

**PALEOGENOMICS AND ARCHAEOLOGY:
RECENT DEBATES ABOUT THE SPREAD OF STEPPE ANCESTRY
IN WESTERNMOST EUROPE**

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The recent development of paleogenetics has had a large impact on much of archaeology. Particularly surprising has been the discovery of a connection between the Iberian Peninsula and the Eurasian steppes, an unexpected link between the first stages of metallurgy at opposite ends of Europe. Recent studies of human remains from Copper and Bronze Age Spain and Portugal have shown a significant presence of genomes of types geneticists attribute to the Yamnaya culture and historical community. Geneticists had already identified this genome in central European archaeological contexts. Interpretation of these results has led to controversy concerning their historical significance and their importance for explaining important cultural changes, such as the origin of the Bronze Age in Iberia. As a result, many Spanish and Portuguese prehistorians have “discovered” the cultures of the steppes. Their inclusion has broadened and enriched debates concerning Iberian prehistory. This article reviews recent literature so as to assess the state of play on the contribution of paleogenetics to Iberian prehistory and to reflect on the impact of the Yamnaya culture’s unexpected burst onto its scene.

Keywords: archaeology, genomic research, radiocarbon chronology, Eurasia, Iberian Peninsula, Chalcolithic, Bronze Age, Bell Beakers, steppe ancestry, haplotype YR1B.

**ПАЛЕОГЕНОМИКА И АРХЕОЛОГИЯ:
ПОСЛЕДНИЕ ДИСКУССИИ О РАСПРОСТРАНЕНИИ
ГЕНОВ СТЕПНОГО ПРОИСХОЖДЕНИЯ В ЗАПАДНОЙ ЕВРОПЕ**

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Недавнее развитие палеогенетики оказало большое влияние на многие аспекты археологии. Одним из них, особенно удивительным, стало соединение евразийских степей с Иберийским полуостровом, установившее неожиданную связь между ранними металлургическими этапами окраин Европы. Недавние исследования человеческих останков из месторождений энеолита и бронзового века в Испании и Португалии показали значительное присутствие характерных геномов генетических типов, которые генетики приписывают ямной историко-культурной общности. Ранее это генетическое наследие также было установлено генетиками в среде населения Центральной Европы. Интерпретация данных результатов вызвала споры относительно исторического значения этого явления и его важности в объяснении базовых культурных изменений, одним из которых может быть само происхождение иберийского бронзового века. В результате этой полемики испанские и португальские исследователи доисторического времен «открыли» для себя степные культуры. Включение этих культур в дискуссию по вопросу о доисторическом периоде полуострова само по себе является весьма плодотворным результатом. Эта статья предполагает представление информации о состоянии этого вопроса, используя самую последнюю библиографию, а также рассмотрение некоторых вопросов, обусловленных неожиданным вторжением ямной культуры на Иберийский полуостров.

Ключевые слова: археология, исследования генома, радиоуглеродный хронологический анализ, Евразия, Пиренейский полуостров, энеолит, бронзовый век, колоколовидные кубки, степное происхождение, гаплотип YR1B.

In principle there is no direct connection between the prehistories of the Iberian Peninsula and the Eurasian steppes. Until very recently few prehistorians of Iberia (Antipina, Morales 2005) knew the specific characteristics or terms that define the culture-historical sequence in the gigantic eastern extension of the European plain (Kohl 2007, Chernykh 1992, 2008). This situation changed unexpectedly because of the synergy between pharmaceutical and paleogenetic

research (Krause, Pääbo 2016, Lewis-Kraus 2019) that opened opportunities for collaboration between paleogeneticists and archaeologists (Morgunova, Turetsky 2019, p. 98-99). Various articles arising from this collaboration (Allentoft et al. 2015, Haak et al. 2015) revealed the significance of a lineage “sharing predominantly R1b Y chromosomes” (Mathieson et al. 2015, Armit, Reich 2021) in the configuration of the genetic map of modern European populations.

This lineage is “associated with the arrival steppe migrants in central Europe after 3000 bc” (Olalde et al. 2018, p. 320, Suppl. Tab. 4). During the 3rd millennium BC these traits would spread rapidly in central European populations, reaching Iberia at the end of that millennium (Olalde et al. 2019), a possibility archaeologists had rejected (Mathieson et al. 2015). This evidence establishes a direct link between the opposite ends of Europe that must be evaluated and interpreted.

This article is dedicated to our friend S.V. Kuzminykh, one of the foremost experts on archaeological record and literature on the earliest metallurgy of Eurasia (Koreniako 2012, Gaydukov et al. 2021). Our contribution takes for granted the historical reality of the occupation of the steppe zone by pastoralists in the 3rd millennium, considers the historical implications of the identification in westernmost Europe of genetic traits associated with these steppe populations, and reiterates the need for a critical discussion of this evidence (Vicent García, Martínez Navarrete 2018).

Palaeogenetics and History

Paleogenetic facts are not, *prima facie*, historical facts except insofar as they are proper archaeological facts. Their historical interpretation depends on their archaeological quality. Their importance can only be established in reference to their context and their spatial and temporal position. The differences in purpose and scale that exist between archaeological and paleogenetic practice make the historical interpretation of the latter difficult.

The goal of palaeogenetics is to explain the configuration of human populations in terms of past demographic events whose echo can be seen in the patterning that exists today (Mathieson et al. 2015, p. 500). The most influential work on the palaeogenetics of western Eurasia is based on “time transects” that isolate periods of change by maximizing the temporal and spatial range of the sample. The resulting data is aggregated into “populations” that are labeled by terms referring to archaeological cultures and/or chronological periods. Inevitably, this creates a false sense that the two registers are identical or at least run in parallel (see the criticisms, some of them self-criticisms, in Calloway 2018, Editorial 2018, Eisenmann et al. 2018). The underlying problem is that palaeogenetic practice assumes that archaeological cultures, understood as units of ethno-cultural identity, are equivalent to homogenous biological populations (Furholt 2020, p. 23-24). Consequently, it is assumed that the palaeogenetic sample of prehistoric individuals

belonging to the same culture-historical entity allows the corresponding population to be characterized as a whole, independently of the specific contexts from which the remains of those individuals were obtained.

Based on this methodology, historical interpretations of the genetic changes are constructed as narratives that refer to the dynamics (migration, substitution, admixture) of the biological populations represented by archaeological cultures. This makes it difficult to avoid a circular argument. Nevertheless, only archaeological contextualization of the palaeogenetic data can establish in what sense and to what degree the palaeogenetic sample represents prehistoric populations and its spatial and temporal distribution is representative of the historical dynamics of the societies to which those populations belonged.

Iberia: The archaeological record and palaeogenetic data

The work of Olalde et al. (2019) in Iberia follows the above methodology. The research is based on a “time transect” of 8000 years (from the Mesolithic to the Modern Era). This is subdivided using the traditional archaeological periods (Mesolithic, Neolithic, Copper Age, Bronze Age, etc.). The results obtained for the 3rd and 2nd millennia calBC seem to indicate that the start of the early Bronze Age (BA) coincides with the almost complete replacement of autochthonous male lineages by others of steppe ancestry (Marshall 2018), although the Y R1b haplotype is marginally present in Copper Age (CA) contexts as of 2500 calBC (Fig. 1). This substitution is much less evident in female lineages (Olalde et al. 2019, p. 1231).

Obviously these results would transform our understanding of processes of late prehistoric prehistory in Iberia. They require an archaeological critique that focuses on cultural and chronological assignation of the individuals in the sample. To assess how representative the Olalde et al. (2019) sample may be, we have reviewed the 142 samples dated between 2500 and 900 calBC, that is to say, from the earliest appearance of the Y R1b haplotype to the latest sample attributed to BA (Fig. 2: Above, and Table). Two male individuals were excluded from the selected sample due to the lack of information about their Y-Chromosome.

First one must consider the archaeological quality of the sample. The supplementary materials (SI 1) for Olalde et al. (2019) show that, with a few valuable exceptions, these proceed from old excavations, *palimpsests* in which it is

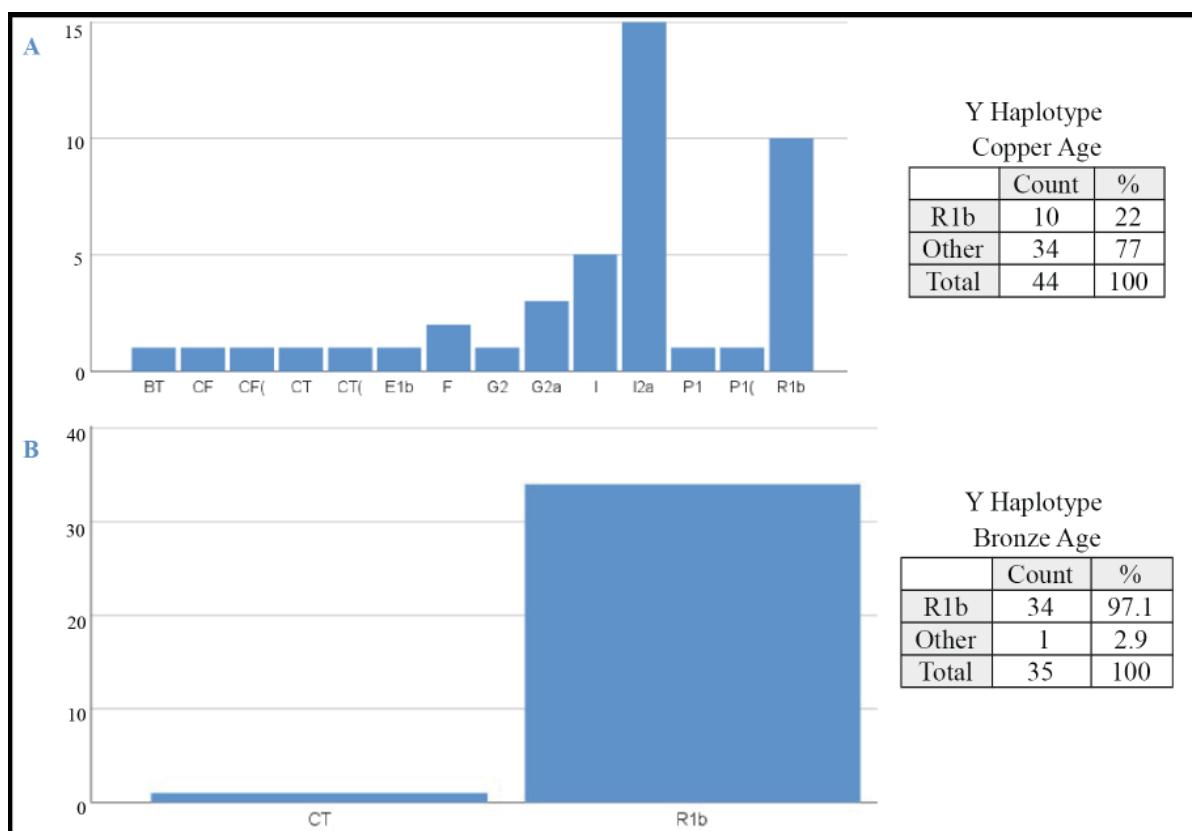


Fig. 1. Distribution of Y haplotypes dated from 2500 to 900 cal BC according to their assigned archaeological phase.

Source: Olalde et al., 2019, Tab. S1.

Рис. 1. Распределение Y гаплотипов, датированных от 2500 до 900 лет до н.э. в соответствии с их установленной археологической фазой. Источник: Olalde et al., 2019, Tab. S1.

difficult to establish the specific context of the human remains, or even finds with no context. Human remains without associated grave goods are assigned to an archaeological complex based on their radiocarbon dates, a circularity that complicates the definition of the CA/BA transition.

This makes the quality of the dating series an important issue. 51 samples (35.9% of the total) (Fig. 3) have direct radiocarbon dates.

The time brackets of the remaining 91 (64.1%, Fig. 4) are based on their contexts (stratigraphic positions, typological associations, etc.) or on combinations of C14 dates for non-human organic materials in those contexts. As already mentioned, these contextual dates are often problematic.

Olalde et al. (2019, p.1231) take for granted the conventional 2200 calBC boundary between CA and BA, but the oldest assigned to BA (28 Castillejo del Bonete) has a 2σ range of 2014-1781 calBC and falls between two samples assigned to CA (26, 29) (Fig. 3). The other direct dates for BA are all later than 1900 BC, while the most recent date from a CA context (29 Camino de las Yeseras) has a 2σ range of 1971-1745 calBC. If one includes the samples that

only have indirect chronological estimates, the problem is accentuated: 21 samples attributed to the Copper Age are later than 2200 calBC. In sum, the direct and indirect dates for the samples show a great degree of indetermination in the 2200-1990 calBC interval. This undoubtedly is the result of the low quality of archaeological cultural assignations. The available data do not permit an archaeological characterization of the CA/BA transition, but Olalde et al. nevertheless treat the boundary in absolute terms, as is usual in large-scale palaeogenetic studies (Furholt 2020, p. 23-24).

This dichotomous treatment also has direct consequences for the sampling strategy. Recent research has shown that CA collective burial chambers continued to be used in BA (Aranda Jiménez et al. 2017). If the criterion used to discriminate between CA and BA is to identify the latter with burials that are individualized and/or associated with Beaker elements, the sampling strategy may have excluded part of the population from the sample. The Beaker phenomenon coincides with the appearance of individualized burial rites, sometimes inside collective burial chambers, but it does not necessarily imply individual inhumation. There is great variability

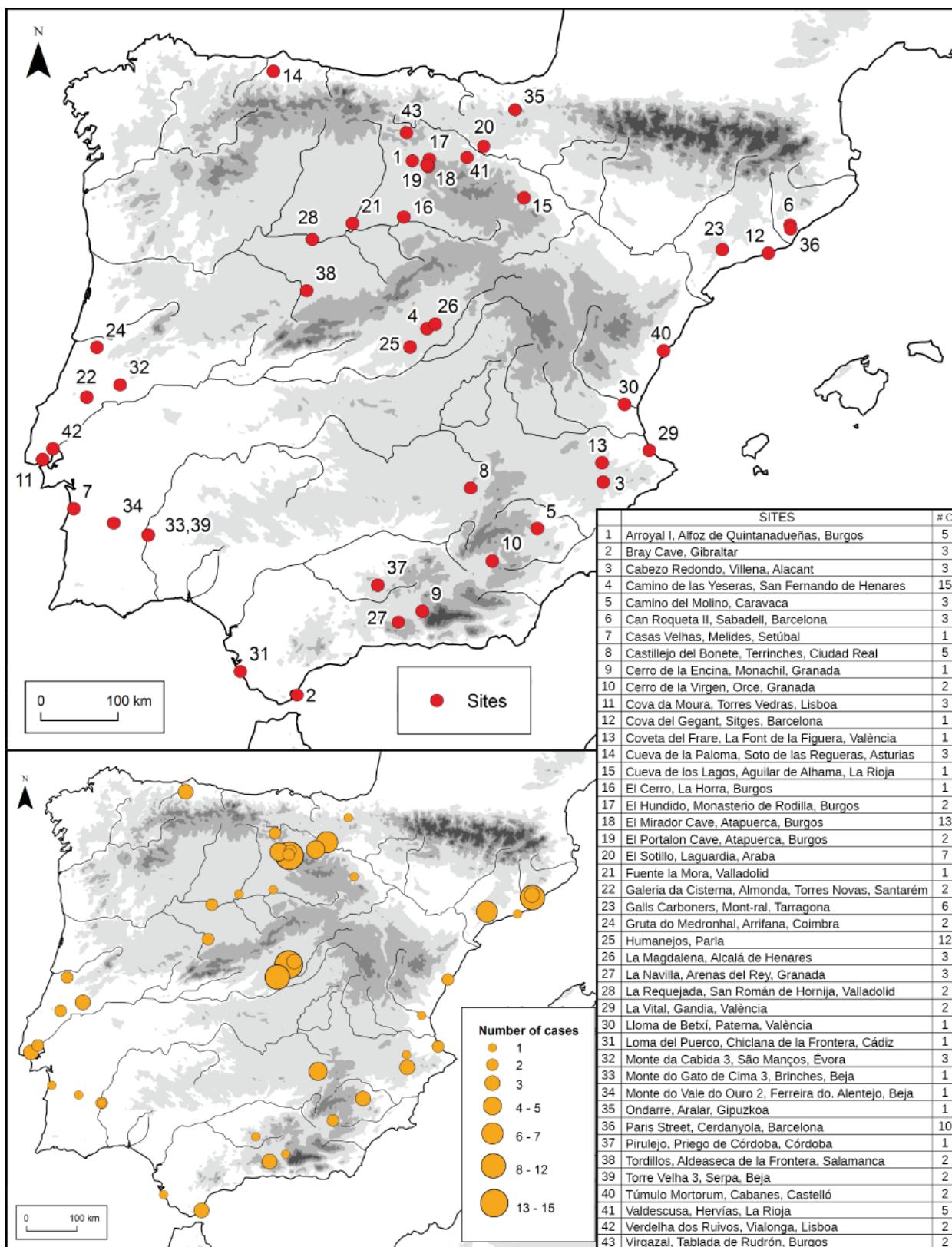


Fig. 2. Above: Geographical distribution of the 43 archaeological sites with samples dated between 2500 and 900 cal BC. For each site the table includes its identification, full name, and number of samples. Below: Cartographic representation of the sample size from those sites.

Source: Olalde et al., 2019, Tab. S1.

Рис. 2. Вверху: Географическое распределение 43 археологических памятников с образцами, датируемыми от 2500 до 900 гг. до н. э. В таблице содержится идентификатор, полное наименование и количество образцов для каждого памятника. Внизу: Картографическое изображение выборки с указанных памятников.

Источник: Olalde et al., 2019, Tab. S1.

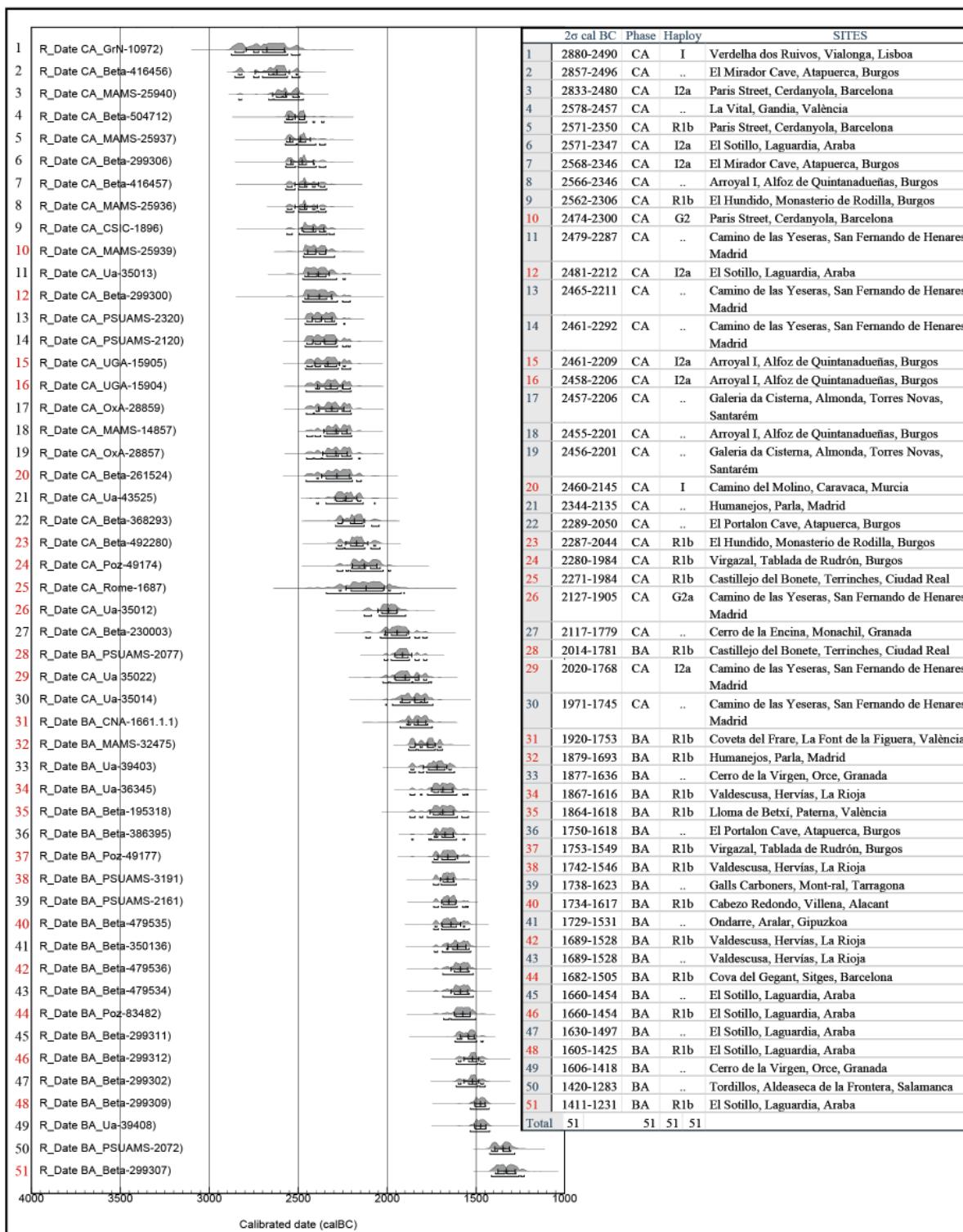


Fig. 3. Calibrations of the 51 ^{14}C -dated genetic samples, including their assigned archaeological phases (CA= Copper Age; BA= Bronze Age) (Source: Olalde et al., 2019, Tab. S1). The number in the column to the left identifies the dates in the table to the right and in the text. Numbers in red indicate those with haplotype Y R1b. The table also includes the 2σ calibration range, the assigned phase, the Y haplotype (absent for female individuals), and the site name. Calibration used the OxCal v4.4.4 program (Bronk Ramsey, 2021 <https://c14.arch.ox.ac.uk/oxcal.html> access october 2021); r:5 Atmospheric data from Reimer et al. (2020).

Рис. 3. Калибровка 51 датированных методом ^{14}C генетических образцов, включая присвоенные им археологические фазы (СА = медный век; ВА = бронзовый век) (Источник: Олалде и др. 2019, Табл. S1). Число в столбце слева обозначает даты в таблице справа и в тексте. Красным цветом обозначены образцы с гаплотипом Y R1b. Таблица также включает в себя диапазон калибровки 2σ , присвоенную фазу, гаплотип Y (отсутствует у лиц женского пола) и наименование памятника. Для калибровки использовалась программа OxCal v4.4.4 (Bronk Ramsey, 2021 <https://c14.arch.ox.ac.uk/oxcal.html>, дата обращения октябрь 2021 г.); r:5 Атмосферные данные по: Reimer et al., 2020.

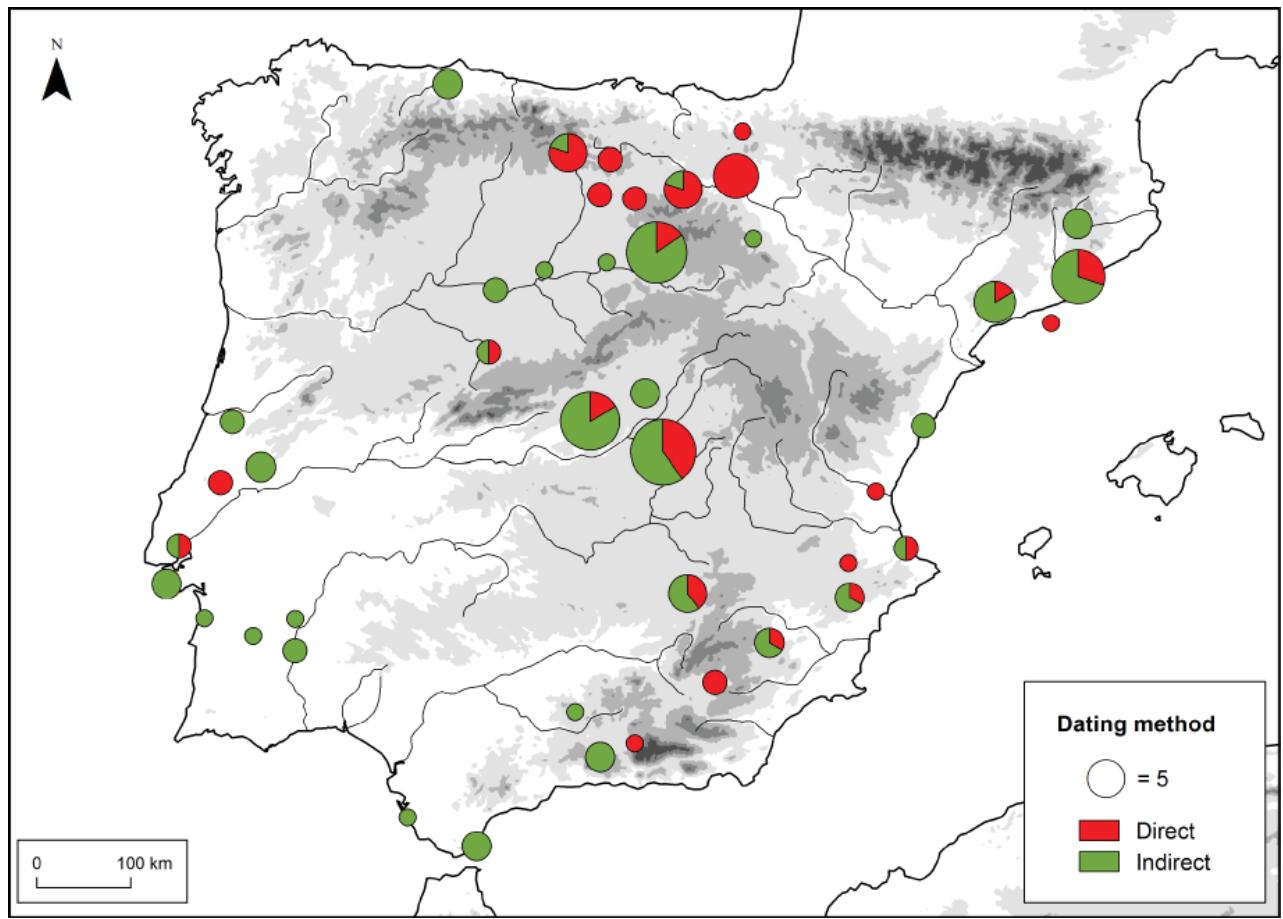


Fig. 4. Cartographic representation of the proportion of direct and indirect dates for each site selected in this article.
Source: Olalde et al., 2019, Tab. S1.

Рис. 4. Картографическое изображение долей прямых и косвенных датировок для каждого памятника, указанного в данной статье. Источник: Olalde et al., 2019, Tab. S1.

that is hard to systematize (Díaz-del-Río et al. 2017, Soriano 2021).

One must also consider the spatial aspect of the sampling. In general, the selection of samples combines opportunism (the availability of samples) with an effort to cover areas throughout Iberia. There are significant gaps, however, in two regions central to CA and BA development in Iberia: the classic Argaric of the southeast and the Guadalquivir drainage, each represented by just one site, Cabezo Redondo de Villena and Cerro de la Virgen respectively.

Another important aspect of the sampling strategy is a degree of regional redundancy. A substantial proportion of the sites that have sampled cluster together (Fig. 2: below and table). As a result, if one of the sites in the cluster has an early occurrence of the Y R1b haplotype, later occurrences within the cluster do not represent a change: they introduce redundancy into the data set instead of broadening the overall sample.

Finally, it is significant that, except for Cueva de la Paloma on the Cantabrian coast (estimated age 2500-2200 calBC), the early occurrences of

Y R1b almost are all in the NE quadrant of Iberia. Castillejo del Bonete is the only site south of the 40th parallel with a direct for a Y R1b individual. The individuals from Monte da Cabida (Évora) and Pirulejo (Córdoba) have estimated dates with a high degree of uncertainty (2200-1700 and 2100-1450 calBC, respectively). If we set these cases aside and consider only the directly dated ones, we can conclude that spread of the Y R1b haplotype beyond NE Iberia occurs after 1950 calBC.

Discussion

We have shown that the archaeological evidence assembled by Olalde et al. (2019) suffers from insufficient contextual integrity, low chronological resolution, potential sampling biases, and uneven geographic distribution. This does not invalidate the paleogenetic significance of the results, but it does limit the possibilities of interpreting them as history. Even so, one can discard some interpretative hypotheses and point to possible directions for future research.

The historical narratives that would explain the results of large-scale palaeogenetic studies

usually refer to concrete historical events, such as migrations, and Olalde et al. (2019) is no exception. According to D. Reich, one of the co-authors, the substitution of CA male lineages in Iberia would be explained as follows: "Every man in Spain was wiped out 4500 years ago by hostile invaders" (Marshall 2018). This formulation was picked up by the Spanish and Portuguese media and gave rise to considerable controversy. In the end, the publication of the results doesn't mention this interpretation and limits itself to a prudent suspension of judgement (Olalde et al. 2019, p. 1231).

Indeed, the Iberian archaeological record shows no sign of the sort of disruption proposed by Reich or even of the less gruesome "massive migrations" postulated by Allentoft et al. (2015) and authors to account for the evidence in central and eastern Europe. If "migration" is understood to mean what one can infer from these interpretations, namely the displacement of entire social units (not isolated individuals), one would suppose that the migrants would bring with them their own material culture and that this assemblage (like the genetic characteristics of their skeletal remains) would form part of the archaeological record of the places they passed through and of their final destination.

As we hope to have shown in the previous section, the data provided by Olalde et al 2019 suggests that the process of substitution of male lineages occurred gradually over the course of the period 2500-1900 calBC. This coincides with the Beaker phenomenon, so that one might suppose that beakers and their associated paraphernalia are the archaeological marker of the immigrants with steppe ancestry in Iberia. There currently exists a certain consensus about the transcultural and transethnic character of the Beaker phenomenon (Olalde et al. 2018) as a vast sphere of interaction and exchange across all of western Europe. Great Britain (Armit, Reich 2021) is a case with reasonably good evidence for a Beaker association with ethnocultural displacements, but as Olalde et al. 2018 note, in general the elements of the Beaker complex are added to local archaeological cultures without replacing them. As we have seen, the spread of the Y R1b haplotype doesn't go beyond the center of Iberia until 1900 calBC. This shows that the genetic diffusion and the Beaker network are causally independent (all the more so if one accepts the date of c. 2750 BC from Portugal [Cardoso 2014] as the earliest for Beakers in all of Europe as Olalde et al. 2018, p. 190 consider to be possible).

The archaeological record for the CA/BA transition in Iberia does not show invasions from across the Pyrenees. The transition appears to have causes that are fundamentally economic and political (Díaz-del-Río 2020, 2022), and are related to changes in metallurgical (Rovira, Montero 2013, Rovira 2017, Montero-Ruiz et al. 2021) and agro-pastoral production like those that occur in the steppes (Antipina, Morales 2005, Wilkin et al. 2021, Curry 2021). The reconstructions of the later prehistoric demography of Iberia using summed calibrated date probability distributions (Balsera et al. 2015, Drake et al. 2017) show a great continuity in an estimated population growth curve that falls within the confidence limits of natural increase without any appreciable disruptions.

In conclusion, both the archaeological record and the palaeogenetic data seem to be incompatible with a migrationist explanation of the genetic change in Iberia (especially a version as extreme as Reich's). The gradual, long-term character of the spread of steppe ancestry (Fig. 5) seems to suggest a percolation model of change, where large-scale outcomes are brought about over the long term as a result of many, local interchanges between communities. These local events affect both the material culture (e.g., Beakers) and the individual reproductive partners that are the locus of genetic intercourse. The association of material and genetic exchanges is compatible with what we know to be the forms of social reproduction in segmentary societies where interchange is based on social values, formalization of alliances, real and fictive kinship, and so on.

This perspective also may help explain something that has concerned the geneticists themselves, namely the "sex bias" in the processes of genetic change. The intercourse that, as we postulate, constitutes the actual basis of genetic change clearly is mediated by the structure of the kinship system. This acts a social filter that regulates the outcomes of purely biostatistical combinations, so that variations in these systems structure what one observes in the paleogenetic record. It is plausible, for example, that exogamous matrilocal groups would be net exporters of Y chromosomes and viceversa. Furthermore the possible practice of polygyny could multiply the gene flow of male lineages.

The processes of genetic change neither demand nor exclude the long-distance displacement of migratory individuals. Genes can flow through relatively immobile populations as can elements of material culture (in many cases associated with reproductive intercourse).

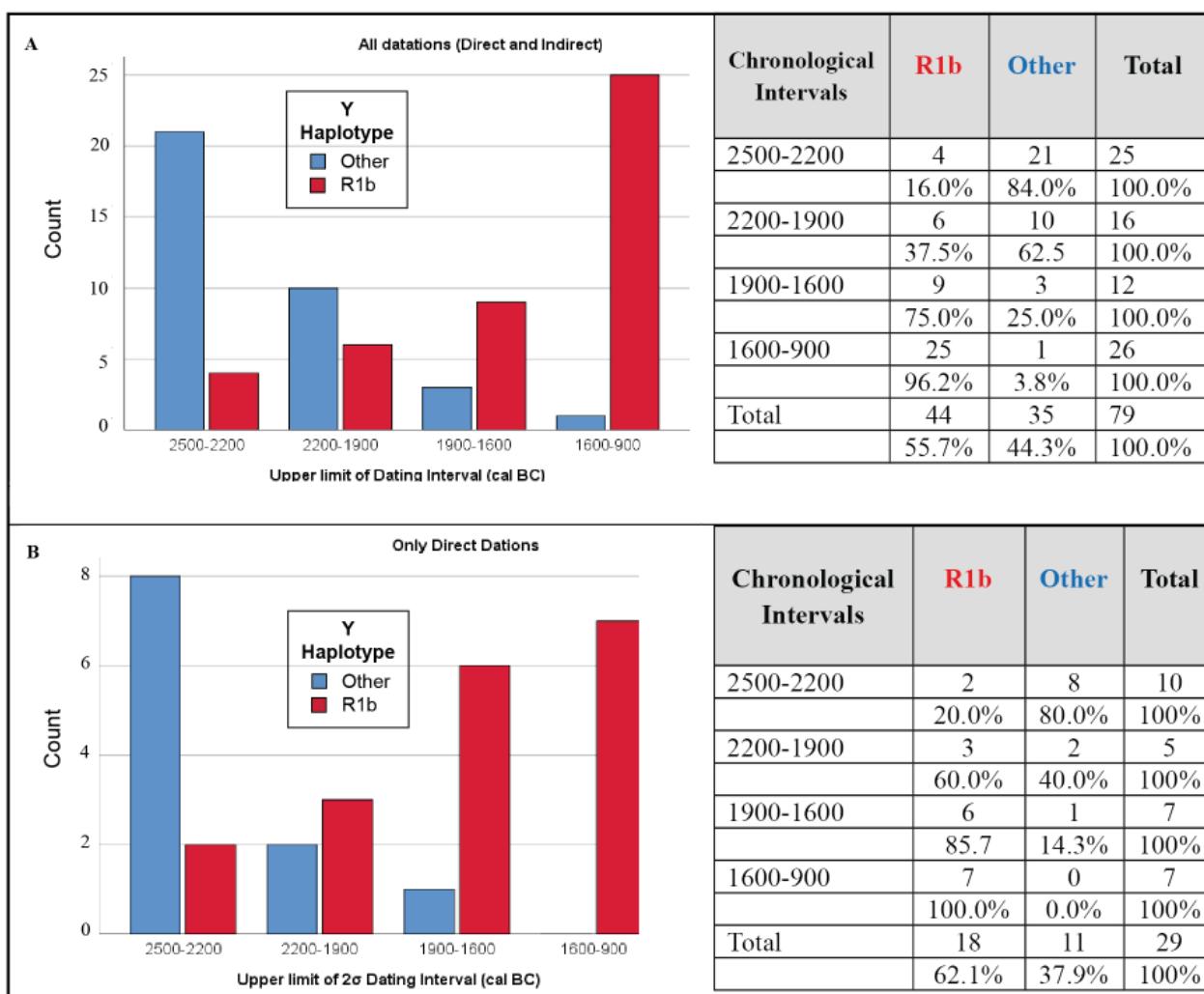


Fig. 5. Frequency distribution of Y haplotypes grouped by the most recent date of their respective chronological intervals. The diagrams represent the number of cases in each group. The Y haplotypes are presented in two classes “R1b” and “Other” (all non-R1b variants). The upper diagram shows all 79 male individuals listed in Olalde et al. (2019, Tab. S1) directly or indirectly dated in the interval 2500–900 cal BC. The lower diagram shows only the samples directly dated by ^{14}C . The tables to the right give the data used to make the diagrams together with percentage frequencies for each time interval and the corresponding marginal totals. Grouping the samples into 300-year intervals (except for the most recent bracket that shows all cases later than 1600 cal BC) reveals the gradual, staggered progression over time of the YR1b variant in Iberia.

Рис. 5. Распределение по частоте гаплотипов Y, сгруппированных по самой недавней дате их соответствующих хронологических интервалов. На схеме указано количество случаев для каждой группы. Гаплотипы Y представлены двумя классами «R1b» и «Прочие» (все варианты, кроме R1b). На схеме вверху представлены все 79 лиц мужского пола, перечисленные Олалде и др. (2019, Табл. S1), прямо или косвенно датированные в интервале от 2500 до 900 гг. до н.э. На нижней схеме представлены только образцы, прямо датированные методом ^{14}C . В таблицах справа приведены данные, использованные для построения схем, а также процентная частота для каждого временного интервала и соответствующие предельные значения. Группировка образцов по 300-летним интервалам (за исключением последней группы, в которой представлены все датировки позже 1600 г. до н.э.) демонстрирует постепенное ступенчатое развитие варианта YR1b в Иберии с течением времени.

The impact of this percolation must be understood in demographic terms (population densities, growth rates, etc.). From this perspective, under conditions of very low demographic density small population units can have a large impact on genetic drift. This seems to be the case in Iberia, and perhaps all of western Europe. This would explain the success of “steppe ancestry” without having to recur to the *deus ex machina*

of massive migrations. This perspective presents new challenges to paleogenetic research: it must undertake the systematic, intensive studies that would complement extensive “time transects” with regional and local approaches that would clarify the concrete mechanisms of genetic interchange and the social filters through which such interchanges must pass. This would require, of course, close attention to archaeological

contexts within a precise chronological framework.

Conclusions

The evidence in Olalde et al. (2019) show that beginning in the middle of the 3rd millennium calBC Iberia entered a process of genetic homogenization with the rest of Europe. This is expressed in the growing weight of male lineages characterized by the Y R1b haplotype, the so-called “steppe” or “Yamnaya” ancestry. This begins during the Beaker episode of trans-regional interaction and culminates in the second quarter of the 2nd millennium calBC, during the Bronze Age (Fig. 5). The absence of significant cultural or demographic disruptions over the course of this process is an argument in favor of a percolation model of the entry of foreign genes as part of normal interchanges between local and/or regional groups. However, the low archaeological and chronological resolution of the available evidence does not permit a clear decision between the percolation model and the classic *Völkerwanderung* narrative that presupposes the arrival of large populations in successive migratory waves. This issue can only be addressed in the future by combining the extensive research strategies over large spatio-temporal scales characteristic of most paleogenetic studies with

a complementary, intensive strategy that will address the “social filters” (kinship systems, local exchange networks) and “archaeological filters” (differential burial practices within and between communities and their degrees of archaeological visibility) that control what enters the paleogenetic record.

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