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Mining Data on the Spread of Early Metallurgy: Revisiting the Carpathian Hypothesis with Ancient Genomes

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Abstract. *This study presents results relevant to understanding the spread of early metallurgy obtained by extracting patterns from a dataset of ancient genomes. It finds that, conservatively, the spread of metallurgy into Italy Remedello Chalcolithic culture can be linked to a probably Bulgaria Chalcolithic-shifted population represented by the genome of an individual associated with Bodrogkeresztúr pottery in Romania. Also conservatively, either a population related to this sample or to populations sampled from the Chalcolithic era Great Hungarian Plain can be associated with Italy North Bell Beakers and some Bell Beakers in France. Traces the samples examined have left give a sense of the geographical spread of the populations they represent. This paper illustrates the use of a data mining technique to support archaeological and humanistic inquiries on cultural developments.*

Rezumat. *Acest studiu prezintă rezultate relevante pentru înțelegerea răspândirii metalurgiei timpurii obținute prin extragerea tiparelor dintr-un set de date de genomuri antice. Se constată că, în ansamblu, răspândirea metalurgiei în cultura chalcolitică Remedello din Italia poate fi probabil corelată cu populația chalcolitică din Bulgaria reprezentată de genomul unei persoane aflată în legătură cu ceramica Bodrogkeresztúr în România. De asemenea, în ansamblu, fie o populație asociată acestui eșantion, fie cu populațiile din perioada chalcolitică din Marea Câmpie Maghiară pot fi asociate cu paharele de tip clopot din nordul Italiei și cu unele pahare de tip clopot din Franța. Urmele pe care probele examinate le-au lăsat ne indică răspândirea geografică a populațiilor pe care le reprezintă. Această lucrare explică modul de utilizare a tehnicii de extragere a datelor, venind în sprijinul cercetărilor arheologice și umaniste privind evoluțiile culturale.*

Keywords: Ancient Autosomal DNA Dataset; Spread of Metallurgy; Chalcolithic Carpatho-Danubian Area; Bodrogkeresztúr.

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Introduction

What can be said about the way of life of the earliest communities that spread metallurgical knowledge in Europe? This is an issue of interest to a general understanding of cultural transformations, and it is from that perspective that this preliminary study was first initiated. Metallurgical activity in Europe attains a high level of development in the fifth millennium BCE. Until now only archaeology could adduce evidence relevant to the transmission of metallurgical know-how and the communities that were implicated. Open-access archaeogenetic tools for unpacking relations among ancient populations can provide additional information in support of an examination of prehistoric cultural processes.

This paper presents the results of examining patterns among recently available ancient genomes of individuals from cultures or populations that the archaeological literature has deemed relevant to the spread of early metallurgy. That the transmission of metallurgical know-how throughout Europe received at least some if not most of its impetus from the Carpatho-Danubian region is a claim that has been broadly accepted. It appears to be generally believed that the transmission of know-how was primarily, if not exclusively, cultural. This study will present evidence that suggests that the transmission had a demic component.

The paper will also suggest there is evidence that some of the populations involved did not disappear at the end of the Chalcolithic. Thus, it will also include results about traces of their presence in post-Chalcolithic periods in some areas of Europe. The data used are samples of ancient and modern autosomal DNA in a curated dataset, which is current as of March 2020. Some geographical zones and eras of European prehistory are unevenly sampled, which might give the impression that populations implicated in the development and spread of metallurgy in Europe disappeared without leaving a trace. For this reason, data on more recent populations are also included.

This paper presents a first look at populations involved in the spread of early metallurgy in Europe obtained through open-access archaeogenetic data and tools.

Methodology

Genomic data from ancient and modern individuals are from the 240K+HO, Version v42.4 dataset at David Reich Lab[2]. The program *qpAdm* (version 810) in the *AdmixTools* package

[2] *David Reich Lab, Harvard University*, March 1, 2020. Online: *https://reich.hms.harvard.edu/downloadable-genotypes-present-day-and-ancient-dna-data-compiled-published-papers*.

distributed by David Reich Lab[3] was used to support inferences about relations among individuals and populations that have not been discussed in publications.

qpAdm models admixture in a target individual or population, given a choice of source and reference individuals or populations[4]. Henceforth, the term "population" will be used to denote either individuals or groups of individuals. Reference populations are populations from which no recent admixture — or more recent than stemming from source populations — into the target has occurred. The choice of reference populations in the analyses performed for this paper closely tracks the extended set used in Mittnik, et al., (2019). This set includes the following populations: Mbuti.DG, Ust_Ishim_HG_published.DG, Ethiopia_4500BP.SG, Russia_MA1_HG.SG, Italy_Villabruna, Papuan.DG, Indian_GreatAndaman_100BP.SG,[5] Han.DG, Karitiana.DG, Iberia_EN, and Germany_LBK_EN.

qpAdm is a means of assessing admixture based on allele frequency correlations between populations. *qpAdm* computes allele correlations for all four-way combinations of proposed populations for analysis —target, sources, and references, one of the latter being chosen as a base— as f_4 statistics. f_4 statistics provide the input to a least squares fitting algorithm, which calculates admixture proportions and standard errors for the proposed sources. A target population can thus be modeled as the result of admixture between source populations. This can be done if the source populations are differently related to at least some of the reference populations. A likelihood ratio test assesses whether the computed admixture proportions are rejected or not. This assessment is the *p*-value ascribed to the admixture proportions. The paper follows a common practice of placing the cut-off point of non-rejection or plausibility at $p \geq 0.05$.

The information included in the Appendix of this paper includes admixture proportions, standard errors, and *p*-values for each target, given proposed sources of admixture and the assumption about relevant reference populations. The Results section is a verbal summary based on the data contained in the Appendix. Because the focus of this study is on the plausibility of admixture of Bodrogkeresztúr from Romania, Bodrogkeresztúr, Tiszapolgár, Late Chalcolithic Baden, as well as Late Neolithic Tisza and Lengyel from Hungary into various target populations, little attention is given to admixture proportions, although they are reported where more than one source population is required. The only condition is that the admixture proportions be biologically feasible. Likewise, because of the focus of the study, the simplest models are entertained. None feature more than two source populations.

To model input from the Pontic-Caspian steppe of the fourth millennium, the currently best available population is Yamnaya Samara, even though it has been found to harbor

[3] *David Reich Lab, Harvard University*, n.d. Online: https://reich.hms.harvard.edu/software.

[4] PATTERSON *et al.* 2012; HAAK *et al.* 2015, Supplementary Information, 94 *ff.*

[5] Out of caution, a nineteenth-century Andamanese replaces modern Onge to stand in for a Southeast Asian population reference. Some of the modern Onge may have recent Western European admixture.

around 13% Early European Farmer admixture[6]. For steppe input from the third millennium into more westerly parts of Europe, an Estonia Corded Ware Culture population was used, since it is less admixed with Early European Farmers than other Corded Ware Culture populations.

As the focus of this study is evidence of admixture from presumed early metallurgists, not steppe admixture, preference is given to models that pass without the latter. If a plausible model reported in the Appendix includes a steppe source, usually Yamnaya Samara, it can be assumed that it is required.

The "allsnps: YES" option was applied in all *qpAdm* runs. Some of the models for low coverage targets were spot-checked using the "allsnps: NO" option, which might allow non-optimal models to be identified as plausible[7]. No material difference in results concerning which models were found to be plausible was noted.

While mixing modern and ancient populations may produce biased results for admixture proportions and rule potentially optimal models out as implausible, in simulations, combining modern and ancient populations as target and sources has not been found to cause implausible models to be assessed as plausible.[8] For this reason, some models that incorporate modern populations as targets will also be included. If they are not rejected, that is information worth noting.

The list of all samples used, their dates and location, is in the Supplement. Sample dates provided in the body of the paper are from this list.

Results

The populations of interest are Early European Farmers of the Chalcolithic. They refer to Urziceni48 — a label used in this paper to name sample I4089 — who is a representative of Bodrogkeresztúr from a necropolis in Vama Urziceni in Romania (4300-4000 cal BCE);[9] Hungary_EarlyC_Tiszapolgar (4500-4000 BCE); Hungary_EarlyC_Tiszapolgar_ Bodrogkeresztur_published (4444-4257 cal BCE); and Hungary_LateC_Baden (various dates; cal BCE dates range between 3359-2929). Steppe admixture is modeled with Russia_EBA_Yamnaya_Samara (various dates; cal BCE ranging between 3335-2622) and, for Bell Beaker populations, Estonia_Corded_Ware (dates ranging between 2871-2340 cal BCE).

Populations from the Late Neolithic were added. They are Hungary_LN_Tisza (samples dated 5000-4500 BCE) and Hungary_LN_Lengyel (samples dated 4800-4500 BCE).

[6] WANG *et al.* 2019.

[7] HARNEY *et al.* 2020.

[8] HARNEY *et al.* 2020, Supplementary Information.

[9] SZÜCS-CSILLIK and VIRAG 2016. For information on Urziceni48, the contact person is Cristian Virag.

The Chalcolithic populations of interest are genetically very close. By-and-large, their genetic origin is in areas occupying the eastern part of the Great Hungarian Plain, but also extending northward into the Bükk Mountains (Appendix, Table 1.) If there is one factor that introduces a difference between them, it is that Urziceni48 may harbor admixture from some Bulgaria Chalcolithic populations. This admixture source is apparent if one restricts the Bulgaria Chalcolithic samples to Varna (various cal BCE dates, ranging between 4711-4374), Smyadovo (various, between 4520-4260 cal BCE), Sushina (various, between 4679-4335 cal BCE), and Dzhulyunitsa (various, between 4452-4246 cal BCE).

Urziceni48 can model admixture in various populations from the Chalcolithic later than it, except Late Chalcolithic Baden. The populations that Urziceni48 can model successfully include Croatia Vucedol, Italy Iceman, and Italy North Remedello Chalcolithic. Croatia Vucedol can also be modeled by some of the other populations of interest from the Chalcolithic or Late Neolithic (Appendix, Table 2.) Nevertheless, of all the source populations of interest from the Chalcolithic and Late Neolithic, only Urziceni48 can successfully model Italy Iceman (3484-3104 cal BCE) and Italy North Remedello Chalcolithic (dates ranging from 3483 to 2578 cal BCE).

For the Bell Beaker period, almost all of our source populations of interest from the Chalcolithic can successfully model low steppe France Bell Beakers from Haute-Savoie and Haut-Rhin (dates ranging between 2832-2135 cal BCE), Switzerland Bell Beakers from Sion-Petit-Chasseur (between 2470-1985 cal BCE), Italy North Bell Beakers from Emilia Romagna (between 2195-1930 cal BCE), and some Lech Valley Bell Beakers from Germany (between 2470-2210 cal BCE). Late Neolithic populations of interest, Lengyel and Tisza Late Neolithic, are not plausible sources of admixture in low steppe France Bell Beakers and Italy North Bell Beakers. Early Chalcolithic Tiszapolgár is also not a plausible source for low steppe France Bell Beakers (Appendix, Table 3.)

For the Bronze Age, among the populations of interest discussed in this paper, only Urziceni48 serves as a source of admixture in Maros Early Bronze Age (also referred to as Periam-Pecica; various dates from 2034 to 1696 cal BCE). Croatia Middle Bronze Age, Hungary Early Bronze Age Protonagyrev, and Italy Remedello of the Early Bronze Age can be modeled not only with Urziceni48 but also with Chalcolithic Bodrogkeresztúr or Late Chalcolithic Baden from Hungary. Lengyel LN and Tisza LN from Hungary are also acceptable sources (Appendix, Table 4.)

A variety of individuals and populations from the Iron Age to the Early Middle Ages from Croatia, northern Italy, Hungary, Bulgaria, and Republic of Moldova have also been examined (Appendix, Table 5.) Most of them can still be modeled as having Early European Farmer admixture derived from Lengyel or Tisza LN, with some exceptions. The following can be plausibly modeled only with Urziceni48 rather than other Early European Farmer sources from the Chalcolithic or Late Neolithic: Italy Iron Age Republic (various dates and locations in northern Italy, between 900-200 BCE), Italy North Early Medieval Langobards, all from Collegno (580-630 CE), and Moldova Scythian 311 (389-204 cal BCE).

Finally, Urziceni48 can model Early European Farmer admixture in the following modern populations: Croatian, Italian North, Moldavian, Romanian, Sardinian, and Tuscan (Appendix, Table 6.)

All the ancient populations examined of all periods that are later than Urziceni48 can be plausibly modeled with Urziceni48 as a source, except for Late Chalcolithic Baden. Remedello Chalcolithic, Iceman, Maros (Periam-Pecica), Republic-era northern Italians, Collegno Langobards, and one of the Moldovan Scythians are modeled preferentially with Urziceni48 over the other ancient populations of interest from the Chalcolithic and Late Neolithic surveyed in this paper. The locations of modern populations that can be modeled with Urziceni48, Croatia, Italy North, Moldavia, Romania, Sardinia, and Tuscany, are consistent geographically with the pattern of admixture of this sample in ancient populations, even in the face of a current lack of ancient samples from significant areas.

Discussion

The choice of populations of interest from the Chalcolithic and Late Neolithic reflects discussions of the early spread of metallurgy in the archaeological literature. Archaeological studies[10] and network-oriented analyses[11] of the early spread of metallurgy in Europe have tended to manifest a preference for cultural transmission.

If we take differential plausibility of admixture from our populations of interest of the Chalcolithic era as an indicator of migration, then there is, at the very minimum, support for small-scale population migration of groups bringing metallurgical knowledge to Italy (Trentino, Lombardy, and Emilia Romagna) and France (Haute-Savoie, Haut-Rhin).

Dolfini (2013) has argued that the earliest spread of metallurgy in Italy progressed very rapidly from the northern Alps to Sardinia[12]. It spread both north and south of the Alps at the same time and came from a region encompassing the north-central Balkans or the Carpathian region[13]. This paper identifies a population represented by Urziceni48 as the likely source of the earliest spread of metallurgical know-how into northern Italy.

Strahm (2005, 2007) has argued that a Carpathian stream is responsible for bringing metallurgical know-how from the north to south Germany and Austria. Metal objects from the latter areas diffused into parts of Switzerland and France. Textual and tabular

[10] DOLFINI 2013; MERKL, SEININGER and STRAHM 2011; STRAHM 2005; 2007.

[11] RADIVOIEVIĆ and GRUCIĆ 2018; ROSENSTOCK, SCHARL and SCHIER 2016.

[12] DOLFINI 2013, 43.

[13] DOLFINI 2013, 41, 49.

information identify, going from east to west, Kodžadermen-Gumelnița-Karanovo, Tiszapolgár-Bodrogkeresztúr, and Lengyel cultures as relays in the chain of transmission. Merkl, Steiniger, and Strahm (2011) suggest populations originating in Late Neolithic central Europe as a preponderant source of this influence[14]. Strahm (2005) believes that Chalcolithic Italy provided the source of metallurgical know-how in France[15]. Merkl, Steiniger, and Strahm (2011) continue to believe that metallurgy in Italy came from north of the Alps[16].

The results of this study allow that most of the Chalcolithic era populations of interest examined, Urziceni48-related, Tiszapolgár Bodrogkeresztúr, or even Late Chalcolithic Baden could have played the role of seeding some early metallurgy in Bell Beaker era France, Switzerland, or Germany. One can exclude Lengyel LN, Tisza LN, and Early Chalcolithic Tiszapolgár as sources in the case of low steppe Bell Beakers in France. Neither Lengyel LN nor Tisza LN looks to be plausible as a source of admixture in Chalcolithic or Bell Beaker era Italy.

Network based or oriented analyses plot correlations between metal artifacts and archaeological cultures. The social network approach in Rosenstock, Scharl, and Schier (2016) associates the spread of copper artifacts with Tiszapolgár and Bodrogkeresztúr cultures,[17] in continuity with earlier cultures of the Great Hungarian Plain, Tisza LN and Lengyel LN, with Tisza playing a greater role than Lengyel.[18] The results reported for this paper are more convincing for Bodrogkeresztúr than Tiszapolgár, although the latter cannot be ruled out except for low steppe Bell Beakers in France. Genetic input from Tisza LN also cannot be ruled out for samples from the Lech Valley and Sion-Petit-Chasseur, but the results in this paper find that a role for Tisza LN is no more compelling than Lengyel LN. Both may represent an earlier population spread not associated with metallurgical know-how. It should also be noted that the Lech Valley and Sion-Petit-Chasseur individuals are among the lowest coverage samples used in this study.

Network analyses, whether in Rosenstock, Scharl, and Schier (2016) or Radivoiević and Grucić (2018), see the metallurgical center of gravity shifting westward from the Kodžadermen-Gumelnița-Karanovo network to the Krivodol-Sălcuța-Bubanj complex, both in present-day Bulgaria, Serbia, and southern Romania. Radivoiević and Grucić (2018) date the shift to around 4100–3700 BC. The authors place Bodrogkeresztúr culture in this period, and view it as occupying a northwestern expanse in relation to the Krivodol-Sălcuța-Bubanj

[14] STRAHM 2005, 30; 2007, 51 and 53–54; MERKL, STEINIGER, and STRAHM 2011, 176–177, and 182–183.

[15] STRAHM 2005, 29–31.

[16] MERKL, STEINIGER and STRAHM 2011, 185–189.

[17] ROSENSTOCK, SCHARL, and SCHIER 2016, 86–88.

[18] ROSENSTOCK, SCHARL, and SCHIER 2016, 101.

complex. They identify Serbian mines in the Krivodol-Sălcuța-Bubanj complex as the source of copper in Bodrogkeresztúr[19].

Siklósi and Szilágyi (2019) note that recently obtained AMS dating shows that the copper supply network linked to metal use in Bodrogkeresztúr culture was contemporary with the end of the earlier Kodžadermen-Gumelnița-Karanovo network and the duration of the Krivodol-Sălcuța-Bubanj complex. The authors see a strong association between Bodrogkeresztúr pottery and metal artifacts but believe that there is currently no evidence that the Great Hungarian Plain was a source of metallurgical technology. Instead, Siklósi and Szilágyi (2019) believe the source of this technology was in neighboring mountainous areas. Furthermore, they suggest that Bodrogkeresztúr communities, because of their mobility, could have been the agents that facilitated the spread of copper artifacts[20].

This paper supports some of the observations concerning the role of communities associated with Bodrogkeresztúr pottery outlined in Radivoiević and Grucić (2018) and Siklósi and Szilágyi (2019) in finding that there might be a difference between Bodrogkeresztúr from the Tisa River area and a culture identified as Bodrogkeresztúr based on its pottery, but located further east and represented by Urziceni48. The latter shows possible admixture with populations from Chalcolithic Bulgaria, which implies close contact with some of the agents at stake in the core metallurgical production area, the networks comprising the Kodžadermen-Gumelnița-Karanovo and Krivodol-Sălcuța-Bubanj complexes.

The samples available from Chalcolithic Bulgaria — Dzhulyunitsa, Smyadovo, Sushina, and Varna —might not be optimal, but they intimate that perhaps not all groups identified as Bodrogkeresztúr based on pottery were the same. The ones represented by Urziceni48 might have played a more significant role in the spread of metal artifacts not only as intermediaries but also through their metallurgical proficiency. The approximately 750 km path from Vama Urziceni to the area encompassing Dzhulyunitsa, Smyadovo, Sushina, and Varna passes through the Arieș River area. A cave in the Cheile Turzii identified as harboring a metallurgical workshop belonging to the late Bodrogkeresztúr period is situated a short distance from this area. The workshop is dated 4100-3900 cal BCE[21]. Evidence from ancient genomes adds weight to perhaps otherwise still incidental evidence that a Bodrogkeresztúr-related population was more than an intermediary for the westward spread of metal artifacts.

There is likely to have been significant interaction between a more eastern situated Bodrogkeresztúr population and Sălcuța, as has been suggested by Roman (1971)[22].

[19] RADIVOIEVIĆ and GRUCIĆ 2018, 114, 119 and Fig. 7.E, 117.

[20] SIKLÓSI and SZILÁGYI 2019, 5281 and 5283.

[21] LAZAROVICI, LAZAROVICI and CONSTANTINESCU 2015, 340.

[22] ROMAN 1971, 130–131.

The interaction with Sălcuța culture, at the minimum, invites closer scrutiny. As of this writing, there is no published sample available for exploring this matter further.

Conclusion

Based on a method of modeling admixture in ancient populations, one can infer that the transfer of metallurgical technology in Europe was not only cultural but probably also involved a small-scale movement of populations. This paper identifies a likely Balkan Chalcolithic-shifted population associated with Bodrogkeresztúr pottery and represented by Urziceni48 as having played role that calls for further elucidation. It suggests, conservatively, that the population this sample represents is currently the best candidate to account for the spread of metallurgy in northern Italy Remedello Chalcolithic culture.

The paper compared similar populations and found that, also conservatively, some Chalcolithic populations including Tiszapolgár Bodrogkeresztúr and Late Chalcolithic Baden are also possible candidates for demic diffusion in Bell Beaker era communities in northern Italy and France. The lingering traces populations of interest examined in this paper left in later populations give a sense of the geographic expanse of their movements.

A greater variety of samples from Chalcolithic-era populations, notably Sălcuța, could bring more clarity to the early transmission of metallurgical know-how and its evolution. Such information should be beneficial to outlining a fuller picture of the social interactions among the populations at stake.

Appendix

Table 1. Possible sources for relevant Chalcolithic-era samples of interest. Populations later used as sources: Urzi48: Urziceni 48; TsPolg: Hungary_EarlyC_Tiszapolgar; Bodrog: Hungary_EarlyC_Tiszapolgar_Bodrogkeresztur_published; Baden: Hungary_LateC_Baden. Green: $p \geq 0.05$

Urziceni48: possible sources	p-value
Bulgaria_C	5.8660E-02
Bulgaria_Chalc**	1.7909E-01
Hung_EarlyC_Tiszapolg_Bodrogker_pub	1.7936E-03
Hungary_EarlyC_Tiszapolgar	4.2779E-03
Hungary_LN_Lengyel	5.5053E-02
Hungary_LN_Sopot	4.1235E-03
Hungary_LN_Tisza	6.4551E-01
Hungary_MN_ALBK_Szakalhat	3.9273E-02
Hungary_MN_ALPc	1.9890E-01
Hungary_MN_ALPc_Bukk	6.9516E-01

Hungary_MN_ALPc_I	2.7101E-02
Hungary_MN_ALPc_III	7.0629E-01
Hungary_MN_ALPc_Szakalhat	3.1114E-01
Hungary_MN_ALPc_Szatmar	3.9517E-03
Hungary_MN_ALPc_Tiszadob	1.1332E-01
Hungary_MN_LBK	2.8223E-03
Hungary_MN_Vinca	3.9861E-03

Hungary_EarlyC_Tiszapolgar	p-value
Bulgaria_C	4.7834E-02
Bulgaria_Chalc**	2.8759E-02
Hungary_LN_Lengyel	6.8254E-02
Hungary_LN_Sopot	2.5149E-02
Hungary_LN_Tisza	6.3640E-02
Hungary_MN_ALBK_Szakalhat	4.3104E-01
Hungary_MN_ALPc	1.5716E-01
Hungary_MN_ALPc_Bukk	2.7266E-01
Hungary_MN_ALPc_I	6.5660E-01
Hungary_MN_ALPc_III	7.7582E-01
Hungary_MN_ALPc_Szakalhat	9.7655E-01
Hungary_MN_ALPc_Szatmar	2.9841E-02
Hungary_MN_ALPc_Tiszadob	1.9904E-02
Hungary_MN_LBK	7.9855E-04
Hungary_MN_Vinca	4.3105E-04

Hung_EarlyC_Tiszapolg_Bodrogker_pub	p-value
Bulgaria_C	2.2203E-04
Bulgaria_Chalc**	4.5455E-04
Hungary_EarlyC_Tiszapolgar	4.2182E-02
Hungary_LN_Lengyel	2.6627E-02
Hungary_LN_Sopot	4.7560E-03
Hungary_LN_Tisza	1.1736E-01
Hungary_MN_ALBK_Szakalhat	1.3003E-01
Hungary_MN_ALPc	1.4132E-01
Hungary_MN_ALPc_Bukk	1.6573E-01
Hungary_MN_ALPc_I	2.8949E-01
Hungary_MN_ALPc_III	4.5670E-01
Hungary_MN_ALPc_Szakalhat	6.5922E-01
Hungary_MN_ALPc_Szatmar	3.9161E-01
Hungary_MN_ALPc_Tiszadob	3.6649E-01
Hungary_MN_LBK	2.9824E-06
Hungary_MN_Vinca	2.3717E-06

Hungary_LateC_Baden	p-value
Bulgaria_C	1.5555E-09
Bulgaria_Chalc**	6.7816E-08
Hung_EarlyC_Tiszapolg_Bodrogker_pub	3.3064E-01
Hungary_EarlyC_Tiszapolgar	1.0398E-02
Hungary_Hunyadihalom_MCHA	7.6621E-01
Hungary_LN_Lengyel	4.5266E-02
Hungary_LN_Sopot	2.8511E-05
Hungary_LN_Tisza	3.2903E-02
Hungary_MN_ALBK_Szakalhat	1.2823E-01
Hungary_MN_ALPc	7.2976E-01
Hungary_MN_ALPc_Bukk	6.8783E-01
Hungary_MN_ALPc_I	4.7971E-01
Hungary_MN_ALPc_III	6.4648E-01
Hungary_MN_ALPc_Szakalhat	5.7571E-01
Hungary_MN_ALPc_Szatmar	1.3303E-02
Hungary_MN_ALPc_Tiszadob	3.5626E-01
Hungary_MN_LBK	4.2088E-15
Hungary_MN_Vinca	2.0530E-13
Urziceni48	3.4061E-02

** Restricted to Varna (4 samples), Smyadovo (3), Sushina (2), Dhzulyunitsa (2). See Supplement for sample ID numbers and dates.

Table 2. Admixture of populations of interest in the Chalcolithic. Sources: Urzi48: Urziceni 48; TsPolg: Hungary_EarlyC_Tiszapolgar; Bodrog: Hungary_EarlyC_Tiszapolgar_ Bodrogkeresztur_published; Baden: Hungary_LateC_Baden; Lengyel: Hungary_LN_Lengyel; TsLN: Hungary_LN_Tisza; YamSam: Russia_EBA_Yamnaya_Samara. Green: $p \geq 0.05$. SE= standard error

Other Ancient	p-value	Urzi48	YamSam	SE	SE
Croatia_LateC_EBA_Vucedol	3.7729E-01	0.726	0.274	0.040	0.040
Croatia_Vucedol	1.4919E-01	1.000			
Hungary_LateC_Baden	3.4061E-02	1.000			
Hungary_LC_EBA_Baden_Yamnaya	6.1265E-01	1.000			
Italy_Iceman_MN	7.0462E-01	1.000			
Italy_North_Remedello_C	3.1628E-01	1.000			

Other Ancient	p-value	TsPolg	YamSam	SE	SE
Croatia_LateC_EBA_Vucedol	2.5495E-01	0.702	0.298	0.034	0.034
Croatia_Vucedol	3.0145E-02	1.000			
Hungary_LateC_Baden	1.0398E-02	1.000			

Hungary_LC_EBA_Baden_Yamnaya	2.8270E-04	1.000			
Italy_Iceman_MN	1.0887E-03	1.000			
Italy_North_Remedello_C	5.0072E-05	1.000			

Other Ancient	p-value	Bodrog	YamSam	SE	SE
Croatia_LateC_EBA_Vucedol	2.0235E-03	0.665	0.335	0.039	0.039
Croatia_Vucedol	8.1247E-02	1.000			
Hungary_LateC_Baden	3.3064E-01	1.000			
Hungary_LC_EBA_Baden_Yamnaya	2.2081E-01	1.000			
Italy_Iceman_MN	3.3799E-05	1.000			
Italy_North_Remedello_C	4.1520E-03	1.000			

Other Ancient	p-value	Baden	YamSam	SE	SE
Croatia_LateC_EBA_Vucedol	2.4563E-01	0.665	0.335	0.033	0.033
Croatia_Vucedol	2.0586E-02	1.000			
Italy_North_Remedello_C	2.1970E-03	1.000			

Other Ancient	p-value	Lengyel	YSam	SE	SE
Croatia_LateC_EBA_Vucedol	3.1839E-01	0.636	0.364	0.033	0.033
Croatia_Vucedol	1.4298E-01	1.000			
Hungary_LateC_Baden	4.90405E-02	0.976	0.024	0.019	0.019
Hungary_LC_EBA_Baden_Yamnaya	1.71651E-02	0.953	0.047	0.023	0.023
Italy_Iceman_MN	3.1700E-04	1.000			
Italy_North_Remedello_C	2.40658E-04	0.934	0.066	0.031	0.031

Other Ancient	p-value	TsLN	YSam	SE	SE
Croatia_LateC_EBA_Vucedol	1.6569E-01	0.677	0.323	0.037	0.037
Croatia_Vucedol	1.8720E-01	1.000			
Hungary_LateC_Baden	3.2903E-02	1.000			
Hungary_LC_EBA_Baden_Yamnaya	2.1784E-01	1.000			
Italy_Iceman_MN	2.7597E-02	1.000			
Italy_North_Remedello_C	5.9709E-04	1.000			

Table 3. Admixture of populations of interest in Bell Beakers.
Sources: Urzi48: Urziceni48; TsPolg: Hungary_EarlyC_Tiszapolgar; Bodrog: Hungary_EarlyC_Tiszapolgar_ Bodrogkeresztur_published; Baden: Hungary_LateC_Baden; Lengyel: Hungary_LN_Lengyel; TsLN: Hungary_LN_Tisza; EstCW: Estonia_CordedWare.SG. Green: $p \geq 0.05$. SE= standard error

Bell Beaker	p-value	Urzi48	EstCW	SE	SE
France_Bell_Beaker_lowSteppe	1.4235E-01	1.000			
Germany_Lech_BellBeaker	6.6357E-01	0.526	0.474	0.043	0.043
Italy_North_BellBeaker	1.4646E-01	1.000			
Switzerland_Bell_Beakerulyu	9.8666E-01	0.422	0.578	0.051	0.051
Bell Beaker	p-value	TsPolg	EstCW	SE	SE
France_Bell_Beaker_lowSteppe	2.2590E-04	0.891	0.109	0.037	0.037
Germany_Lech_BellBeaker	6.6973E-02	0.493	0.507	0.040	0.040
Italy_North_BellBeaker	6.1361E-02	0.830	0.170	0.030	0.030
Switzerland_BellBeaker	8.4197E-01	0.416	0.584	0.048	0.048

Bell Beaker	p-value	Bodrog	EstCW	SE	SE
France_Bell_Beaker_lowSteppe	2.5559E-01	0.864	0.136	0.042	0.042
Germany_Lech_BellBeaker	2.1960E-01	0.465	0.535	0.039	0.039
Italy_North_BellBeaker	2.2749E-01	0.807	0.193	0.037	0.037
Switzerland_BellBeaker	9.4854E-01	0.383	0.617	0.048	0.048

Bell Beaker	p-value	Baden	EstCW	SE	SE
France_BellBeaker_lowSteppe	1.3990E-01	0.890	0.110	0.035	0.035
Germany_Lech_BellBeaker	2.9899E-01	0.465	0.535	0.036	0.036
Italy_North_BellBeaker	3.3140E-01	0.824	0.176	0.028	0.028
Switzerland_BellBeaker	9.9985E-01	0.381	0.619	0.044	0.044

Bell Beaker	p-value	Lengyel	EstCW	SE	SE
France_Bell_Beaker_lowSteppe	5.7582E-03	0.839	0.161	0.036	0.036
Germany_Lech_BellBeaker	2.6816E-01	0.440	0.560	0.330	0.330
Italy_North_BellBeaker	2.9047E-02	0.775	0.225	0.028	0.028
Switzerland_BellBeaker	9.9757E-01	0.361	0.639	0.042	0.042

Bell Beaker	p-value	TsLN	EstCW	SE	SE
France_Bell_Beaker_lowSteppe	1.5358E-02	0.909	0.091	0.042	0.042
Germany_Lech_BellBeaker	3.2000E-01	0.480	0.520	0.040	0.040
Italy_North_BellBeaker	2.6839E-02	0.841	0.159	0.035	0.035
Switzerland_BellBeaker	9.9998E-01	0.380	0.620	0.044	0.044

Table 4. Admixture of populations of interest in the Bronze Age.
Sources: Urzi48: Urziceni48; TsPolg: Hungary_EarlyC_Tiszapolgar;
Bodrog: Hungary_EarlyC_Tiszapolgar_ Bodrogkeresztur_published; Baden: Hungary_LateC_Baden;
Lengyel: Hungary_LN_Lengyel; TsLN: Hungary_LN_Tisza; YamSam: Russia_EBA_Yamnaya_Samara;
EstCW: Estonia_CordedWare.SG. Green: $p \geq 0.05$. SE= standard error

Bronze Age	p-value	Urzi48	EstCW	YamSam	SE	SE	SE
Bulgaria_EBA	6.7426E-01	0.866		0.134	0.029		0.029
Croatia_MBA	6.1695E-01	0.764		0.236	0.033		0.033
Hungary_EBA_Protonagyrev	3.7296E-01	0.646	0.354		0.044	0.044	
Hungary_Maros	7.5294E-02	0.540	0.460		0.046	0.046	
Italy_North_Remedello_EBA	9.5380E-01	1.000					

Bronze Age	p-value	TsPolg	EstCW	YamSam	SE	SE	SE
Bulgaria_EBA	4.1500E-04	0.832		0.168	0.021		0.021
Croatia_MBA	1.9337E-01	0.740		0.260	0.025		0.025
Hungary_EBA_Protonagyrev	8.4370E-01	0.624	0.376		0.038	0.038	
Hungary_Maros_EBA	2.3266E-03	0.535	0.465		0.042	0.042	
Italy_North_Remedello_EBA	2.0313E-01	1.000					
Bronze Age	p-value	Bodrog	EstCW	YamSam	SE	SE	SE
Bulgaria_EBA	1.6969E-01	0.800		0.200	0.025		0.025
Croatia_MBA	1.4168E-01	0.711		0.289	0.030		0.030
Hungary_EBA_Protonagyrev	3.6456E-01	0.598	0.402		0.042		0.042
Hungary_Maros_EBA	8.6894E-04	0.499	0.501		0.048	0.048	
Italy_North_Remedello_EBA	3.5493E-01	1.000					

Bronze Age	p-value	Baden	EstCW	YamSam	SE	SE	SE
Bulgaria_EBA	3.5939E-01	0.806		0.194	0.018		0.018
Croatia_MBA	1.7668E-01	0.697		0.303	0.025		0.025
Hungary_EBA_Protonagyrev	7.7858E-01	0.591	0.409		0.036	0.036	
Hungary_Maros_EBA	6.4445E-04	0.443	0.557		0.037	0.037	
Italy_North_Remedello_EBA	2.6610E-01	1.000					

Bronze Age	p-value	Lengyel	EstCW	YamSam	SE	SE	SE
Bulgaria_EBA	5.9001E-04	0.786		0.214	0.019		0.019
Croatia_MBA	3.2315E-01	0.675		0.325	0.025		0.025
Hungary_EBA_Protonagyrev	7.5463E-01	0.561	0.439		0.035	0.035	
Hungary_Maros.SG	3.7797E-02	0.468	0.532		0.038	0.038	
Italy_North_Remedello_EBA.SG	2.2326E-01	1.000					

Bronze Age	p-value	TsLN	EstCW	YamSam	SE	SE	SE
Bulgaria_EBA	5.0329E-02	0.836		0.164	0.025		0.025
Croatia_MBA	9.1065E-01	0.727		0.273	0.028		0.028
Hungary_EBA_Protonagyrev	2.5948E-01	0.707	0.293		0.031	0.031	
Hungary_Maros.SG	1.2214E-02	0.484	0.516		0.042	0.042	
Italy_North_Remedello_EBA.SG	3.0312E-01	1.000					

Table 5. Admixture of populations of interest in the Iron Age and Early Medieval periods.
Sources: Urzi48: Urziceni48; TsPolg: Hungary_EarlyC_Tiszapolgar; Bodrog: Hungary_EarlyC_Tiszapolgar_Bodrogkeresztur_published; Baden: Hungary_LateC_Baden; Lengyel: Hungary_LN_Lengyel; TsLN: Hungary_LN_Tisza; YamSam: Russia_EBA_Yamnaya_Samara. Green: $p \geq 0.05$. SE= standard error

Iron Age & Medieval	p-value	Urzi48	YamSam	SE	SE
Bulgaria IA	1.1434E-01	1.000			
Croatia_EIA	6.9926E-01	0.734	0.266	0.036	0.036
Hungary_ScythianDA195	3.1376E-01	0.628	0.372	0.043	0.043
Hungary_ScythianDA198	9.4863E-02	0.702	0.298	0.040	0.040
Italy_IA_Republic	3.1439E-01	0.697	0.303	0.023	0.023
Italy_North_EarlyMedieval_Langobards	7.4849E-01	0.652	0.348	0.021	0.021
Moldova_Scythian300	8.6676E-01	0.725	0.275	0.043	0.043
Moldova_Scythian192	7.5784E-01	0.638	0.362	0.039	0.039
Moldova_Scythian197	3.4183E-01	0.667	0.333	0.047	0.047
Moldova_Scythian305	5.1543E-01	0.581	0.419	0.050	0.050
Moldova_Scythian311	7.4192E-02	0.432	0.568	0.047	0.047
RISE569 Czech_Early_Slav	1.6962E-01	0.474	0.526	0.038	0.038
Slovakia Poprad DA119	1.6015E-01	0.511	0.489	0.042	0.042

Iron Age & Medieval	p-value	TsPolg	YamSam	SE	SE
Bulgaria IA	1.1857E-03	0.884	0.116	0.033	0.033
Croatia_EIA	1.2115E-01	0.720	0.280	0.031	0.031
Hungary_ScythianDA195	3.2607E-02	0.619	0.381	0.038	0.038
Hungary_ScythianDA198	2.9082E-01	0.716	0.284	0.035	0.035
Italy_IA_Republic	2.4039E-05	0.684	0.316	0.018	0.018
Italy_North_EarlyMedieval_Langobards	1.2862E-06	0.646	0.354	0.015	0.015
Moldova_Scythian300	6.7672E-03	0.711	0.289	0.039	0.039
Moldova_Scythian192	1.9859E-02	0.638	0.362	0.035	0.035
Moldova_Scythian197	5.4661E-02	0.647	0.353	0.040	0.040
Moldova_Scythian305	9.5749E-02	0.608	0.392	0.049	0.049
Moldova_Scythian311	4.7404E-04	0.431	0.569	0.051	0.051
RISE569 Czech_Early_Slav	4.3939E-02	0.502	0.498	0.037	0.037

Slovakia Poprad DA119	2.2942E-01	0.500	0.500	0.038	0.038

Iron Age & Medieval	p-value	Bodrog	YamSam	SE	SE
Bulgaria IA	5.4015E-05	0.858	0.142	0.038	0.038
Croatia_EIA	3.2666E-01	0.672	0.328	0.034	0.034
Hungary_ScythianDA195	2.5979E-01	0.536	0.464	0.036	0.036
Hungary_ScythianDA198	3.2410E-01	0.656	0.344	0.037	0.037
Italy_IA_Republic	5.4429E-03	0.653	0.347	0.022	0.022
Italy_North_EarlyMedieval_Langobards	1.5056E-04	0.610	0.390	0.020	0.020
Moldova_Scythian300	5.7179E-02	0.682	0.318	0.042	0.042
Moldova_Scythian192	5.8835E-02	0.588	0.412	0.037	0.037
Moldova_Scythian197	1.1793E-01	0.608	0.392	0.043	0.043
Moldova_Scythian305	3.6804E-01	0.571	0.429	0.051	0.051
Moldova_Scythian311	4.1430E-03	0.383	0.617	0.047	0.047
RISE569 Czech_Early_Slav	3.6539E-02	0.439	0.561	0.034	0.034
Slovakia Poprad DA119	6.4718E-01	0.452	0.548	0.036	0.036

Iron Age & Medieval	p-value	Baden	YamSam	SE	SE
Bulgaria IA	5.9633E-05	0.857	0.143	0.032	0.032
Croatia_EIA	7.0623E-01	0.678	0.322	0.029	0.029
Hungary_ScythianDA195	1.7045E-01	0.521	0.479	0.034	0.034
Hungary_ScythianDA198	7.9830E-03	0.660	0.340	0.033	0.033
Italy_IA_Republic	1.1939E-04	0.629	0.371	0.014	0.014
Italy_North_EarlyMedieval_Langobards	1.1886E-04	0.598	0.402	0.012	0.012
Moldova_Scythian300	1.9872E-02	0.628	0.372	0.035	0.035
Moldova_Scythian192	4.9366E-02	0.559	0.441	0.032	0.032
Moldova_Scythian197	3.2455E-03	0.585	0.415	0.037	0.037
Moldova_Scythian305	8.2921E-02	0.480	0.520	0.043	0.043
Moldova_Scythian311	1.9725E-03	0.352	0.648	0.043	0.043
RISE569 Czech_Early_Slav	2.1601E-01	0.418	0.582	0.032	0.032
Slovakia Poprad DA119	4.0783E-01	0.426	0.574	0.033	0.033

Iron Age & Medieval	p-value	Lengyel	YamSam	SE	SE
Bulgaria IA	2.9099E-02	0.826	0.174	0.032	0.032
Croatia_EIA	2.5785E-01	0.653	0.347	0.029	0.029
Hungary_ScythianDA195	2.2200E-01	0.522	0.478	0.035	0.035
Hungary_ScythianDA198	1.2079E-01	0.638	0.362	0.035	0.035
Italy_IA_Republic all	3.5106E-03	0.623	0.377	0.017	0.017
Italy_North_EarlyMedieval_Langobards	1.3500E-04	0.586	0.414	0.014	0.014
Moldova_Scythian300	2.1655E-01	0.661	0.339	0.038	0.038
Moldova_Scythian192	1.2886E-01	0.563	0.437	0.033	0.033

Moldova_Scythian197	5.4240E-02	0.040	0.040	0.571	0.429
Moldova_Scythian305	2.4577E-01	0.523	0.477	0.046	0.046
Moldova_Scythian311	1.3729E-02	0.362	0.638	0.042	0.042
RISE569 Czech_Early_Slav	1.9866E-01	0.409	0.591	0.031	0.031
Slovakia Poprad DA119	1.7836E-01	0.425	0.575	0.035	0.035

Iron Age & Medieval	p-value	TsLN	YamSam	SE	SE
Bulgaria IA	7.7696E-02	0.858	0.142	0.034	0.034
Croatia_EIA	5.0105E-01	0.702	0.298	0.033	0.033
Hungary_ScythianDA195	1.4259E-01	0.538	0.462	0.036	0.036
Hungary_ScythianDA198	1.4586E-01	0.662	0.662	0.037	0.037
Italy_IA_Republic	3.6605E-02	0.66	0.34	0.02	0.020
Italy_North_EarlyMedieval_Langobards	4.1714E-03	0.618	0.382	0.017	0.017
Moldova_Scythian300	2.9287E-01	0.665	0.335	0.041	0.041
Moldova_Scythian192	4.9980E-01	0.583	0.417	0.035	0.035
Moldova_Scythian197	4.0367E-01	0.610	0.390	0.043	0.043
Moldova_Scythian305	3.3893E-01	0.502	0.498	0.045	0.045
Moldova_Scythian311	2.8007E-02	0.384	0.616	0.045	0.045
RISE569 Czech_Early_Slav	2.2519E-01	0.443	0.557	0.035	0.035
Slovakia Poprad DA119	2.0668E-01	0.441	0.559	0.037	0.037

Table 6. Admixture of Chalcolithic populations of interest in modern populations. Sources: Urzi48: Urziceni48; Bodrog: Hungary_EarlyC_Tiszapolgar_ Bodrogkeresztur_published; Baden: Hungary_LateC_Baden; YamSam: Russia_EBA_Yamnaya_Samara. Green: $p \geq 0.05$. SE= standard error

Modern	p-value	Urzi48	YamSam	SE	SE
Albanian	7.5248E-03	0.639	0.361	0.022	0.022
Bulgarian	3.6836E-02	0.578	0.422	0.019	0.019
Croatian	3.0943E-01	0.527	0.473	0.020	0.020
Czech	2.1406E-06	0.482	0.518	0.020	0.020
French	4.4085E-03	0.562	0.438	0.018	0.018
Greek	3.7528E-04	0.634	0.366	0.020	0.020
Hungarian	4.9372E-05	0.495	0.505	0.018	0.018
IBS (Iberian)	5.2494E-03	0.647	0.353	0.020	0.020
Italian_N	3.9145E-01	0.667	0.333	0.020	0.020
Moldavian	5.1869E-02	0.575	0.425	0.020	0.020
Romanian	3.0352E-01	0.546	0.454	0.019	0.019
Sardinian	5.2500E-01	0.874	0.126	0.025	0.025
TSI (Tuscan)	9.4428E-02	0.664	0.336	0.020	0.020
Ukrainian	3.3461E-08	0.431	0.569	0.019	0.019

Modern	p-value	Bodrog	YamSam	SE	SE
Albanian	3.9027E-14	0.592	0.408	0.021	0.021
Bulgarian	2.2182E-12	0.535	0.465	0.019	0.019
Croatian	5.6826E-06	0.489	0.511	0.017	0.017
Czech	1.7586E-07	0.456	0.544	0.019	0.019
French	1.9568E-06	0.522	0.478	0.017	0.017
Greek	6.6511E-20	0.585	0.415	0.019	0.019
Hungarian	1.9013E-08	0.455	0.545	0.017	0.017
IBS (Iberian)	1.9914E-12	0.602	0.398	0.019	0.019
Italian_N	1.8217E-10	0.617	0.383	0.020	0.020
Moldavian	9.2742E-12	0.543	0.457	0.019	0.019
Romanian	7.7738E-09	0.509	0.491	0.018	0.018
Sardinian	3.2338E-06	0.819	0.181	0.023	0.023
TSI (Tuscan)	4.8224E-14	0.618	0.382	0.019	0.019
Ukrainian	3.5990E-09	0.400	0.600	0.017	0.017

Modern	p-value	Baden	YamSam	SE	SE
Albanian	1.2643E-24	0.566	0.434	0.015	0.015
Bulgarian	8.0316E-18	0.513	0.487	0.013	0.013
Croatian	5.2189E-07	0.461	0.539	0.013	0.013
Czech	4.7506E-10	0.418	0.582	0.014	0.014
French	9.6456E-10	0.492	0.508	0.010	0.010
Greek	2.1132E-44	0.547	0.453	0.012	0.012
Hungarian	4.7865E-15	0.423	0.577	0.012	0.012
IBS (Iberian)	4.2282E-24	0.569	0.431	0.010	0.010
Italian_N	3.3345E-22	0.598	0.402	0.012	0.012
Moldavian	6.5068E-19	0.513	0.487	0.013	0.013
Romanian	5.3771E-13	0.482	0.518	0.012	0.012
Sardinian	3.0849E-16	0.809	0.191	0.012	0.012
TSI (Tuscan)	2.6548E-35	0.594	0.406	0.011	0.011
Ukrainian	6.4080E-15	0.360	0.640	0.013	0.013

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