archaeological perspective and thus were chosen first in order to characterise the genomic profiles of BB-associated individuals. With very few exceptions, most of these individuals date to after 2400 BC and more broadly overlap with the emerging Early Bronze Age phases ca. 2300/2200/2000

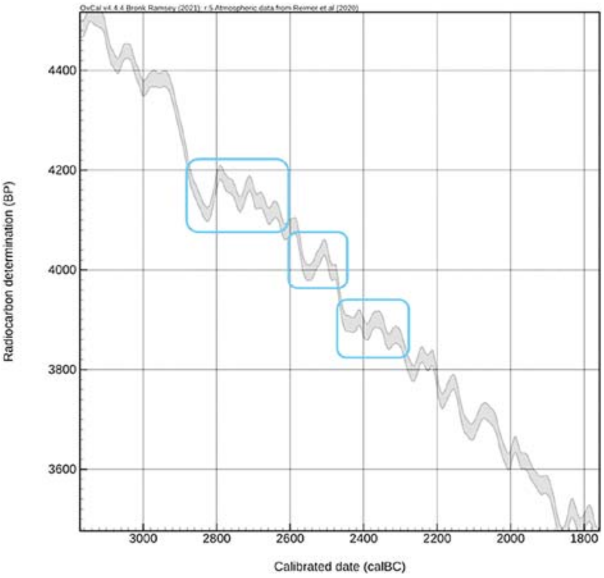

Fig. 12. Radiocarbon date calibration curve of temporal range that spans the 3rd millennium BC (Reimer et al. 2020). Blue squares highlight ranges of wiggles that are challenging for the fine chronologies of the Bell Beaker and preceding periods. (Image by W. Haak)

BC in many regions. However, the transitional phases leading up to the 'classical/late' BB phase remain ephemeral. The difficulty to address this issue is hampered by a well-known plateau in the calibration curve for radiocarbon dates, which hinders a finer resolution for the radiocarbon years equivalent to centuries ca. 2500–2300 BC (*Fig. 12*) (Reimer *et al.* 2020).

A systematic and integrated archaeological and genomic survey would be needed to shed more light onto the transition period. This involves thorough and critical assessments of stratigraphic evidence where possible, a critical revision/re-evaluation and/or universal applicability of typo-chronological approaches. IBD links between individuals are another promising avenue of research. Here, with the help of a denser dataset, it will be a matter of time to find critical 'cross-cultural' links, either between BB-associated individuals and those of preceding steppe ancestry-carrying individuals, or between the former and Late Copper Age from potentially local contexts. These could provide regional or even cross-regional anchor and reference points outside the calibration curve plateau. Moreover, pedigrees of more closely related individuals can offer resolution of generational order at the local scale, which can be used for Bayesian modelling and evaluation of typochronologies.

Even if we cannot pinpoint the exact timing and onset of the BBP at the moment, if we are considering the phenomenon to be linked to the major demographic and cultural transformation of the later 3rd millennium BC then some of the prevailing views of the past decades warrant re-evaluation. A point of contention that was also raised at the Riva conference was the reliability of the context and the radiocarbon from the Tagus valley in Portugal that are still building the main arguments for an expansion of the BBP from West to East. Historically, the BBP was defined on the basis of characteristic pottery, the iconic bell-shaped vessels, then expanded to include other grave goods (e.g., arm plate, dagger, arrowheads, etc.). The traditionally postulated origin in the Iberian Peninsula was based on stylistic evaluations, which generally applies a development from simple to complex decoration. This put the less decorated vessels from Iberia at the start of the evolutionary series and the all-over-ornamented beakers towards the end. This chronological sequence became henceforth the paradigm in Beaker-focussed archaeological research (Schmidt 1913; Bosch-Gimpera 1926; del Castillo Yurrita 1928; Sangmeister 1976; Harrison 1977; 1980). This dogmatic view was challenged only by the so-called 'Dutch model', which delineated the vessel type and decoration styles from the CW on the basis of stylistic comparisons and the first emerging radiocarbon chronologies (Lanting –Van der Waals 1976; Van der Waals 1984). The presence of CW analogies in western Europe had already been addressed by Edward Sangmeister (Sangmeister 1957; 1976; 1984), who in defence of the Iberian origin had developed the *Rückstrom* (reflux) theory. Equally non-parsimonious explanations were found for the chronological overlap of vessel types in southern Germany (as discovered by Ullrich 2008) and the problem of the so-called *Begleitkeramik* (accompanying pottery) in BB-associated contexts of the Upper Danubian region and the Carpathian Basin, which suggested an east-to-west trend of diffusion.

Another attempt to challenge and deconstruct the dogmatic hypothesis of the Iberian origin was offered only recently by Jeunesse (2015) who argues that much of the prevailing view is owed to the strong influence of charismatic scholars and the uncritical transmission rather than a systematic re-evaluation and/or integrated of new lines of evidence. However, more progressive takes by younger scholars and more recent reassessments have shed new light on the contested topic. For instance, Volker Heyd, who in 2001 still attested to the *Begleitkeramik* being a foreign element in the Danubian sphere that could have only been introduced alongside a late Bell Beaker phase, is now proposing the Upper Rhine region as a candidate for emergence of the phenomenon at the interface of western-most late CW groups, late local farming groups and possible influences from the Upper Danubian region (Heyd 2021).

However, despite many detailed regional studies available today, not all of these take on a critical stance. Furthermore, there has not been a systematic Pan-European (re-)assessment of regional typologies and absolute dates (Vander Linden 2024), no doubt a monumental undertaking given more than a century of archaeological data.

In the light of the presented archaeogenomic data above, we argue for the need of multi-proxy studies and integrated ways forward: these could include a systematic investigation of strata and potential reservoir effects and/or marine offsets, especially in coastal regions and/or estuaries, through the evaluation of dietary isotopes and comparison with livestock with a clear terrestrial signal. A focus on combined archaeological, anthropological and genomic evidence from transitional periods and contexts with mixed assemblages holds the promise of chronological placements either via refined radiocarbon chronologies or IBD networks of closer biological relations or a combination of both.

At a different scale, biogeochemistry can also contribute to clarify the strategies and trajectories of mobility through the BB network. As demonstrated by several studies, strontium, oxygen and sulphur isotope composition in human bones and teeth may highlight individual movements throughout the lifetime and generate “life histories”, emphasising the role of single, meaningful individuals inside macro-trend related to cultures and populations (Price *et al.* 2004; Parker Pearson *et al.* 2016; Knipper *et al.* 2017). Further, the parallel investigation of domestic animals, as well as emerging diseases such as zoonoses throughout the 3rd millennium BC will be necessary to trace the movement, mobility and trading patterns of humans and animals alike and potential routes of transmission. Finally, a solid record of the ecological and economic background during this time period is critical in order to evaluate the demographic and cultural transformations of the 3rd millennium BC as a holistic approach.

The potential and limitations of aDNA studies to reconstruct human prehistory will continue to be subject of scholarly debate and refinements of contextual as well as genetic scale and resolution. After all, archaeogenomics is only one tool in the toolbox of archaeological research. Human prehistory still leaves a lot to discover and the demographic processes that underpin the genetic data still need much better understanding. Here, spatially explicit modelling of demographic scenarios, informed by multiple lines of evidence, promises powerful and exciting areas of research in the future (Racimo *et al.* 2020). For example, what are the processes that shaped and reduced the Y chromosome diversity during the spread of steppe ancestry in the 3rd millennium BC such that there is only one dominant, nearly exclusive lineage in Bronze Age western Europe (Olalde *et al.* 2018; 2019; Villalba-Mouco *et al.* 2021)? Interestingly, despite millions of recombinant variants, in such cases there is a decent chance for a comeback of uniparentally-inherited genetic lineages (i.e. the paternal Y chromosome), which could help unravel such a process at genealogical level of detail.

To reconcile this new form of genetic data with the archaeological record and to build and test new hypotheses remains a common task for all disciplines that share a common interest in the complex dispersal and admixture history of humankind. However, since the origin and evolution of prehistoric societies is also a topic of significant interest and appeal to the general public, it is paramount to interweave the lines of evidence from the various disciplines involved in the best possible and most informed way.

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The *Transformation of Europe in the Third Millennium BC, Part 1* presents the proceedings of the second Riva del Garda conference on the Bell Beaker phenomenon (c. 2700–2000 BC), exploring one of the great turning points of European prehistory. With 32 contributions, grouped into six chapters, authored by 54 scholars from over 15 countries, the book brings together latest discoveries and exciting research results from across Europe. It spans topics like the origins and spread of Bell Beakers, their social and ideological dimensions, regional identities, ritual and economic practices, mobility and migrations, and the far-reaching impact of ancient DNA. Being part 1 of a two-part international conference project, the book offers a fresh synthesis of how Beaker groups connected distant regions and so shaped the cultural landscapes of the western half of the European continent.

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