“A River Runs Through It- Ancient DNA Data on the Neolithic Populations of the Great Hungarian Plain”

Dissertation
Zur Erlangung des Grades
Doktor der Naturwissenschaften

Am Fachbereich Biologie
der Johannes Gutenberg-Universität Mainz

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Mainz, 2014

Tag der mündlichen Prüfung: 19.05.2015

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1.1.1 The Mesolithic period in Europe

Europe was first settled by anatomically modern Humans (AMH) approximately 45000 years ago (Benazzi et al. 2011; Collins et al. 2011; Mellars 2006). As the last ice age reached its maximum about 25 000 years before now (Dansgaard et al. 1993; Petit et al. 1999; Yokoyama et al. 2000), human occupation of the continent became restricted to refuge areas in southern Europe and the Eastern European Plain (Straus 1995; Dolukhanov et al. 2001). The end of this period and thus the last ice age marked a major climatic and ecological change. As much of the continent became covered by temperate woodlands, the large migratory herds that had frequented the tundra were replaced by woodland animals and edible plants and aquatic resources became more readily accessible (Bogucki & Crabtree 2004, pp.126–127). This in turn changed human subsistence patterns and strategies. This period, which lasted from the beginning of the Holocene until the advent of agriculture, is referred to as the Mesolithic[1].

The archaeological record of the Mesolithic in western Europe- especially northwestern Europe- is extensive and encompasses several millennia, as in the case of the southern Scandinavian *Maglemose-Kongemose-Ertebølle* sequence. In Central Europe, Mesolithic hunter-gatherers apparently had a preference for upland regions, in particular the lake basins of the Alps. Mesolithic settlements in France were frequent in the Paris Basin, the upper and lower Rhone Valley, southern Brittany, southwestern France and the Pyrenees (Meiklejohn et al. 2010). The Iberian Peninsula also featured a range of distinct Mesolithic cultures occupying the resource-rich coastal regions and river estuaries (Meiklejohn 2009; Meiklejohn et al. 2009)

The Mesolithic record in southeastern Europe is less defined. From Greece, several cave sites are known; some of these, for instance the *Franchthi* cave on the Peloponnes, were in use over several millennia from the Paleolithic until the Neolithic, but were intermittently abandoned (Bailey 2000; Merkyte 2003). In the Balkans, Mesolithic sites are known from Bulgaria, Croatia, Albania and Montenegro, as well as from the shores of the Black Sea (Bailey 2000, pp.32–36; Merkyte 2003 and citations therein).

The richest archaeological record of Mesolithic life in Southeastern Europe was found in a just 130 km long stretch along the Danube banks: The Danube gorges of the “Iron gates” contained settlements

[1] In studies concerning southeastern Europe, the period between the beginning of the Holocene and the appearance of agriculture is also referred to as the „Epipaleolithic“, in particular by researchers who regard the cultural changes that occurred in southestern Europe during this time as less severe than those observed in northwestern Europe

spanning about 6000 years from the late Paleolithic up to the Neolithic. Important sites are *Cuina Turcului, Lepenski Vir, Padina, Vlasac* and *Schela Cladovei* (Srejović 1971; Boroneanţ 1970; Boric 2002; Jovanovic 1987). The Mesolithic population of the Iron Gates apparently relied heavily on aquatic resources (Bonsall et al. 2004; Borić et al. 2004; Bonsall et al. 1997), used their settlements all year round, and the elaborate construction of dwellings and storage facilities suggests that they- if not fully sedentary- had a considerably decreased range of mobility.

1.1.2 The Neolithic Transition in the Near East

The change from a hunter-gatherer subsistence strategy to food production occurred independently in different regions of the world (Diamond 2002). Among these "Neolithisation centres", the Near East was the earliest to emerge and the one that drove the subsequent Neolithisation of Europe and parts of Central Asia. The "Fertile Crescent" - a term coined by the American archaeologist J.H. Breasted (Breasted 1916)- stretches from the Levant over Southeastern Anatolia into Mesopotamia, and is regarded as the core area of this process.

Cultural succession

Following the end of the last ice age, the climatic improvements and the development of the Natufian Culture in the Levant, which lasted from 15000- 12000 cal BP, "set the stage" for the development of agriculture and animal husbandry in the "Fertile Crescent". The core area of the Natufian lay in the Mediterranean Levant (Figure 1) (Bar-Yosef 1998). Important settlements in this period were *Ain Mallaha, Hayoim, Nahal Oren* and *Beidha* and *Rosh Zin*, which marked the southern boundaries of the Natufian "homeland". The Natufians were hunter-gatherers, but some communities were already (semi)sedentary (Simmons 2007, p.58). Skeletal isotope data and stone tools (grinding stones, mortars, microwear patterns on blades) show that Natufian groups habitually harvested and consumed wild cereals. However, evidence for actual grain domestication during the Natufian is inconclusive (Simmons 2007, p.64; Wilcox 2004). Also absent are signs of domesticated animals other than dogs (Horwitz et al. 1999; Tchernov & Valla 1997; Simmons 2007, pp.61–63).

The late phase of the Natufian roughly coincided with the Younger Dryas event, an unusually cold and dry period immediately predating the Holocene; cultivation of grains may have been intensified during that time to compensate for the worsening climatic conditions (Hillman et al. 2001; Simmons 2007, p.85; Bar-Yosef 1998). The sites of *Mureybe*t and *Abu Hureira* in northern Syria show that the territory of the Natufian culture had expanded northwards by this time. Archaeological traces of the Natufian in the Levant from the end of the Younger Dryas are sparse, suggesting that the populations abandoned the area (Blockley & Pinhasi 2011).

The Natufian was succeeded by the Pre-pottery Neolithic (PPN), which is most commonly split into two phases (PPNA and PPNB). The PPNA has been dated to the fairly wide range of 11700-10500 cal BP,

which may be partly due to regional variation and calibration difficulties for radiocarbon dates of this particular period (Simmons 2007, p.89). Important sites of the PPNA are *Jericho*, *'Ain Ghazal* in Jordan, *Tell Aswad* in southern Syria and *Göbekli Tepe* in Southeast Anatolia. The onset of the PPNA coincided with the beginning of the Holocene and may thus have been a cultural response to the improving climate (Blockley & Pinhasi 2011). During the PPNA, villages grew larger and plant cultivation became more intense, although there is still considerable debate about the presence of morphologically domesticated plant species (Simmons 2007, p.104). The population was by now predominantly sedentary. Some of the earliest examples of communal architecture date to this time, such as the tower of *Jericho* or the site of *Göbekli Tepe* (Kenyon 1957; Schmidt 2000).

During the PPNB the domestication of various grains and animal species was well underway (Simmons 2007, p.140). Dwellings became larger, and the traditional circular huts were abandoned for rectangular buildings with walls made from mud bricks or stone (Hauptmann & Özdoğan 2007, p.32). Clay and lime plaster were already known as working materials and used in buildings and figurines. For unclear reasons, many settlements in Mesopotamia and Palestine were abandoned towards the end of the PPNB (Hauptmann & Özdoğan 2007, p.34).

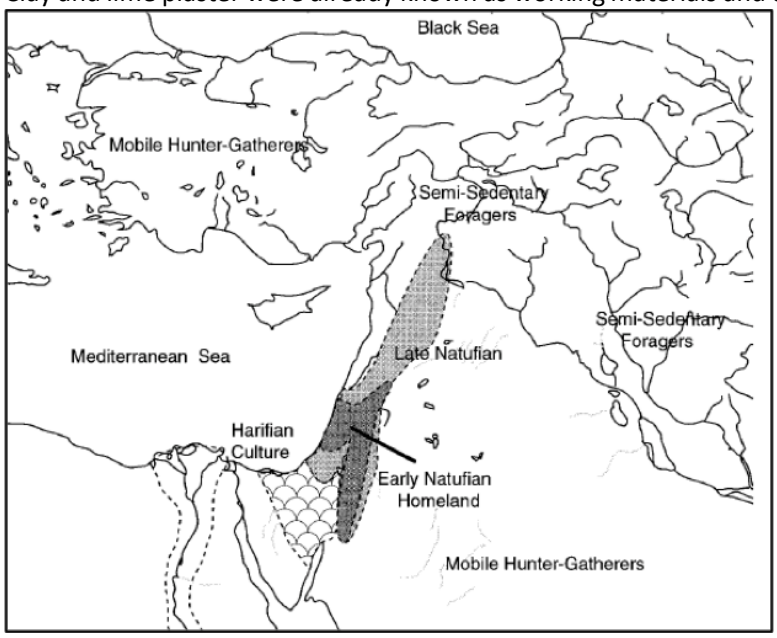

Figure 1: The territory of the Natufian culture The Harifian culture emerged during the late Natufian in the southern parts of the Levant including the Sinai peninsula and may be a regional variant of the Natufian rather than an independent cultural entity; from (Bar-Yosef 1998, p.160).

During the Pottery Neolithic (PN), which followed the PPNB from 9000-6900 cal BP, clay and lime plaster were first used for the construction of vessels (Simmons 2007, p.201). In the Fertile Crescent, this phase marked the late Neolithic, and the previous cultural uniformity dissolved into several local traditions defined by pottery and architectural styles. In Anatolia, the architectonic traditions from the preneolithic were continued (Hauptmann & Özdoğan 2007, p.35).

1.1.3 The way into Europe

The Neolithic subsistence strategy spread to Central Anatolia, Crete and Cyprus during the PPNB (Guilaine 2007; Perlès 2001; Evans et al. 1964). Around 7000 BC, Neolithic settlements first appeared

in western Anatolia, reaching the Aegean and Marmara coasts during the later 7th millennium BC (Özdoğan 2007, p.153). While settlement structure and subsistence strategies were much the same in Central/eastern and western Anatolia, the western Anatolian Neolithic sites lack the monumental architecture and prestige goods which were common in the east (Özdoğan 2007, p.153). The expansion of the Neolithic into western Anatolia occurred in three phases. The first phase occurred in preceramic times and appears to have been small-scale. The second phase was characterized by dark monochrome wares and is referred to as the "Fikirtepe culture" after one of its prominent sites. It stretched from western Anatolia into Thrace and parts of Bulgaria. The third phase is characterised by red wares, which were sometimes polished or decorated with white paint (Özdoğan 2007, pp.155–157). This type of pottery has been linked to traditions going back to Central Anatolia, from where it appears to have spread towards the Aegean Sea following river valleys. Similar pottery also accompanied the early Neolithic in Greece (Sesklo) and the Balkans (Karanovo I and Starčevo-Körös-Criş) (Özdoğan 2007, p.157).

In the light of the PPNB-findings on Cyprus and Crete, there has been some debate about the existence of a pre-pottery Neolithic on the Greek peninsula, but the evidence is inconclusive. The beginning of the "Neolithic proper" in Greece- as evidenced by pottery- is dated to around 6500- 6400 cal BC (Budja 2009; Reingruber & Thissen 2009; Lespez et al. 2013).

Thessaly shows the largest concentration of settlements, important sites being *Argissa*, *Nea Nikomedeia* and *Sesklo* (Bogucki & Crabtree 2004, p.220), but early Neolithic settlements have also been recovered further north in the Greek province of Macedonia (Karamitrou-Mentessidi et al. 2013; Lespez et al. 2013; Rodden 1962). The characteristic culture of the early Greek Neolithic is the Sesklo culture, named after the site where it was discovered. It lasted from 6500 to 5900 cal BC (Perlès 2001). From the Aegean region and the southern Balkans, the first farming populations took two different routes (Figure 2): One led westwards along the Mediterranean coastline, the other one went northwards into the Balkans, subsequently turning westward towards the Carpathian Basin and finally Central Europe; Eastern Europe was likely settled by farmers splitting from this branch towards the Pontic Steppe.

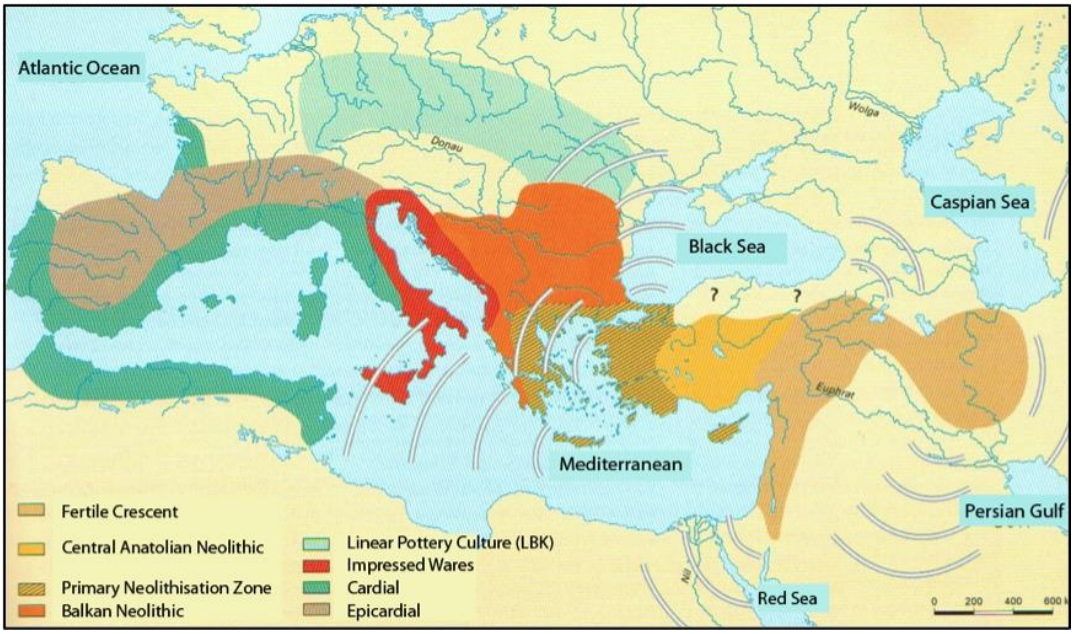

Figure 2: The Neolithisation of Europe. Question marks denote areas where archaeological traces of the Neolithic would be expected, but have not been found. Adapted from (Özdoğan 2007, p.151).

From the Balkans to Central Europe- the "continental route"

The defining cultures of the early Neolithic in the southern Balkans are Karanovo I and Kremovci, which appeared in southern Bulgaria about 6200 BC and are characterized by red and white painted wares (Bogucki & Crabtree 2004, p.238).

The first pottery in the northern Balkans and southwestern Carpathian Basin appeared around 6300 cal BC and belonged to the so-called Starčevo-Körös-Criş complex (Budja 2009; Whittle et al. 2002). The earliest Neolithic pottery found in the Iron Gates was also associated with this complex, but evidence from Lepenski Vir indicates that farming and stockbreeding were adapted only later on. In a similar case of "Mesolithic-Neolithic overlap", the trapezoidal buildings at Lepenski Vir and Padina are associated with Neolithic pottery, while they already occur in a Mesolithic context at the nearby site of Vlasac (Merkyte 2003; Boric 2002; Radovanovic 2006; Borić 2007). Meanwhile, contemporaneous neolithic settlements in the vicinity of Lepenski Vir clearly belonged to the Starčevo-Körös cultural complex (Merkyte 2003).

The Starčevo culture expanded into the western Carpathian Basin, finally reaching Transdanubia around 5800 cal BC. The eastern Carpathian Basin, encompassing the Great Hungarian Plain and parts of Romania, was settled by the Körös and Criş cultures at roughly the same time.

The neolithisation of Central Europe had its starting point in the vicinity of Lake Balaton in Transdanubia. Here, the Starčevo culture gave rise to the Transdanubian Linearbandkeramik (TBLK) about 5600 cal BC (Bánffy & Oross 2007; Oross & Bánffy 2009). The Linearbandkeramik (LBK) then rapidly spread further west and north into Austria, Slovakia and the Czech Republic, reaching eastern Germany about 5500 cal BC. At its maximum extent, the LBK stretched from the Paris Basin to the

Ukraine. Apart from the eponymous pottery style, important cultural features of the LBK were the construction of longhouses and the emphasis on cattle breeding as opposed to the sheep and goat favoured by the more southerly Neolithic groups. The decline of the LBK at the end of the 6th millennium BC marks the "beginning of the end "of the early Neolithic in Central Europe. The LBK was succeeded by numerous locally circumscribed Neolithic cultures (see for instance (Brandt et al. 2013) for description of the cultural succession in the Middle-Elbe-Saale region of Germany).

The Mediterranean route

Around 6200 BC, a pottery tradition characterized by impressed decorations developed on the Adriatic side of the Greek peninsula (Guilaine 2007). The "Impressed Wares" tradition spread westwards through the Adriatic (Forenbaher 2011) and along the Dalmatian coast, reaching Apulia on the southeastern Italian Peninsula about 5900 BC (Costantini & Stancanelli 1994; Price 2000, pp.11–12 and citations therein). The Tavoliere Plain in the province of Apulia appears to have been one of the focal points of Neolithic settlements (Malone 2003; Brown 1991). From Apulia, the Neolithic settlemets steadily expanded northwards along the Adriatic coast, while the settlement of the Tyrrhenian coast was more punctual (Malone 2003 and citations therein). In northern Italy, there appears to have been continuity with Mesolithic traditions, as evidenced by settlement location, raw materials and lithic techniques (Malone 2003). The earliest Neolithic settlements from northwestern Italy (Liguria) feature impressed wares and date to 5800 cal BC (Gehlen 2010; Müller 1994, p.257). Three small settlements which can be directly linked to Liguria or Tuscany have been found in France (Guilaine & Manen 2007). They date to around 5800-5600 cal BC.

The nearly contemporaneaous C-14 dates for Neolithic sites in northern Italy, France and the Iberian Peninsula, have been interpreted as evidence of "maritime" pioneer colonization, which allows for faster expansion than land-based migration (Zilhao 2001)

In France, the Impressa tradition was succeeded by the so-called Cardial culture, which emerged between 5600 and 5400 years cal BC (Guilaine & Manen 2007; van Willigen et al. 2009) . While toolmaking techniques and pottery decoration link the early farmers of southern France to those of Northwestern Italy, the Cardial culture is a separate entity from the Ligurian/Italian impressed wares tradition (Gehlen 2010).

Via the Languedoc and the Provence the Cardial culture spread into the Iberian peninsula (Guilaine & Manen 2007). The archaeological record shows the coexistence of hunter-gatherer on the Iberian Peninsula during the Early Neolithic in some regions, especially Valencia and Portugal (Medved 2013).

1.1.4. Models of Neolithisation

While the time frame and the cultural entities associated with the Neolithisation of Europe are reasonably well established, the nature of the process itself is less clear. Historically, the debate has oscillated between two opposing viewpoints: The "acculturationist" approach envisioned a process

where the “Neolithic package” was culturally transmitted from the first farming communities to neighbouring hunter-gatherer groups, who in turn adapted the novel technologies based on their own intimate knowledge of their surroundings. The “migrationist” point of view favoured a migration of Neolithic farmers across Europe and the replacement of the local hunter-gatherers. Proponents of either theory have drawn evidence from many areas of research besides “classical archaeology”, such as physical anthropology (Pinhasi & von Cramon-Taubadel 2009; Pinhasi & Cramon-taubadel 2012) , linguistics (Renfrew 1996) and genetic studies of both modern and ancient populations (Bramanti et al. 2009; Haak, Forster, et al. 2005; Chikhi et al. 1998; Menozzi et al. 1978; Chikhi et al. 2002; Richards 2003a). While the debate between the two schools of thought is still ongoing in parts of the research world (in particular among geneticists), the focus of archaeological research has shifted from sweeping “theories of everything” to the regional level, tracking local changes during circumscribed phases of cultural development. This has been accompanied by the development of “integrationist” models, which include both migration and acculturation as contributing factors (see (Gronenborn 2007; Richards 2003b) for an overview).

Nowadays the most widely accepted model with the best support by evidence is the “demic diffusion” or “wave of advance” model, where the spread of farming was mainly migration-driven, but acculturation gained importance towards the margins of the “farmer territory”,e.g. Scandinavia and the Baltic, where hunter-gatherers and farmers coexisted for considerable lengths of time. Variations on this model are “leapfrog colonization” and “(maritime) pioneer colonization” ((Zvelebil 2000; Gamba et al. 2012; Zilhao 2001).

The margins or “contact zones” in turn are of particular interest to researchers who maintain the position that local hunter-gatherers shaped and and influenced the developing European Neolithic (Bánffy 2004; Bánffy 2005; Whittle 1996).

1.2 The prehistory of the Great Hungarian Plain (Alföld)

The Great Hungarian Plain (hung. *Nagy Alföld* or simply *Alföld*) is a lowland area in the eastern part of the Carpathian Basin, encompassing about 52000km^2. Most of the Alföld lies in in Hungary, but Romania, Slowakia, the Ukraine, Serbia and Croatia each also share parts of it. The Hungarian Alföld is bounded by the Tisza-Danube interfluve to the west, the foothills of the Carpathian mountains to the North and East and the Maros floodplain in the South (definition adapted from (Yerkes et al. 2009)). Its main drainage system consists of the Tisza, which traverses the Alföld north to south, and its two main tributaries, the Körös and Maros rivers, which flow from east to west. The northeastern part of the Alföld (the Nyírség region) and the Tisza-Danube interfluve are sandy regions which are largely unsuitable for agriculture, while the present and former flood plains have fertile loess soils. Before the extensive drainage works of the last two centuries, the Alföld used to be a marshy landscape dominated by flood plains and backswamps, with fluvial terraces and elevated “islands” dispersed

throughout the low-lying marshlands. The Alföld has a continental climate with warm summers (Dfb in the Köppen-Geiger system), defined as having an average temperature above 10 °C in the warm months, and a coldest month average below −3 °C and no marked seasonal differences in precipitation (Peel et al. 2007; Sümegi et al. 2002). The vegetation is mostly of a steppe-forest type, while the bordering foothills of the Carpathians are covered in deciduous and mixed forests.

1.2.1 The Mesolithic period of the Alföld

The Alföld shows a remarkable dearth of Mesolithic findings. The reason for this is not entirely clear; two possible reasons are the general low population density of hunter-gatherer populations and the fact that nomadic communities leave fewer durable traces, i.e. pits or permanent dwellings, than sedentary ones. It has also been proposed that remains from the Mesolithic period may be buried too deep in alluvial sediments to be detected. However, at least in the Körös region even in-depth-probing did not yield any Mesolithic remains (Makkay 1996).

The fluctuations of hazel pollen in sediment records from northern Hungary during the late Mesolithic have been interpreted as the result of periodic forest-clearing by hunter-gatherers, but this is not uncontested (Bácsmegi et al. 2012; Magyari et al. 2012; Kertész 2002). What is certain is that the areas surrounding the Alföld were inhabited by Mesolithic populations: To the North, the Ukrainian Nezvisko–Oselevka culture occupied areas north of the Tisza and along the Dniestr (Kertész 1996; Kertész 2002, and references therein). To the South, the Danube Gorges were the territory of the "Iron Gates Mesolithic".

To date, there are three known Mesolithic sites in Romania (Paunescu 1964; Nicolăescu-Plopşor & Pop 1959; Eichmann 2004). On Hungarian territory, archaeological research has brought to light a few sites in Central Hungary on the Tisza-Danube interfluve and the Jászság region (Kertész 1996).

The only Hungarian Mesolithic sites that have been archaeologically explored in depth are *Jásztelek* and *Jászberény*, which lie in the Jászság region at the foot of the Mátra Mountains (Kertész 2002). The excavated remains included the foundations of a circular hut and numerous tools, most of which were microliths fashioned from local flint. No human remains were recovered. Radiocarbon dates of shells from kitchen refuse and and sediment carbonate at *Jászberény I* lay between 8030 ±250 BP and 7154 ±62 BP[2]. The style of the lithic tools links the Jászság to the "western technocomplex" spanning much of western and Central Europe (Kertész 2002; Bogucki & Crabtree 2004, p.173; Kertész 1996).

There are three more hints of a Mesolithic presence from the Alföld: A disarticulated skull from Maroslele-Pana (grave no. 7) was dated to 6300-6200 cal BC, which predates the assumed beginnings

[2] The C-14 data reported in the original study was uncalibrated. When calibrated with the web-based tool OxCal v. 4.2 (Ramsey 2009; Reimer et al. 2013) (IntCal 13 calibration curve, 95.4% probability), the dates for the shells and the Mesolithic culture-bearing layer are given as 6999 ± 544 cal BC and 6007 ± 107 cal BC, respectively.

of the early Neolithic in the Alföld by about 300 years. Furthermore, the individual's isotope values indicated a high consumption of freshwater fish, distinguishing it from the Neolithic individuals (Whittle et al. 2002). At *Ecsegfalva,* a Körös culture site that was occupied between 5800 and 5650 cal BC, cattle bones (*Bos sp.*) could be dated to 6950-7750 cal BC, hinting at human occupation sometime prior (Whittle & Bálint 2007, chap.10). Finally, excavations in the southern Alföld (Hódmezővásárhely) have yielded sporadic Mesolithic remains, but the detailed archaeological results are yet to be published (A. Marcsik *et al*., pers. communication).

1.2.2 Early Neolithic [6000-5500/5400 cal BC]

Neolithic technologies were introduced to the Alföld by the Körös Culture, which originated in the northern Balkans as part of the "Starčevo -Körös-Criş" complex. By 6000 cal BC, the Körös culture had reached the Maros (e.g. *Maroslele-Pana*). It then spread north and east along the major rivers of the Alföld, such as Tisza, Körös and Berettyó (Whittle et al. 2002). While the Neolithic settlers generally steered clear of the Tisza-Danube interfluve with its sandy soils, several dozen densely clustered Körös settlements were found in the southern part of the interfluve, for instance at *Szakmár-Kisüles* (Bánffy 2012).

By 5800 cal BC the Körös culture had reached the central Alföld. This is where *Ecsegfalva*, one of the best-studied Körös sites, is situated. By 5700 cal BC settlements north of the eponymous Körös river had been established, such as *Tiszaszőlős-Domaháza* (Whittle & Bálint 2007, chap.10; Domboróczki et al. 2010; Raczky et al. 2005). The upper Tisza region was settled roughly between 5600 and 5500 cal BC, as data from the northern Hungarian site of *Ibrány* indicate (Domboróczki & Raczky 2010 and citations therein). There is some archaeological evidence- mainly from the northeastern site of *Méhtelek* – that the Upper Tisza region was (also) settled from the northeast by groups originating in Romania, which has a solid record of Criş/Körös sites (Domboróczki 2010; Domboróczki & Raczky 2010; Mester & Rácz 2010; Raczky et al. 2005).

Körös settlements were erected close to rivers, preferentially elevated above the floodplain on hills or terraces. They consisted of groups of rectangular huts with saddle roofs, supported by wooden beams and with walls made of clay-daubed wattling (Bartosiewicz et al. 2003, p.100). The high settlement density, the absence of vertical stratigraphy and the comparatively "light" construction of the buildings has been taken as a sign that Körös settlers were highly mobile (Whittle et al. 2002; Bailey 2000, p.58). In the northern part of the Alföld, settlements were smaller and less numerous than in the south, indicating an even higher degree of mobility (Domboróczki & Raczky 2010; Domboróczki 2009).

The Körös farmers presumably practiced an intensive form of agriculture on small fields; pollen records are consistent with small-scale forest clearing and coppicing of hazel (Magyari et al. 2012). Sheep and goat were bred and used for meat and likely also small-scale dairying (Bartosiewicz 2005; Craig et al. 2005). Farming was supplemented by hunting, fishing and foraging, possibly as compensation for poor

agrarian yields, especially in the northern Alföld (Bartosiewicz 2005; Raczky et al. 2005). The Alföld itself is poor in lithic resources, so Körös farmers relied on imports from the surrounding mountains in Hungary and Romania. Sought-after materials included obsidian, Szentgál radiolarite, Hornfels, dolerites and flint (Whittle & Bálint 2007, p.746; Mester & Rácz 2010). Hunter-gatherers and early farmers used lithic materials from the same sources, but the tools they fashioned differ markedly from each other (Kertész 1996). The existence of Körös settlements in the Upper Tisza region within reach of the foothills of the Carpathians suggests that the Körös farmers were able to gather and trade some lithic resources within their own cultural group (Domboróczki & Raczky 2010).

Körös pottery is characterized by rounded vessel shapes and pinched decorations. The majority of wares were unpainted, but painted-on linear decorations in white, brown and black were occasionally used. Körös farmers also frequently formed animal and human figurines (idols) from clay (Kalicz 1990a; Bartosiewicz et al. 2003). Graves were situated within the settlements, sometimes inside the buildings; there were no formal cemeteries. During the early Neolithic, grave goods were not a regular feature of burials, nor were they particularly lavish (Bíró et al. 2003, p.99; Bailey 2000, pp.122–123).

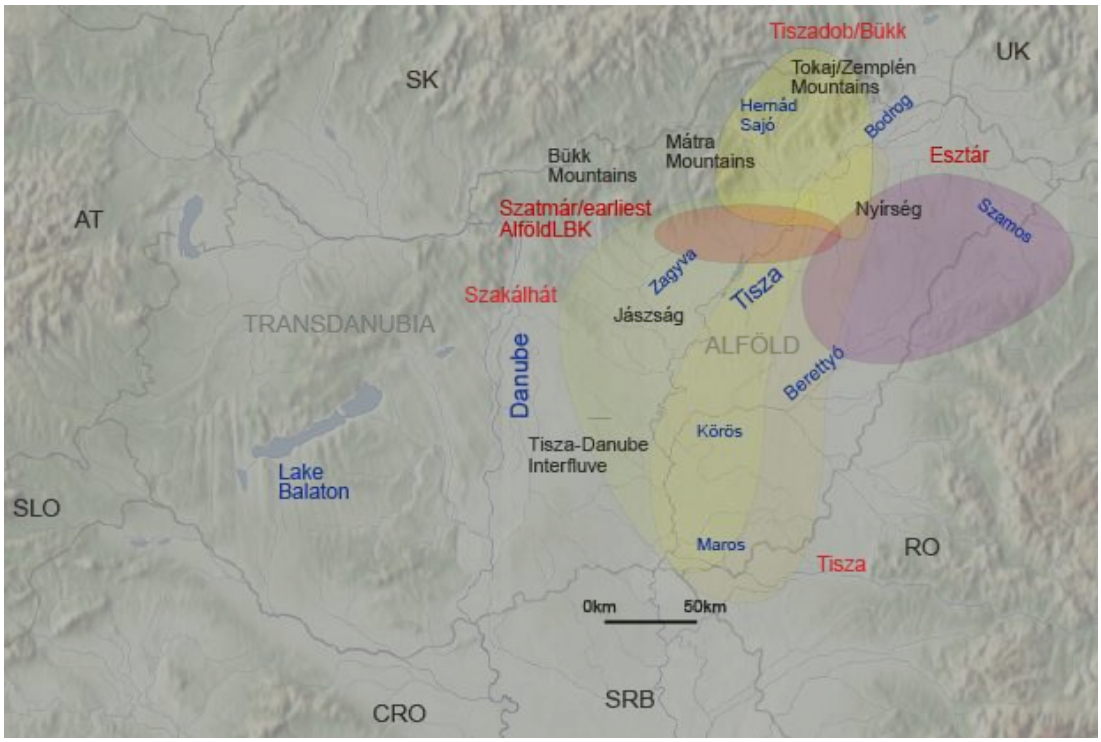

Figure 3: Map ofhe Hungarian part of the Carpathian Basin. Names of rivers and lakes are in blue, countries and regions are black, archaeological cultures are red. The coloured shapes mark the approximate distribution areas of the Alföld Neolithic cultures and their subgroups (red= Szatmár/earliest ALBK, purple = Esztár group, yellow= Tiszadob/Bükk group, green=Szakálhát group, yellow= Tisza culture) (Körös culture not depicted, see text for description of its territory) UK=Ukraine, SK= Slovakia, AT= Austria, SLO= Slovenia, CRO= Croatia, SRB=Serbia, RO= Romania. (Topographic map courtesy of the Institute of Archaeology at the Hungarian Academy of the Sciences, Budapest)

1.2.3 Middle Neolithic [5600/5400-5000 cal BC]

The middle Neolithic of the Alföld is represented by the Alföld-Linearbandkeramik (ALBK), which emerged in the northern Alföld around 5500 BC.

The Szatmár group and the beginnings of the Alföld LBK

The transition from the early Neolithic Körös culture to the Middle Neolithic Alföld LBK is closely associated with the Szatmár group. There is some debate as to whether this group can already be regarded as the earliest phase of the ALBK or whether it is a separate cultural entity, but its intermediate position between the Körös culture and the "proper" ALBK is undisputed. Its core area was the northern Alföld, especially close to the Bükk and Matra mountains (Figure 3, see also map in (Domboróczki 2009). Important sites from this period are *Füzesabony-Gubakút* and *Mezökövesd-Mocsolyás.* The appearance of the Szatmár group/earliest ALBK has been dated to about 5630-5560 cal BC (Domboróczki et al. 2010; Kalicz & Makkay 1977; Domboróczki & Raczky 2010; Domboróczki 2009). The earliest remains of longhouses, which are characteristic of the ALBK as well as of other forms of the LBK, date to around 5400 cal BC (Domboróczki et al. 2010). The pinched decoration and

incised lines on the Szatmár/ earliest ALBK pottery and their shape(s) show links to Körös ceramics, but there are also linear patterns similar to later ALBK decorations (Kalicz & Makkay 1977, p.21). As in the Körös culture, the dead were buried within the settlements, most lying on their left side in a crouched position. The graves were generally oriented in a SE-NW direction and furnished with only few, simple grave goods, if at all (Kalicz & Koós 2001).

In their seminal work "Die Linienbandkeramik der Ungarischen Tiefebene", Nándor Kalicz and János Makkay proposed a Mesolithic origin for the ALBK, which was at the time supported by the apparent lack of overlap between Körös and early Alföld LBK territories (Kalicz & Makkay 1977, p.29). This was further compounded by environmental studies suggesting that the agricultural technology of the Körös culture was not suitable for the climate and soil conditions of the northern Alföld (Sümegi et al. 2002). A mix of environmental factors and pushback from hunter-gatherers supposedly created an "agro-ecological barrier" in the Carpathian Basin, which was only overcome after an extensive adaptation process involving the local Mesolithic population (Sümegi et al. 2002) .

However, the discovery of Körös sites in the northern Alföld showed that the Alföld LBK did not emerge on "virgin territory" free of Neolithic background. Furthermore, pottery, settlement layout, buildings and burial rites of early Alföld LBK sites show strong similarities to Körös sites, suggesting continuity (Domboróczki 2009; Szilágyi & Szakmány 2007; Kalicz & Koós 2001). It is nevertheless undisputed, that the emergence of the ALBK was accompanied by changes in lifestyle and technology, and while a large-scale involvement of local hunter-gatherers seems unlikely given the sparse evidence of their existence, the meeting between the two branches of the Körös culture in the Upper Tisza region and the existing trade networks may have played an important role in this cultural change. Thus the concept of the agroecological barrier was remodeled to a "mental-marginal-zone"(Raczky et al. 2005) and finally reinterpreted as a zone for interaction (Bánffy & Sümegi 2012).

During the ALBK, hunting and fishing became less important as part of the daily subsistence, and the focus of livestock breeding shifted to cattle and pigs, which were better suited to the colder and wetter climate of the Alföld (Raczky et al. 2005). Woodland management in the form of burning and coppicing increased and pollen records from northeastern Hungary show an increase of meadowland, either used for pasture or fallow (Magyari et al. 2012; Gardner 2002).

The ALBK pottery bears the eponymous incised linear patterns, while the formerly popular pinched decorations became rare (Kalicz & Makkay 1977, pp.34–37). Obsidian and flint were mined in the northern mountains and exported to the lowlands. Tools were fashioned from stone, bone and antler or clay. Spondylus beads and pendants were frequently used as personal adornments. Anthropomorphic vessels and small idols were found throughout the Alföld (Kalicz & Makkay 1977, pp.56–59). As in the Körös culture, there are no cemeteries in the ALBK. The dead were buried in the settlements, but it has been argued that this burial space was reserved for high-ranking members of

the community (Siklósi & Csengeri 2011). Grave goods were sparse and mostly limited to ochre, spondylus jewellery and pieces of pottery (Kalicz 1977 pp 73-83). The dead were buried in a crouched position, and the majority of graves are oriented in SE-NW direction.

The further development of the ALBK

From its region of origin, the ALBK proceeded to spread across the entire Alföld, from the Maros River in the south to the river valleys in the Bükk Mountains in the north. Unlike its Transdanubian counterpart, which eventually expanded beyond the Carpathian Basin, the ALBK remained largely confined to the Alföld, a few "outposts" in modern-day Slovakia and Romania notwithstanding (see also Oross & Bánffy 2009). Instead, it split into several regional groups, which are distinguished mainly by their pottery styles. The regionalisation set in around 5300 BC and lasted until the end of the middle Neolithic around 5000 BC (based on (Hertelendi et al. 1995)).

The *Szakálhát* group is one of the earliest regional styles- findings from the Middle Tisza region show that it directly succeeded the early Alföld LBK there (Kalicz & Makkay 1977, p.106). Its core area stretched from the Middle Tisza region towards the Maros in the south, covering large parts of former "Körös territory". In the northern and eastern Alföld, it overlapped with the territories of the earliest ALBK/Szatmár, Bükk and Esztár groups. Major sites of the Szakálhát group are *Battonya*, *Cegléd*, *Abony* and *Pusztataskony.* The pottery is sand- or chaff-tempered, thin-walled and often brown, dark grey or red. Typical Szakálhát decorations include spiral patterns, and pottery was often painted in monochrome red (Kalicz & Makkay 1977, pp.88–90). The Szakálhát group was well connected to the other Alföld LBK groups, which was probably facilitated by spatial overlap of the respective territories. There also was also a trade connection to Transdanubia, in particular to the Notenkopf and early Zseliz groups of the late middle Neolithic. In the South, the cultural influence of Szakálhát group stretched far into the territory of the Vinča culture (B2 phase) in northern Serbia and the Banat region of Romania (Kalicz & Makkay 1977, pp.107–108 and citations therein; Bartosiewicz et al. 2003, chap.4).

The core area of the *Esztár* group lies in the eastern Alföld north of the Körös. Linear decorations are rare in Esztár wares, but their shape(s) link them to the ALBK tradition. Fine ware was sometimes red-slipped and often painted in monochrome (Kalicz & Makkay 1977, pp.54–56). The painted decorations show some similarities to ceramics from the Szamos region of neighbouring Romania, which has led to the term "Esztár-Szamos region Painted Pottery Group" (Bánffy 2006).

Around 5300 BC, the *Tiszadob* group emerged in the Upper Tisza region and was quickly succeeded by the *Bükk* group. The Tiszadob/Bükk territory stretched from northeastern Hungary to southern Slovakia. Settlements were not only found on the plain, but also in the Bükk and Mátra mountains,

following the river valleys of the Hernád and Bodrog (Kalicz & Makkay 1977, p.39). Characteristic for Tiszadob and Bükk pottery are the dark clay, sand-tempering and the polishing of the finished wares (Kalicz & Makkay 1977, p.38). Bükk pottery was of high quality and traded far beyond the limits of the northern Alföld, as far as southern Poland and Central Serbia (Csengeri 2010b; Kalicz & Makkay 1977, p.45 and citations therein). In the Upper Tisza region, the settlement area of the Bükk culture partially overlapped with those of the Zseliz, Esztár and Szakálhát groups (Kalicz & Makkay 1977, p.44; Raczky & Anders 2009). It has been hypothesized that the Tiszadob and Bükk groups received a major input from Mesolithic hunter-gatherers, who are thought to have occupied the mountainous areas (Domboróczki 2009 and citations therein).

The *Szilmeg* group has so far yielded less findings than the other groups. Its territory stretched from the foot of the Bükk and Mátra mountains to the Hortobágy in the east. The pottery was not decorated with the typical linear band incisions, but location and cultural features place it among the regional variants of the Alföld LBK. Szilmeg-type pottery was also recovered from Esztár and Szakálhát sites, pointing to territorial overlap and/or trade connections between these groups (Kalicz & Makkay 1977, pp.51–52).

1.2.4 Late Neolithic [5100-4500/4400 cal BC]

The dominant culture of the late Neolithic on the Alföld is the Tisza culture, which appeared around 5100 cal BC (Hertelendi & Horváth 1992). In Transdanubia, this period corresponds with the late Notenkopf and Zselisz groups as well as the first phase of the Sopot culture. The core territory of the early Tisza culture was the southern Alföld between the Tisza and the Transsylvanian Carpathians, with the Körös as northern boundary (Kalicz & Raczky 1987). Well-known sites from this area are *Vésztő-Mágor*, *Hódmezővásárhely-Gorza* and *Békés-Povádzug* (Hegedüs & Makkay 1987; Horváth 1987; Kalicz & Raczky 1987). This area largely overlaps with the Szakálhát territory, and Tisza settlements were frequently erected directly on top of Szakálhát settlements. Tisza pottery shows some degree of continuity with Szakálhát material as well (Kalicz & Makkay 1977). The earliest phase of the Tisza culture also overlapped with the Bükk and Szilmeg groups of the ALBK, and Bükk imports were found in the lowest layers of some tell settlements (Raczky & Anders 2012, pp.21–22).

In its classical phase, the Tisza culture spread to the Middle and Upper Tisza, where *Pusztataskony* and *Polgár-Csőszhalom* are important sites. Unlike the southern Alföld, where the Tisza culture was the sole representative of the late Neolithic, the northern Alföld and Upper Tisza Valley also harboured other late Neolithic cultural groups (Kalicz 1994; Kalicz & Raczky 1987): In the valleys of the rapid Körös and the Berettyó, the Herpály culture developed, whereas the Upper Tisza region and Bodrog valley gave rise to the Csőszhalom culture. The former had ties with Transsylvania to the east, while the latter shows some Transdanubian and Polish/Slovakian influence (Bartosiewicz et al. 2003, chap.4). The

"Tisza-Herpály-Csőszhalom" complex was roughly contemporary with Lengyel I–II cultures in Transdanubia and northern Hungary, the Iclod group and the PetreƔti culture in Transsylvania, and the Vinča B2-D2 phases in the northern Balkans (Yerkes et al. 2009; Kalicz & Raczky 1987; Bánffy & Oross 2007).

An important characteristic of the Tisza culture are its tell settlements (Bailey 2000, p.168). Tells were common in the Neolithic Levant and the southern Balkans, but the Tisza culture is the northernmost representative of this settlement style. Apart from "real" tells (3-4m height), the Tisza culture also featured tell-like settlements (1-2.5m) and horizontal or "flat" settlements. Tell settlements were more frequent in the southern Alföld, with the exception of the Herpály culture, which left a large number of small tell sites along the Körös and Berettyó (Kalicz & Raczky 1987). Settlements were built on elevated locations, lay close to waterways and were often surrounded by ditches (Kalicz & Raczky 1987). Houses were built on a rectangular floor plan with timber frames and wattle-and-daub walls, but rammed-earth structures have also been observed (Kalicz & Raczky 1987). The dead were buried in crouched positions, often in wooden coffins and/or wrapped into woven mats. There were few grave goods, except for red ochre. Burials were often clustered in the non-functional parts of the settlement (Kalicz & Raczky 1987; Bailey 2000, p.195).

While their early pottery shows stylistic similarities to Szakálhát wares, the Tisza farmers also added new shapes to the repertoire, such as amphora-shaped vessels and pedestalled bowls. The "diagnostic decoration" of the Tisza culture is an incised meandering pattern that presumably mimics woven textiles. Another innovation was the coating of vessels with bitumen, sometimes with chaff pressed into it (Kalicz & Raczky 1987). As in the preceding cultures of the Alföld, lithic materials were imported from the surrounding regions, probably using the Tisza and its tributaries for transport (Kalicz & Raczky 1987).

Hunting became a significant part of subsistence again during the Tisza culture, with aurochs and deer being the preferred prey (Bartosiewicz 2005; Kalicz & Raczky 1987). The detection of Lengyel pottery at Tisza sites deep in the Alföld indicates some connections between the two groups (Sebők 2012; Kalicz 1994). Another important trading partner was the Vinča culture (Kalicz & Raczky 1987).

During the late Neolithic, it appears that copper began to replace Spondylus as prestige material (Siklósi & Csengeri 2011). The actual Copper Age on the Alföld, however, started with the Tiszapolgár culture, which succeeded the Tisza culture.

1.2.5. The Neolithic in Transdanubia

The Neolithisation of Transdanubia was largely comtemporaneous with the developments on the Alföld, give or take a few decades. The earliest Neolithic culture in Transdanubia was the Starčevo culture (Bíró et al. 2003, p.102; Kalicz 1990b; Kalicz 1990a), which reached the vicinity of Lake Balaton around 5800 BC and lasted until 5400 BC (Kalicz 2010). Here, the Transdanubian

Linearbandkeramik (TLBK) emerged around 5600 cal BC and expanded to the regions northwest of the Carpathian Basin while still in its formative phase (Bánffy & Oross 2007; Oross & Bánffy 2009; Bánffy 2004; Bánffy 2000). In its later phase, which lasted until 4900 cal BC the TLBK split into several groups: the Kestzhely group in the south and Zselisz and Notenkopf in the north (Bánffy & Oross 2007 and citations therein). While the TLBK held sway in northern Transdanubia, southern Transdanubia was also influenced by the Vinča culture (Oross & Bánffy 2009 and citations therein). The late Neolithic of Transdanubia was characterized by two cultures: The Sopot culture originated in the northern Balkans (Bíró et al. 2003, p.102) and spread to Transdanubia about 5000 cal BC, lasting until 4800 cal BC. It was succeeded by the Lengyel culture (5000-4300 cal BC), which shows influences from the late TLBK and Slovakia/ Southern Poland and extended into present-day Austria (Bíró et al. 2003, p.102).

1.3 Mitochondrial DNA and human prehistory

1.3.1 Mitochondrial DNA

Mitochondria are cell organelles in eukaryotic organisms and serve important functions in the cellular energy metabolism, i.e. the citric acid cycle and oxidative phosphorylation. Cells can contain several thousand of mitochondria (Campbell & Reece 2003a), with especially high numbers in tissues that require a lot of energy, e.g. muscle and liver tissue. They are surrounded by two membranes and retain their own genome and ribosomes. The human mitochondrial genome was first sequenced in 1981, with minor revisions made in 1999 (Anderson et al. 1981; Andrews et al. 1999). This genome has since been used as a reference sequence ("(revised) Cambridge Reference Sequence"= rCRS), which means that mutations are identified and named in relation to the rCRS. The circular genome comprises 16569 bases and contains 37 genes, which code for 2 ribosomal RNAs, 22 tRNAs and 13 proteins of the mitochondrial inner membrane. The two strands of mtDNA are denoted as "heavy"(H) and "light" (L) strand. The 1122 base pair (bp) long region between the nucleotide positions (np) 16024 and 16577 does not code for RNAs or proteins (Anderson et al. 1981), but contains the H strand replication origin, the transcription origins for both strands and binding sites for regulatory factors, which is why it is also referred to as "control region". Mitochondria typically contain multiple genome copies, and a eukaryotic cell approximately contains between 1000 and 10 000 copies of mtDNA (Clayton 1982; Clayton 1984; Larsson & Clayton 1995). According to the widely accepted "endosymbiotic theory", mitochondria are most likely derived from prokaryotic organisms that were at some point integrated into another prokaryotic cell via phagocytosis (Campbell & Reece 2003b). The mitochondrial DNA of mammals and most other vertebrates is inherited maternally (Hutchison III et al. 1974; Giles et al. 1980). In mammals, paternal mitochondria are tagged with

ubiquitin during spermatogenesis and subsequently destroyed by the proteasomes of the oocyte (Sutovsky et al. 1999; Sutovsky et al. 2004). In mice, paternal/maternal heteroplasmy can be induced by crossing inbred strains (Gyllensten et al. 1991), and there has been a documented case of paternally inherited mtDNA in humans resulting in heteroplasmy (Schwartz & Vissing 2002). These cases notwithstanding, paternal inheritance of mtDNA is exceptionally rare in mammals. The same goes for mitochondrial recombination: Some studies have reported mtDNA recombination in heteroplasmic human cells *in vitro* (D'Aurelio et al. 2004; Kraytsberg et al. 2004) and extant human populations (Hagelberg et al. 1999; Awadalla 1999). However, the statistical methods soon came under criticism (Kivisild et al. 2000; Sun et al. 2011) and a reanalysis of the datasets did not confirm the results (Elson et al. 2001; Piganeau & Eyre-Walker 2004). Additional experiments *in vivo* detected no germ line mitochondrial recombination (Hagström et al. 2013). The observed ubiquitous low-level heteroplasmy in human populations is mostly due to inherited and somatic mutations, which are more frequent in mitochondrial than in nuclear DNA (Payne et al. 2013; Li et al. 2010).The current consensus is that for all intents and purposes, mtDNA can be regarded as a non-recombining system.

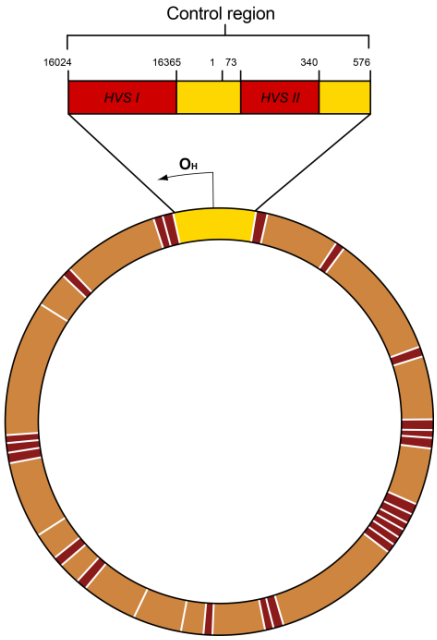

Figure 4: A schematic representation of the human mitochondrial genome.
The control region with the replication origin of the H strand (O_H) is depicted in yellow. The coding region is coloured brown, with interspersed red segments which code for tRNAs (modified from (Jobling et al. 2004, p.40)) Note: the limits of the HVS regions vary slightly between publications ((see also Andrews et al. 1999))

Mitochondrial DNA mutates at a substantially higher rate than nuclear DNA (Brown et al. 1979). The low accuracy of mitochondrial polymerase (Kunkel & Loeb 1981), high levels of oxidative stress due to proton/electron leakage from the electron transport chain and deficiencies in mismatch repair and nucleotide excision have been discussed as causes (Bogenhagen 1999; Shigenaga et al. 1994). Mutation rates are site specific, and the mitochondrial genome in particular shows large rate differences between sites. Since the coding region codes for a number of essential parts of the cellular energy generation, it is subject to natural selection, especially for mutations that cause amino acid changes (nonsynonymous changes) (Elson et al. 2004; Kivisild et al. 2006). It therefore contains comparatively few hypervariable nucleotide positions and appears to evolve at a relatively steady rate (a Torroni et al. 1994; Kocher & Wilson 1991; Howell et al. 1996; Ingman et al. 2000; Henn et al. 2009). The non-coding control region is under significantly less selective

pressure and therefore tends to accumulate mutations. It has been shown to diverge 10 times faster than the coding region (Greenberg et al. 1983; Aquadro & Greenberg 1983; Soares et al. 2009) and shows considerable site heterogeneity (Hasegawa & Horai 1991; Excoffier & Yang 1999; Wakeley 1993).

There are two highly polymorphic regions within the control region, referred to as Highly Variable Sequences (HVS) I and II (Aquadro & Greenberg 1983; Greenberg et al. 1983; Kocher & Wilson 1991; Vigilant et al. 1991). The mutation rate for the HVS-I, which contains five of the ten fastest sites of the entire mitochondrial genome, was estimated to be 4.95×10^{-5} transitions/ year (Forster et al. 1996). The HVS-II mutates at approximately half that rate (Soares et al. 2009).

1.3.2 The mitochondrial molecular clock

Provided they are neutral, i.e. do not influence the function of the final product, nucleotide and amino acid substitutions tend to accumulate at a steady rate, a phenomenon that was first described by Pauling & Zuckerkandl and dubbed the "molecular clock" (Zuckerkandl & Pauling 1965). The molecular clock can be used to reconstruct and date entire phylogenetic relationships between species and/or populations when nucleotide substitution rates are known. The nucleotide substitution rate is determined either directly by pedigree analysis or indirectly from a known and dated divergence point for different branches of the phylogenetic tree. In human phylogeny, traditionally the split between human and chimpanzee lineages is used, which has been dated to about 6 Mya (Stoneking et al. 1992; Vigilant et al. 1991). More recently, mitochondrial genomes from hominids, i.e. Neanderthals and Denisovans, and ancient humans have been used as a closer root for the Homo sapiens tree (Soares et al. 2009; Fu et al. 2013). Pedigree analyses yield much higher mutation rates than phylogenetic studies (Howell et al. 1996; Parsons et al. 1997; Sigurğardóttir et al. 2000; Henn et al. 2009). This time-dependency of the molecular clock has several plausible causes:

1. Site heterogeneity, as pedigree studies are more likely to observe mutations at fast sites, which leads to higher substitution rate estimates. Likewise, estimates based on phylogenetic studies rely on mutations at slow and moderate sites while "missing" mutation events at the fast sites due to homoplasy and back mutations (Heyer et al. 2001; Pääbo 1996).
2. Purifying selection: phylogenetic studies only detect those mutations that have become fixed in the population, missing those mutations that were lost by drift or selection (Ho & Larson 2006; Kivisild et al. 2006; Elson et al. 2004).
3. Demographic factors: In humans, demographic history may further have influenced this time-dependency of the molecular clock, with serial bottlenecks in the past and a relatively recent population growth/ relaxed selective constraints? (Henn et al. 2009).

These factors have led to often considerably diverging estimates for mitochondrial mutation rates.

1.3.3 Mitochondrial phylogeny and phylogeography

Mitochondrial genomes can be divided into haplogroups or clades that are defined by certain mutation motifs. These groups can be further divided into ever more finely resolved subclades. Mutations are named in reference to the rCRS, i.e. “16304C” means that the sequence in question differs from the rCRS at nucleotide position 16304 by having a C instead of a T. The rCRS belongs to haplogroup H2a2a, a subclade of haplogroup H, an extremely common haplogroup in Europe. Phylogenetically, H is found in the “middle” of the mitochondrial gene tree. To avoid confusion, it has been proposed to change to a reference sequence that represents a truly basal human mitochondrial genome. Based on the current human mtDNA phylogeny and the available hominid mt genomes, a ”Revised Sapiens Reference Sequence” (RSRS) sequence was reconstructed recently, but the usefulness of this new reference has been disputed (Behar et al. 2012; Malyarchuk 2013).

The most ancient mitochondrial clade, L, is specific to African populations and is characterized by a *HpaI* restriction site at np3592 (Chen et al. 1995; Cann et al. 1987; Denaro et al. 1981). Originally divided into two subclades, is has since been split into clades L0-L6 which are nested within L* (Van Oven & Kayser 2009). All non-African haplogroups are descendants of subclade L3, which arose 60-96 kya (Ingman et al. 2000; Fu et al. 2013). The two major non-African macro-haplogroups M in (south)eastern Asia and N in (north)western Eurasia coalesce at 50-70 kya (Soares et al. 2009). One of the subclades of N, R, is sometimes regarded as a further founding clade. R contains most of the haplogroups found in contemporary Europeans and populations of European descent, such as J,U (and its subclade K),T, and the haplogroups of the R0 clade: HV, H and V. The sister clades of R are I, W and X, which are also found in Europe, and A, O, S and Y, which are native to Eastern Asia and Australia (Figure 5).

The most comprehensive overview over the current phylogeny is offered by the regularly updated website *www.phylotree.org* (Van Oven & Kayser 2009).

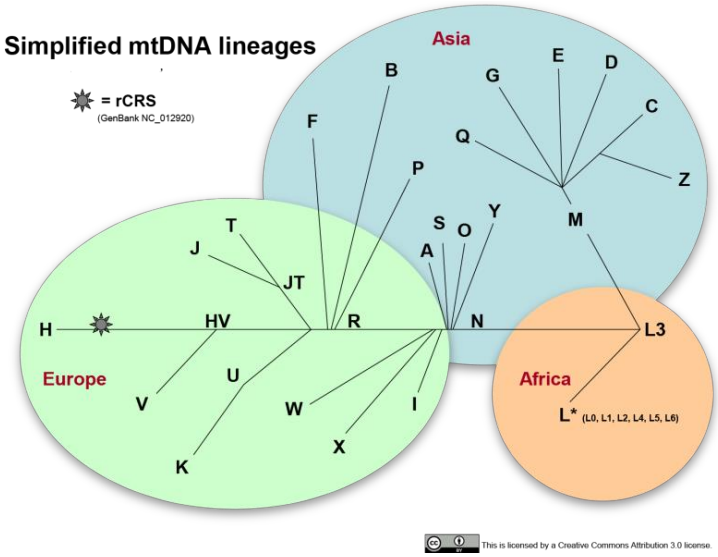

Figure 5: Simplified phylogeographic tree of the major mitochondrial haplogroups. Adapted from MITOMAP (MITOMAP: A Human Mitochondrial Genome Database. http://www.mitomap.org, 2013).

1.3.4 The phylogeography of Europe and its inferred population history

In the mid-nineties, researchers identified four lineages that together comprised about 60% of extant European mitochondrial diversity; they were named H, I, J and K (A. Torroni et al. 1994). A subsequent study on HVS-I data from native Europeans and Middle Easterners resulted in five groups which largely matched those established by Torroni *et al.*, with the addition of U4/U5 (Richards et al. 1996). The resolution of T, V, W and X completed the capture of the most common European mitochondrial haplogroups (Torroni et al. 1996).

Unlike autosomal and classical markers, the first mtDNA studies performed on European populations showed no clear clinal pattern in haplogroup distribution (A. Torroni et al. 1994; Torroni et al. 1996; Richards et al. 1996). With finer haplogroup resolution and increased sample sizes, later studies finally detected some geographic structuring, but it was weaker than the autosomal marker pattern and mostly limited to the Mediterranean (Cavalli-Sforza & Minch 1997; Simoni et al. 2000). The weak correlation between geography and mtDNA variability was explained variously as a remainder of a uniform Palaeolithic population, a result of increased female mobility due to partrilocal marriage patterns or simply as the result of the high mutation rate in the HVS/D-Loop region (Richards et al. 1996; Cavalli-Sforza & Minch 1997).

Richards *et al.* used the estimated divergence times for five major European haplogroups (H, I, J, K, U4/U5) groups as a proxy for their time of entry into Europe. The geographic origins of all five haplogroups were traced to the Near East and their arrival in Europe was dated to the Palaeolithic (Richards et al. 1996). With an expanded Near Eastern database and the inclusion of more haplogroups, there were attemps to identify “founder lineages” in the European gene pool (Richards et al. 2000). According to these analyses, U5 was already present in Europe during the Early Upper Paleolithic. HV, I and U4 developed during the Middle Upper Paleolithic, while the current distributions

of H, K, T, W and X were regarded as the result of post-LGM reexpansion during the Late Upper Paleolithic. The Neolithic mitochondrial input was limited to T1, J and U3, putting the overall proportion of Neolithic lineages in the European gene pool at about 15% (Richards et al. 2000; Richards et al. 1996). However, from the start there was considerable debate as to whether the age of any given haplogroup and its entry into Europe where actually so closely linked. (Richards et al. 1996; Cavalli-Sforza & Minch 1997).

Nowadays, U4 and U5 are accepted as remainders of the preneolithic European population, with U4 and possibly some clusters of U5a originating in Eastern Europe and U5b having a (south)western source region (Richards et al. 2000; Soares et al. 2009; Malyarchuk et al. 2008; Soares et al. 2010). Another member of the U clade, U8a, is probably also a remnant of a preneolithic substrate (Soares et al. 2010). While it is also present in the Near East, its deep phylogeny in southwestern European populations (Basques) and the recent discovery of U8 in paleolithic human remains from Central Europe (see aDNA section for details) suggest an early arrival in Europe (González et al. 2006; Fu et al. 2013) U5b3 has been identified as a subclade that arose in a glacial refugium on the Italian peninsula (Pala et al. 2009) U4 and some U5a clades (as well as some subclades of HV) have also been dated back to preneolithic times and could have (re)dispersed from Eastern European refugia (Malyarchuk et al. 2010; Malyarchuk et al. 2008).

About 40% of modern Europeans belong to Haplogroup H. Frequencies decline towards the East, but remain readily detectable as far as Central Asia (Loogväli et al. 2004; Roostalu et al. 2007; Richards et al. 1996). Hg H can be resolved into numerous subclades (currently about 90) (Roostalu et al. 2007; Van Oven & Kayser 2009). Some subclades show distinct geographic distribution patterns: H1 is the most common subhaplogroup in Europe and the Caucasus. It has a frequency peak of about 46% (among Hg H) on the Iberian peninsula, with gradually declining frequencies towards the northeast and south (Pereira et al. 2004). H3 shows a similar pattern (with a frequency peak of 17%) and is exclusively European (Pereira et al. 2004; Quintáns et al. 2004; Pereira et al. 2005). H1b and H7 are more common in Eastern Europe and the Caucasus, H2a and H4 even extend into the Arabian Peninsula and Central Asia. H6 is most frequent in Central Asia, and its coalescence time in this region dates to 40kya (Loogväli et al. 2004). One of the very few H-subhaplogroups that can be identified by its HVSI sequence alone is H5, which reaches a frequency peak at 20% in the Caucasus (Roostalu et al. 2007), while its subhaplogroup H5a is common in the Balkans.

The frequency distributions of haplogroup V and the subclades of H raised the question of a population event that occurred *between* the initial settling of Europe and the arrival of farming. The estimated age of H in Europe is 20-25 kya, (Pereira et al. 2005; Richards et al. 2000). The total age of 30kya and the extant variability in the Near East suggest an arrival in Europe from the Near East before the LGM (Pereira et al. 2005). Its spread has been associated with the paleolithic Gravettian tradition (Achilli et

al. 2004; Torroni et al. 1998). Among the subclades of the dominant European haplogroup H, the ages and distribution of the common subhaplogroups H1 and H3 show a pronounced gradient from Southwest to Northeast, which do not correspond with a presumed expansion from the Near East. However, this pattern would be in concordance with a postglacial expansion from the Iberian Peninsula, although it has not been established yet whether this expansion occurred directly after the LGM or later at the beginning of the Holocene (Torroni et al. 1998; Achilli et al. 2004; Pereira et al. 2005; Soares et al. 2010). There may also have been a southward expansion into North Africa, as indicated by H1, H3 and a rare subclade of U5 in North African populations (Achilli et al. 2005; Achilli et al. 2004; Cherni et al. 2009). More recently, subclade H5 has also been linked to postglacial reexpansion from Iberia (Soares et al. 2010).

In one study, haplogroup V was found to be most frequent in northern Spain (particularly among Basques) and among the Saami of northern Scandinavia, with decreasing frequencies to the North and Near East (Torroni et al. 1998). A more comprehensive study revealed that V was older (16kya, albeit with considerable uncertainty) and more diverse in Western Europe than in the East (8.5kya)(Torroni et al. 2001). This fit well with a putative population expansion from the Iberian Peninsula after the end of the LGM. However, haplogroup V could not be detected in prehistoric Basque populations (Izagirre & de la Rúa 1999). Furthermore, it was found to lack a gradual distribution pattern between the two extremes in Iberia and northern Scandinavia (Simoni et al. 2000). It is thus likely that the exceptionally high levels of V in Basque and Saami are the result of genetic drift in isolated populations rather than late glacial remnants.

While Richards dated the origin of J and T in Europe to the Neolithic, recent age estimates based on whole mitochondrial genomes suggest that certain subclades of J and T (J2a1, J1b1b and T2b) as well as I, W and N1a1b1 arrived in Europe shortly after the LGM from a Near Eastern refugium, which would set back their presumed entry time into Europe by several thousand years (Pala et al. 2012; Olivieri et al. 2013).

1.4 Ancient DNA

1.4.1 Taphonomy

In a living cell, the DNA is protected from damage by a number of highly complex repair mechanisms, e.g. mismatch repair, base excision repair and nucleotide excision repair (Sancar et al. 2004 and citations therein; Friedberg 2003). These mechanisms ensure that the information carried by the DNA remains uncorrupted.

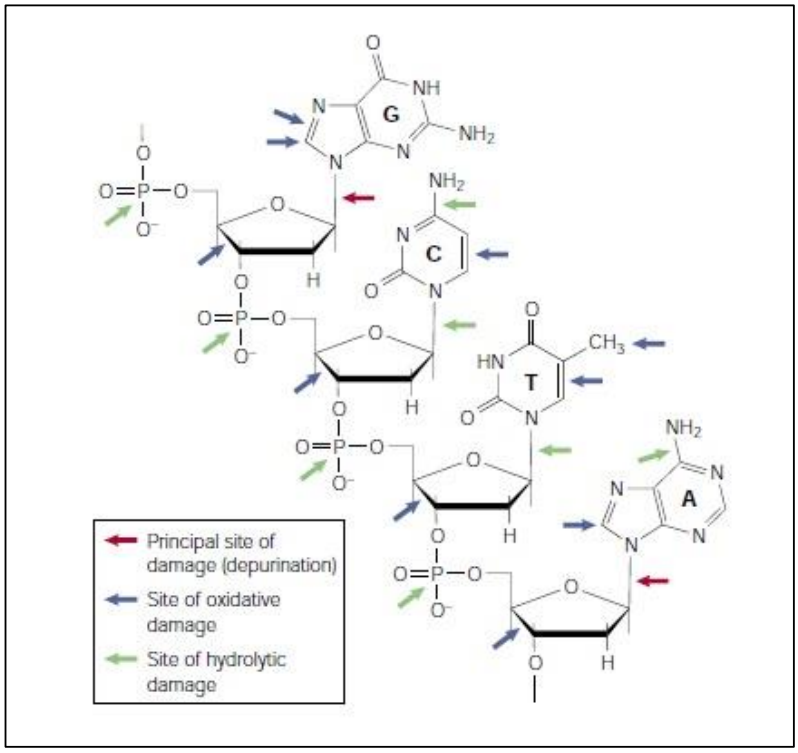

Figure 6: Target sites of DNA damage (from Hofreiter 2001).

After death, the tissues and cellular structures of an organism start to break down. The rate of decay of the organism is determined by environmental factors: Enzymatic and microbial action, ionising/ UV-radiation, humidity, acidity and heat all affect DNA preservation. The mineralised hard tissues of the body (bone and teeth) offer some degree of protection to the cellular remains, but they are not impenetrable. Bone porosity is a major factor in bone diagenesis: High porosity means high water uptake and high accessibility for microorganisms, which facilitates decay and further increases bone porosity (Hedges 2002; Jans et al. 2004; Nielsen-Marsh & Hedges 2000). Acidic and wet environments leech mineral compounds out of the bones/teeth, exposing the DNA within to harmful influences (Bollongino, Tresset, et al. 2008). The collagen of the bone matrix is lost mainly due to microbial attack (Balzer et al. 1997).

Important types of DNA damage are strand breakage, cross-links and base modifications.

Strand breaks are caused by hydrolysis, free radicals (e.g. reactive oxygen species (ROS)), which are formed during redox-reactions, or by ionising radiation. Specialized enzymes (nucleases) can also induce strand breaks, for instance during excision repair, autolysis or microbial digestion (Kohn 1983). DNA fragmentation sets in immediately *post mortem*, first in the DNA regions not protected by nucleosomes, then across the entire molecule (Dong et al. 1997; Johnson & Ferris 2002). It has been shown that the remaining DNA in ancient samples is highly fragmented (Pääbo 1989).

Cross-links can either form between strands of DNA or between DNA and proteins. Their formation is usually mediated by chemical compounds that interlink strands, e.g. cis-platinum (II) complexes. They interfere with DNA replication and transcription. *In vitro,* they inhibit the Polymerase Chain Reaction (PCR). Protein-DNA cross-links can be facilitated by the same compounds that also cause DNA-cross-links, but also by ionising and ultraviolet radiation (Kohn 1983). Aside from affecting DNA replication,

DNA-protein crosslinks may also interfere with DNA extraction methods that rely on the separation of proteins from nucleic acids based on differing solubility in organic solvents.

The structure of bases may be altered by multiple causes, for instance ionising radiation, UV radiation, hydrolysis, ROS and compounds that also cause cross-links (Sancar et al. 2004; Lindahl 1993 and citations therein). Base modifications can inhibit DNA replication, corrupt coding information and distort the shape of the double helix.

In ancient DNA, the oxidative modification of the pyrimidine bases (C and T) to hydantoins can completely inhibit PCR (Höss et al. 1996). A major contributing factor to post-mortem DNA decay is the hydrolytic cleavage of the β-N glycosicic bond between ribose and bases. Purine bases are affected at about a 20-fold higher rate than pyrimidine bases (Lindahl 1993; Cooper et al. 1992). Also relevant to aDNA research are "miscoding lesions", which do not halt DNA replication, but lead to the incorporation of "false" bases. Because of the low number of target molecules in ancient samples, strands carrying miscoding lesions can be amplified to such a high degree that the "original" sequence may not be recognisable anymore. A prominent example of miscoding lesions is the hydrolytic deamination of cytosine to uracil (Lindahl 1993). Uracil serves as a substitute for thymine in RNA and pairs with adenine. When cytosine is deaminated to uracil on one DNA strand, subsequent DNA replication will lead to the erroneous incorporation of adenine on the complementary strand. During the next replication, this strand will in turn pair with a thymine- it appears as if the cytosine was replaced by a thymine (C-T transition). The complementary strand will accordingly show a G-A transition. Gilbert *et al.* also tentatively identified a transition that starts with modification of guanine and its subsequent transition to adenine, but did not identify the responsible mechanisms (Gilbert et al. 2003; Gilbert et al. 2007). C-T transitions (and the corresponding G-A change) are referred to as type 2 transitions, and they have been identified as the leading cause of miscoding in ancient DNA, accounting for 50%- 88% of all miscoding lesions (Pääbo 1989; Gilbert et al. 2007; Lamers et al. 2009; Gilbert et al. 2003).

The less frequent type 1 transitions occur at only 2-3% of the rate of type 2 transitions. The most common target for type 1 transition is adenine, which deaminates to hypoxanthine, an anaologue of guanine (Lindahl 1993 and citations therein). This results in a transition from A to G, and a corresponding T to C transition on the complementary strand. The rarity of type 1 transitions in ancient DNA data has led some researchers to believe that they do not represent "authentic" damage, but rather misincorporations during PCR (Gilbert et al. 2007).

Transversions occur due to oxidative damage. The most common transversion is the hydroxylation of guanine to 8-hydroxyguanine. This preferentially pairs with adenine instead of cytosine, resulting in a G-T transversion (and C-A on the complementary strand) (Lindahl 1993; Lamers et al. 2009). Like

transitions, transversions can be divided into two types. The G-T transversion belongs to type 2, which is the dominant cause of transversions.

1.4.2 The history of aDNA research and its current state

Prior to the development of the PCR, low DNA amounts in a sample severely restricted the possibilities for experiments and analysis.

The earliest aDNA studies, performed in the eighties, worked around this by cloning ancient DNA in order to amplify it. Since molecular cloning is untargeted, the desired DNA squences had to be detected by hybridization to target-specific probes. Using this method, first aDNA results were generated from Egyptian mummies and a museum specimen of the quagga (*Equus quagga*), an extinct African equid (Pääbo 1985; Higuchi et al. 1984). An analysis of 8000 year old human remains from a North American peat bog showed the presence of human mtDNA, but a high contamination rate from the surroundings and extensive postmortem degradation were noted (Doran et al. 1986). With the development of the PCR in the mid-eighties, it finally became possible to amplify minute amounts of DNA and target specific sequences (Mullis & Faloona 1987; Saiki et al. 1985). The uses of this technique for aDNA research were soon recognized (Pääbo 1989; Pääbo et al. 1989). After the first aDNA studies had relied on preserved soft tissues, the development of an extraction method for bones and teeth (Hagelberg et al. 1989) finally made aDNA analysis widely applicable to archaeological remains. The field expanded notably in the following years. The variety of materials tested and the age of the samples were ever-increasing, culminating in several studies claiming the successful extraction of DNA from samples several million years old, such as fossilized dinosaurs and plants (DeSalle et al. 1992; DeSalle et al. 1993; Woodward et al. 1994; Golenberg et al. 1990).

It soon became apparent that the more spectacular results- and Svante Pääbo's initial mummy- could not be replicated and were in fact most likely contaminations (Zischler et al. 1995; Pääbo & Wilson 1991; Austin et al. 1997; Handt et al. 1994). While safeguard measures for ensuring authentic results had been proposed early on, few labs were adhering to these suggestions. At the turn of the millennium, two papers outlining new guidelines for aDNA work were published (Cooper & Poinar 2000; Hofreiter et al. 2001). They expanded on several criteria for reproducible aDNA work that had already been outlined in earlier studies:

a) Phylogenetic sense: the results should correspond with the position of the individual/species in the established phylogeny

b) Non-template controls included in each extraction, PCR and cloning to test for and assess the"background levels" of contamination in the laboratory.

c) At least two independent extractions per individual to mitigate the effects of contamination in the individual

d) Amplification efficiency should be antiproportional to PCR product size: In ancient samples, most of the surviving DNA is highly fragmented, with longer fragments being the exception. Therefore, amplifications of small fragments are expected to yield better results than those of larger fragments.

and introduced several additions:

e) The use of dedicated ancient-DNA facilities to prevent contamination introduced by recent DNA

f) Cloning of PCR products to assess the frequency and type of contaminations present within the PCR product

g) Independent replication of results at another institution

h) DNA quantification: prior to performing a PCR, the amount of DNA present in the sample should be quantified. When the initial testing shows extremely low levels of DNA in the extract, subsequent results may be due to contamination.

i) Testing for preservation status of other biomolecules, such as collagen, as well as aDNA preservation in associated (faunal) remains: when the general preservation of a sample is bad, aDNA results should be treated with caution.

1.4.3 Applications of aDNA

Ancient DNA can be used to determine the phylogenetic relationships of extinct species. The fauna of the last ice age has been of particular interest to researchers, such as the European cave bear, the cave lion and the woolly mammoth (Dabney et al. 2013; Hofreiter et al. 2004; Knapp et al. 2009; Loreille et al. 2001; Noonan et al. 2005; Burger et al. 2004; Barnett et al. 2009; Hagelberg et al. 1994; Miller et al. 2008).

Museum specimens are often available from those species that have gone extinct in more recent times, for instance the Moa, passenger pigeon, the Falkland Islands wolf and the thylacine (Huynen et al. 2003; Cooper et al. 1992; Baker et al. 2005; Hung et al. 2013; Austin et al. 2013; Krajewski et al. 1992; Miller et al. 2009).

In Palaeoanthropology, the relationship of modern humans with other hominins has drawn a lot of attention. Especially the genetics of our close relative, the Neandertal, have been studied in depth. Starting with mitochondrial sequences and pieces of genomic sequences (Noonan et al. 2006; Krings et al. 1997; Green et al. 2006; Krings et al. 2000; Ovchinnikov et al. 2000), research progressed to complete mitochondrial genomes and finally a complete (draft) Neandertal genome in 2010 (Green et al. 2008; Green et al. 2010). The aDNA analysis of a fossil found in a Siberian case resulted in the identification of a new hominin species, dubbed “Denisovan” after the site where it was found (Krause, Fu, et al. 2010; Reich et al. 2010; Meyer et al. 2012). Comparisons to extant human genetic data showed that- like Neandertals- the Denisovans had also contributed to the modern gene pool of

Eurasians. A 300ky old hominin fossil from Spain has proven to be closely related, but not identical to, Denisovans, while sharing many morphological features with Neandertals (Meyer et al. 2013).

In a more methodological approach, human aDNA data has also been used to calibrate the molecular clock for the human mitochondrial genome (Fu et al. 2013).

Historical figures and the identification of their remains are a popular application for aDNA, especially if circumstantial evidence is inconclusive. Members of (pre)historic royalty with known genealogies are a popular study subject: aDNA analysis has been undertaken to identify the Romanovs- the family of exectuted Russian Czar Nikolaus II- as well as the Egyptian pharaoh Tutankhamun and several putative relatives (Gill et al. 1994; Ivanov et al. 1996; Rogaev et al. 2009; Hawass et al. 2010). However, the results have been called into question as being conspicuously good for a skeleton from a hot climate (Lorenzen & Willerslev 2010). aDNA analysis was also employed in the case of Kaspar Hauser, an orphan of unknown origin who was found in Nuremberg in 1828. He was hypothesized to the be a direct descendant of the Baden dynasty, but a comparison of his DNA with living members of the Baden family did not bear this out (Weichhold et al. 1998).

Another high-profile case was the identification of the body of Josef Mengele, former doctor at the Auschwitz concentration camp (Jeffreys et al. 1992). The oldest "identity case" to date is the burial from Chaolcilithic Germany: at the Corded-Ware site of Eulau, two adults and two children could be identified as a family by mitochondrial, Y-chromosomal SNPS and autosomal STR (Haak et al. 2008).

Ancient DNA studies have also become a useful tool to analyse the origin, spread and nature of past epidemics and pandemics (Anastasiou & Mitchell 2013; Zink et al. 2002). Pathogens that have been detected in ancient remains include tuberculosis (*Mycobacterium tuberculosis*) (Spigelman & Lemma 1993; Zink et al. 2002; Donoghue et al. 2004; Baron et al. 1996; Zink et al. 2001; Donoghue et al. 2011), bubonic plague (*Yersinia pestis*) ((Drancourt et al. 2004; Drancourt et al. 1998; Schuenemann et al. 2011; Bos et al. 2011; Harbeck et al. 2013), and Leprosy (*Mycobacterium leprae*) (Rafi et al. 1994; Haas et al. 2000; Montiel et al. 2003; Taylor et al. 2000; Economou et al. 2012).

As for congenital conditions, studies have been undertaken on HLA-27B, a marker that is associated with the degenerative joint disease ankylosing spondylitis (Haak, Gruber, et al. 2005; Leden et al. 2009), HLA-DQ2.5, a marker for risk of celiac disease (Gasbarrini et al. 2012) and ΔF508, the most common mutation responsible for cystic fibrosis, a disease that disproportionately affects people of European descent (Bramanti et al. 2003).

An inherited variant that is not only non-pathogenic, but confers an evolutionary advantage, is lactase persistence. Carriers produce the enzyme lactase throughout adulthood, enabling them to digest unfermented dairy products containing lactose. The majority of Europeans is lactase persistent, and within Europe this trait is associated with a single mutation (-13910*T), indicating a single origin of the trait. The appearance of lactase persistence in Europe has been linked to the Neolithisation and the

concomitant introduction of livestock and dairy production (Burger et al. 2007; Itan et al. 2009; Gerbault et al. 2011)

Ancient DNA can also elucidate the domestication of animals. For instance, the European Aurochs and its phylogenetic relationship with European domestic cattle has been explored in a series of publications (Edwards et al. 2007; Bollongino, Elsner, et al. 2008; Bollongino, Ruth; Edwards, CJ; Burger, J; Alt, KW; Bradley et al. 2006; Edwards et al. 2010). Similar research has been undertaken for pigs (Larson et al. 2005; Larson et al. 2007; Ottoni et al. 2012) and goats (Fernández et al. 2006; Kahila Bar-Gal et al. 2002; Naderi et al. 2008).

1.5 The population history of Europe as told by ancient DNA

Apart from the applications outlined in section 1.4.3, aDNA can make extremely valuable contributions to research on the history of ancient and modern populations.

Ancient DNA allows a direct survey of genetic variation in the past, while conclusions about past events drawn from modern DNA have to relie on assumptions and models that can be a source of error. However, population history based on ancient DNA data also poses unique challenges that differ from modern DNA work: For one thing, ancient DNA research frequently has to contend with very small datasets due to the limited number of (pre)historic remains and the often extensive degradation of the sample material. Furthermore, the correct interpretation of the results is always tied to the ability to correctly date the finds and/or assign them to the right cultural context.

The population history of Europe in particular has been the subject of much attention and debate (see section 1.3.4). Over the last two decades, the field of aDNA research has steadily expanded its body of data and is now in a position to provide a perspective independent of modern population studies.

Currently, the story of the peopling of Europe is told mostly from the mtDNA-perspective, as this high-copy number molecule is the most likely to survive in tissues over extended periods of time. With the advent of new, highly effective sequencing methods the amount of available genetic information is expected to increase: Already, successful attempts at the detection of nuclear markers have been made (Olalde et al. 2014; Wilde et al. 2014). The same goes for Y-chromosomal data, which elucidate the paternal population history (Raghavan et al. 2014; Lacan, Keyser, Ricaut, Brucato, Duranthon, et al. 2011).

1.5.1 The Preneolithic period

Central and Eastern Europe

There are several Palaeolithic individuals from Eastern and Central Europe for which aDNA data is available. The sequencing of the mitochondrial genome from a 33 000- 30 000 year old skeleton found in *Kostenki*, Russia, showed that it belonged to haplogroup U2 (Krause, Briggs, et al. 2010). The exploration of the Palaeolithic site of Dolni-Vestoniče (Czech Republic) yielded remains of three

humans of ca 31 000 cal BP that belonged to basal clades of U and U8 (Fu et al. 2013). A particularly interesting case is the genome of a 24 000 year old male skeleton from the Upper Paleolithic of *Mal'ta*, Lake Baikal. While this site lies well beyond the geographic boundaries of Europe, the genomic data from the Mal'ta individual - including mitochondrial and Y-chromosomal markers- shows affinities to modern western Eurasian populations and Native Americans, but not to modern East Asians (Raghavan et al. 2014). Three individuals from the Late Upper Paleolithic in Germany (*Hohler Fels, Oberkassel*) from 12 500- 11 000 years BC showed U5b and U, respectively (Bramanti et al. 2009; Fu et al. 2013).

One of the first studies on the genetics of Mesolithic hunter-gatherer populations in prehistoric Europe appeared in 2009 and contained mtDNA data on 21 mesolithic (and one Palaeolithic) hunter-gatherers from Germany, Poland Lithuania and Russia (Bramanti et al. 2009). The age of the Mesolithic individuals ranged from 6850-2250 cal BC, and all of the individuals where a HVS-I sequence could be obtained belonged to U4, U5a and U5b. Mesolithic individuals from *Loschbour* (Luxemburg), the *Blätterhöhle* cave site in Western Germany and from southern Sweden were found to belong to U5a, U5b and U2e (Bollongino et al. 2013; Lazaridis et al. 2013; Fu et al. 2013; Delsate et al. 2009).

Mitochondrial haplogroups H, U4 and U5a (but not U5b) have also been found in in Mesolithic northeastern Europe (Der Sarkissian et al. 2013). The researchers also detected C1, an eastern Eurasian haplogroup that may represent introgression from Asia (Der Sarkissian et al. 2013).

More recently, entire genomes could be obtained from multiple individuals, including a) two mesolithic skeletons from *Loschbour* (Lazaridis et al. 2013) b) one 8000 year old hunter-gatherer from *Motala*, Sweden and c) three Scandinavian late Mesolithic hunter-gatherers of the PWC (Skoglund et al. 2012). The Loschbour individuals appear to have had dark skin and blue eyes, a combination of phenotypic traits that is rare in modern European populations (Lazaridis et al. 2013; Olalde et al. 2014). All preneolithic individuals fall outside extant European genetic variation, with some proximity to Europeans/Finnish populations as opposed Southern Europe and the Near East (Olalde et al. 2014; Lazaridis et al. 2013). The Loschbour individual clusters together with a Spanish Mesolithic individual, while the the PWC and Motala individuals form a distinct group, suggesting some population substructuring in preneolithic hunter-gatherers (Lazaridis et al. 2013). However, it has to be kept in mind that the PWC likely does not represent a purely preneolithic hunter-gatherer- population (Malmström et al. 2009; Skoglund et al. 2012).

In general, the Central and Eastern European preneolithic aDNA data support the deep roots of haplogroup U in Europe that were presumed based on modern DNA data. Haplogroup apparently H was also present in Europe before the Neolithic expansion, but with currently only one preneolithic instance of this haplogroup- found in northeastern Europe- it is not possible to determine which subclades are included in this.

Southwestern Europe

Nearly all of the existing aDNA data on the preneolithic population of southern Europe was obtained from sites on the Iberian Peninsula. Three Palaeolithic (Magdalenian, ca. 10 000 years BC) and one Mesolithic individual from Cantabria exhibited U5, H, H6 and U5b1, respectively (Hervella et al. 2012). Unfortunately, the phylogeny of two individuals carrying H could not be resolved further, because the study contained HVSI and HVSII sequence data only. An aDNA study on mesolithic hunter-gatherers from coastal and estuarine sites in Portugal revealed that the individuals belonged to haplogroups U4, U5, N* and H (Chandler et al. 2005). Haplogroup N* is an interesting case: In studies based on modern DNA, this haplogroup has been overlooked, probably due to its low frequencies in extant populations. The mitochondrial genomes obtained from two 7000-year old skeletons from *La Braña* (Northwestern Spain) belonged to U5b2c1. Additionally, whole genome shotgun-sequencing was performed on both individuals. The results showed that the two individuals fall close to, but not within the extant genetic variation of Europe. Genetic continuity with Basque populations was not evident, although the results need to be interpreted with caution due to the incomplete genome coverage (Sánchez-Quinto et al. 2012).

A whole-genome-study was undertaken for one of the 7000 year old *La Braña* individuals (Olalde et al. 2014). Like the Loschbour individuals, the individual from *La Braña* was shown to have dark skin and blue eyes, and the two individuals appeared to be genetically similar.

Currently there are three studies containing preneolithic aDNA-data from the Italian peninsula (Mannino et al. 2012; Caramelli et al. 2003; De Benedetto et al. 2000). Two Palaeolithic (ca 24kya) individuals from the *Paglicci cave* in Apulia were assigned to haplogroups HV/pre-HV and N* based on HVS-I data, coding region SNPs and RFLP (Caramelli et al. 2003). A third Palaeolithic individual from the cave exhibited the CRS sequence in its HVS-I. Unfortunately, it could not be unambiguously assigned to a haplogroup due to a lack of SNP and RFLP- data (Caramelli et al. 2008). A late Palaeolithic[3] individual from *Villabruna* (Veneto, Eastern Italien Alps) examined by De Benedetto *et al.* was identified as belonging to haplogroup H in the original study, but the haplotype was poorly reproduced and further confirmation, for instance by coding region SNPs, was lacking.

One Mesolithic hunter-gatherer from *Egadi Island*, Sicily was shown to belong to haplogroup HV1, based on HVS-I data only (Mannino et al. 2012).

In contrast to Central and Eastern Europe, preneolithic populations in Southwestern Europe apparently do not exhibit U2 and U8- although the limited size of the dataset needs to be kept in mind. They do however contain various subclades haplogroup H, which is dominant in extant European populations, as well as closely related haplogroups such as HV. The presumed paleolithic origin and postglacial

[3] Referred to as "Mesolithic" in the De Benedetto *et al.*, but the associated C-14 date of 13831–14267 cal BP puts it into the late Palaeolithic.

expansion of V and HV from the Franco-Cantabrian Glacial refugium is not directly supported by ancient DNA, since these haplogroups have so far not been detected in preneolithic populations on the Iberian peninsula. The picture is inconclusive on H1 and H3, which are also candidates for postglacial expansion from the Iberian refuge: H has been detected, but its resolution in the aDNA studies is often insufficient (see Caramelli *et al.* 2008).

Table 1: Mitochondrial haplogroups observed in preneolithic Europeans.

	South/West Europe	Central Europe	Eastern Europe
Palaeolithic	(pre)HV, N*, U5, H, H6	U, U5b, U8	U, U2
Mesolithic	U5b, H, H1, U4, N*, HV1	U4, U5a, U5b, U2e	U4, U5a, U2e, C1, H

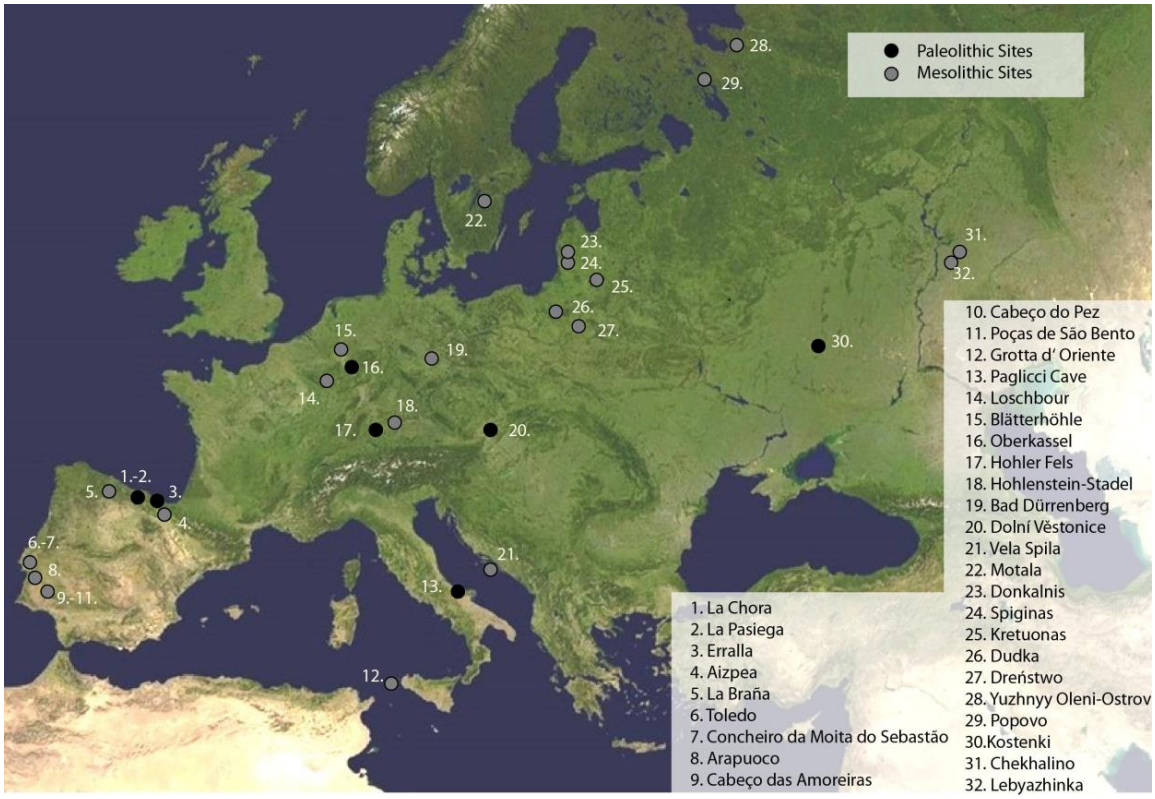

Figure 7: Preneolithic sites in Europe for which aDNA data is available.
Data from these sites was used for the population genetic analyses (section 2.9.2). The geographic subdivisions are: southwestern Europe (HGS), sites 1-13; Central Europe (HGC): sites 14-27, Eastern Europe (HGE): 28-32. Not depicted: Mal'ta, which was included in the HGE set (map: NASA satellite image, public domain, retrieved from http://no.wikipedia.org/wiki/Fil:Europe_satellite_orthographic.jpg)

1.5.2 The Neolithic

Central and Eastern Europe

There are several reasons for the prominent role of the Linearbandkeramik (LBK) in aDNA studies: is archaeologically well defined; it was the first Neolithic culture in much of Central Europe and it covered a large area of Europe from the Ukraine to modern-day France. Therefore, the area from where

samples can be obtained is quite large (meaning more sample material and better chances of obtaining well-preserved samples). Furthermore, due to the extensive archaeological record of the LBK- including many radiocarbon dates- its spread across Europe could be studied in detail. In their 2005 paper, Haak *et al.* presented mtDNA data on 24 LBK farmers from present-day Hungary, Austria, Central and southwestern Germany (Haak, Forster, et al. 2005). Eighteen of the sampled individuals belonged to H/V, T, K, U3 and J, which are still present in the European gene pool today. Six individuals, however, belonged to haplogroup N1a, which is extremely rare in modern European populations. The authors concluded that the first farmers had left no significant maternal imprint on the European populations. At the time, some of the detected lineages (H/V, T and K) were still considered to date back to the paleolithic in Europe, and comparison data on Central European hunter-gatherers was not yet available. The aDNA analysis of six skeletons from the LBK site of *Vedrovice* (Czech Republic) yielded T2, H5, K, J and H/HV/R (was not further resolved) (Bramanti 2008). N1a was not found. The available dataset expanded when 17 additional individuals from the LBK site of *Derenburg*, which had already featured in the 2005 study by Haak *et al*., were analysed. This time, the HVS-I data was complemented by data on 22 coding region SNPs that define the most common Western Eurasian haplogroups, and a multiplex for Y-chromosomal markers (Haak et al. 2010). Apart from the previously observed haplogroups, the sample contained three individuals of haplogroup W, one with V, and one individual carrying U5a. Analysis of the haplotypes showed a genetic affinity to extant Near Eastern populations, hinting at the possible origin of the first European farners. A large transsectional aDNA study focusing on LBK and subsequent cultures from the Middle Elbe-Saale region in Saxony-Anhalt (Germany) added even more details to the picture (Brandt et al. 2013): The LBK had a lasting impact on its successors in central Europe. However, the extant genetic variability of Europe was also decisively shaped by further prehistoric populations movements, namely a) expansion of the Funnel Beaker Culture from Scandinavia around 3000 cal BC, carrying a substantial percentage of hunter-gatherer-lineages such as U4 and U5 b) the expansion of the Corded Ware Culture from Central/Eastern Europe around 2800 cal BC, “contributing” I and U2 and c) the Bell Beaker Culture from the Iberian Peninsula (2500 cal BC), which contained a high percentage of H (Brandt et al. 2013). When studying 37 mitochondrial genomes from the Middle Elbe-Saale region belonging to haplogroup H, it appeared that H1 and H3 were the dominant subclades represented in the sample. Based on modern population data, these sublcades of H have been hypothesized to have originated on the Iberian Peninsula sometime around the LGM. According to this study, they expanded into Central Europe during the (late) Neolithic, probably associated with the Bell Beaker Culture (Brotherton et al. 2013).

In Central and northern Europe, there are instances of gene flow between farming and hunter-gatherer communities. A classic example for this is the Scandinavian Pitted Ware Culture (PWC). A study of

whole mitochondrial genomes showed that PWC individuals carried high levels of U5a, U4/H1b and U5, hinting at a gene pool that was largely uninfluenced by incoming farming populations (Malmström et al. 2009; Skoglund et al. 2012). In contrast, a late Mesolithic (ca. 3000 cal BC) hunter-gatherer site in Ostorf, northern Germany yielded decidedly "Neolithic" haplogroups: J, K and T2. During this time, the site was surrounded by settlements of the Neolithic Funnelbeaker culture, so the "non-U" haplotypes likely point to genetic introgression from its neighbours (Bramanti et al. 2009). The results by Brandt *et al*. indicate that the Funnel Beaker culture received a substantial amount of Mesolithic maternal genetic input in turn and redistributed these lineages across Europe (Brandt et al. 2013). Another interesting site is the *Blätterhöhle* in Western Germany. This cave site was used as a burial place from 9000 cal BC to 3000 calBC, thereby spanning the Mesolithic, Early and Middle Neolithic in Germany. The Mesolithic individuals, as mentioned above, belonged to the expected U-clades. However, the Neolithic inhabitants could be divided into two distinct groups based on diet (as evidenced by C/N isotope values: the group whose signature matched the standard "neolithic" diet showed typical neolithic-associated haplogroups such as H and J as well as some U5b. The group whose signature indicated a forager lifestyle heavily reliant on freshwater fish showed exclusively subclades of U5 (Bollongino et al. 2013). In the latter case, however, it has to be mentioned that the different phases of occupation followed each other very closely, so that a distinction between groups is somewhat arbitrary.

Southwestern Europe

In the 2005 Chandler study, 23 Neolithic individuals from Portugal were included. The sampled individuals covered the range from early to late Neolithic, including one megalithic site (5500-3000 cal BC). All individuals belonged to H, V, U5a and U5b. The haplogroups that are frequent in Central European Neolithic cultures- J, T2 and N1a- were entirely missing. The results of a study on Cantabria/Basque Neolithic samples performed by Hervella *et al.* matched these findings: High frequencies of H, U, with only minor contributions from J, K, T2, (Hervella et al. 2012).

Samples from the Catalonian Epicardial also show H, U5, K and T2, but neither J nor N1a (Lacan, Keyser, Ricaut, Brucato, Tarrús, et al. 2011). A study combining Cardial and Epicardial sites from Catalonia and Aragon added N* (and X1) to the picture alongside H, K and U5, closely mirroring the Mesolithic and Neolithic results from Portugal (Gamba et al. 2012). Taking the middle Neolithic data from Sampietro *et al.* and modern population data from the Iberian Peninsula and the Near East into account, the authors concluded that their findings showed a Near Eastern influence on their early Neolithic Samples, with subsequent heavy genetic drift explaining the differences between early and middle Neolithic data. Based on these results, they proposed a "pioneer colonization" model of neolithisation, with the genetic signal of the first (and few) farmers soon diluted by the larger proportion of acculturated native hunter-gatherers.

The samples from the middle to late Neolithic of Catalonia (3500-3000 cal BC), showed a different picture: while one third of the samples still belonged to haplogroup H (similar to earlier findings and results from Portuga), the remaining individuals belonged to haplogroups that could also be detected in the Central European Neolithic: J, T2, I and W (Sampietro et al. 2007). These findings suggested a demic diffusion rather than a pure acculturation, and were the first hint that the neolithisation process was not necessarily uniform even between neighbouring regions.

Results on 29 individuals of a late Neolithic (3000 cal BC) necropolis of the Treilles group from southern France yielded H1, H3, HV0, V, K1a, T2b, U, U5, U5b1c, X2, and J1 (Lacan, Keyser, Ricaut, Brucato, Duranthon, et al. 2011). Eighteen of the individuals could also be typed for Y-chromosomal haplogroups. Sixteen males belonged to G2a, a haplogroup that has been associated with the Neolithic expansion, while two males belonged to I2a, which is considered to be a remnant of preneolithic populations, similar to mitochondrial haplogroup U4/U5 (Lacan, Keyser, Ricaut, Brucato, Duranthon, et al. 2011). Here, four of the typed five males belonged to G2a and one to E1b1b1a1b, which is present in modern-day southern Europe, especially close to the Mediterranean (Lacan, Keyser, Ricaut, Brucato, Duranthon, et al. 2011).

The samples from both Lacan studies were so well preserved that they could also be tested for the lactase-persistance-associated allele LP-13910C/T. All of the succesfully typed individuals (33 out of 36) were homozygous wild type for this marker and thus probably lactose intolerant as adults.

To date, there are only three individuals from Neolithic Italy, which have been genetically analysed. The haplogroups from two middle Neolithic individuals from the Alps dating to 6400-5900 cal BP -T2, H- could derive from either the Central European or Mediterranean farmer populations (De Benedetto et al. 2000). A very prominent find from the Alps is the “Tyrolean Iceman”, an adult male whose mummified body was found in 1991 at the Tisenjoch on the Austrian/Italian border. “Ötzi”,as the individual was also nicknamed, has become one of the most extensively studied mummies worldwide. According to radiocarbon dating he died around 3350-3100 cal BC, which puts him at the transition phase between the late Neolithic and early chalcolithic (Kutschera et al. 2000). DNA analysis showed that Ötzi belonged to mitochondrial hg K (K1*) (Ermini et al. 2008; Endicott et al. 2009), which was common in the Central European Neolithic. Whole genome analysis established a link between “Ötzi” and present-day Sardinians (Keller et al. 2012).

Haplogroup N1a, which is prominent in Central European early and middle Neolithic populations, is almost completely absent in southwestern Europe. To date, it has only been found in one skeleton from a French megalithic burial (4500-4000 cal BC) (Deguilloux et al. 2011). Interestingly, the HVS-I sequence matches LBK individuals from Hungary *and* Central Germany, suggesting a Central European maternal ancestry for this individual.

1.6 Thesis purpose

The purpose of this thesis was to investigate the maternal gene pool of the population of the Great Hungarian Plain during the Neolithic, and study how it relates to preneolithic populations, neighbouring contemporary populations in Transdanubia and the rest of Europe

Archaeologists have frequently proposed a strong involvement of local hunter-gatherers in the Carpathian Basin cultures, be it as a presence blocking the spread of the Neolithic, trade partners or people who adapted the imported Neolithic to the local circumstances.

Therefore two questions to be addressed in this thesis are:

a) **Is there genetic continuity between the Neolithic cultures of the Great Hungarian Plain and the Mesolithic population who inhabited the Carpathian Basin/Central Europe?**
b) **Is there genetic continuity from the early to the late Neolithic in the Great Hungarian Plain?**

The high degree of regionalisation in the ALBK, which set in after the earliest phase and flourished during its late phase, sets it apart from its closest "cultural relative", the Transdanubian LBK.

It would have also been interesting to study whether regional differences may date back to the early Neolithic, i.e. the proposed southern and northern branch of Körös expansion on the Alföld. However, the sample set of Körös individuals was too small and lacked sites from the Upper Tisza Valley, a crucial area, so that this question could not be addressed.

Because the groups of the Alföld LBK each have their "core" area (albeit often overlapping with other groups), the investigation of regionality on the Alföld necessarily involves a mixed definition of "region" that takes into account both archaeology and geography. The Tisza culture, on the other hand, is culturally rather uniform across the Great Hungarian Plain. Nevertheless, the Tisza culture covered the entire southern half of the Great Hungarian Plain and reached the Upper Tisza valley during its middle and later phases. Therefore, the question arises whether the long distances could have also led to regional differentiation.

A second set of research questions therefore deals with the finer patterns in the gene pool of the Neolithic population of the Alföld:

c) **Is the regional differentiation of the ALBK that is apparent from cultural traits also reflected in the maternal gene pool?**
d) **Does regionality exist in the late Neolithic Tisza culture?**

Finally, this thesis addresses the question of how the Alföld Cultures genetically relate to neighbouring (and distant) contemporary populations. Archaeologically, the Alföld Neolithic springs from the same source as the Transdanubian Neolithic- it comes from the Balkan tradition of red-painted wares. The Carpathian basin was an important waypoint on the "continental route" of Neolithisation. The stylistic

similarities of the Alföld LBK to the Transdanubian LBK- and, by proxy, the Central European LBK- may be reflected in the maternal gene pool.

e) **How do the Alföld Neolithic Cultures genetically relate to the Transdanubian Neolithic? Can a common origin of Alföld and Transdanubian cultures be proposed?**
f) **How do the Alföld Cultures genetically relate to Central European Neolithic cultures, which are known to have been heavily influenced by the LBK?**
g) **How does the Alföld Neolithic relate genetically to contemporaneous Cultures from Western and Eastern Europe?**

Haplogroup H is the most frequent haplogroup in modern populations and contains a multitude of subclades which are phylogeographically structured. In recent years, the history of H in European populations has increasingly come into focus for researchers. The increasing availability of whole mitochondrial genomes and development of primer systems targeting specific subclades have expanded the prehistoric dataset on the variety of H in acient populations. Since haplogroup H was resolved with a multiplex approach in the samples analysed for this study, it could be compared to other European populations where haplogroup H was resolved. While the data is not sufficient to allow sweeping conclusions, a final research question to address was:

h) **How does the variability of haplogroup H in the Alföld Neolithic fit into the European context? Is a geographical structure observable and how does the observed variability of H in the Alföld fit with the presumed origin/history of certain H-clades, for instance H1?**

2 Materials and Methods

2.1 The samples

A total of 320 individuals from the early, middle and late Neolithic were sampled at several universities, archaeological magazines and local museums. The excavation date of the sites varied between the 1930's and 2010 (see Table 2). The skeletal remains had been stored in paper bags or cardboard boxes at room temperature. Most remains had been washed and anthropologically examined. Some, in particular fragmented skulls, jaw bones and teeth, had been glued back together and/or were coated with protective lacquer.

Sites

Table 2: The Neolithic Alföld sites sampled for aDNA.

Site	Year of Excavation	Chronology	settlement structure	Ref.
Abony, Serkeszék-dűlő 60. lh.	2003-2006	classical ALBK, Szakálhát group, Tiszapolgár culture (Copper Age)	flat settlement with intramural burials and/or burials in adjoining living spaces	(Kovács 2011; Kovács & Rajna 2005)
Adács, Mancsos-rét	2005	Szakálhát group	flat settlement with longhouses and burials in adjoining living spaces	(Domboróczki 2006)
Békés-Povádzug	1953-1958	Tisza culture	tell settlement, burials in adjoining living spaces;	(Trogmayer 1962; Zalai-Gaál 1958; Gulyás & Turcsányi 2009; Turcsányi 2007; Farkas 1975, p.61)
Berettyóújfalu, Nagy-Bócs dűlő	2004	Körös culture, Esztár group, one medieval burial	flat settlement, burials in adjoining living spaces and storage pits	(Dani et al. 2006; Zoffmann 2007, p.46)
Cegléd, Városi-Hodula-dűlő, 4/1 lh.	2003-2004	classical ALBK, Szakálhát group	flat settlement with intramural burials and/or burials in adjoining living spaces	(Kovács 2011)
Cegléd, Ipari-Park	2000	late Szakálhát group	flat settlement with intramural burials and/or burials in adjoining living spaces	(Tari 2001)
Csanytelek-Újhalastó	1979	Szakálhát group	flat settlement with remains of longhouses and intramural burials	(Hegedűs 1985; Zoffmann 2001, p.26)
Debrecen, Tócópart Erdőalja	2008-2009	Esztár group	flat settlement, burials within the settlement	(Hajdú & Nagy Emese 2009; Hajdú & Nagy Emese 2010)
Deszk, -1. olajkút	1966	early Körös culture, Szakálhát group	flat settlement	(Trogmayer 1969; Lipták 1976, p.313 Tab. 2)
Deszk- Ordos	1976	Tisza culture	flat settlement	(Kalicz & Raczky 1987, p.28; Hertelendi & Horváth 1992; Horváth 1977; Farkas & Marcsik 1988)
Ebes, Zsong-völgy út	2003	Ezstár group, Iron Age remains	flat settlement	(Dani 2004)
Ebes, Sajtgyár 19.lh.	n.d.	Ezstár group	flat settlement	Personal communication (J. Dani)

Site	Year of Excavation	Chronology	settlement structure	Ref.
Füzesabony-Gubakút	1995	earliest ALBK/Szatmár group, classical ALBK	flat settlement with several houses, burials within the settlement	(Domboróczki 2009)
Garadna, Elkerülő 2.lh	2003	late Tiszadob , early Bükk groups	flat settlement, burials among the settlement features	(Csengeri 2010a; Csengeri 2010b; Kővári & Szathmáry 2004).
Hajdúnánás, Eszlári út, M3-45	2004-2005	late ALBK (phase III-IV), Tiszadob, Bükk and Esztár elements	flat settlement enclosed by multiple ditches, burials within the settlement	(Raczky & Anders 2012), graves unpublished
Hejőkürt, Lidl logisztikai központ	2005	earliest Tiszadob group, Copper Age	flat settlement, burials within the settlement	(Kővári & Szathmáry 2006)
Hódmezővásárhely-Kökénydomb	1928-1944	Tisza culture	tell settlement, burials in the uninhabited adjoining living spaces	(Hertelendi & Horváth 1992; Horváth 1992; Farkas & Szalai 1992)
Hódmezővásárhely-Kökénydomb, Vörös tanya	1940	Tisza culture	Flat settlement, burials adjacent to refuse pits	(Banner & Foltiny 1945; Farkas 1975, p.68)
Hódmezővásárhely - Gorzsa	1978-1996	Tisza culture	tell settlement, burials in the uninhabited adjoining living spaces	(Horváth 1987; Gulyás et al. 2010; Hertelendi & Horváth 1992; Horváth 1982; Farkas & Marcsik 1988)
Hódmezővásárhely Kotacpart	1932-1933	Körös culture		(Trogmayer 1969; Banner 1935; Farkas 1975)
Kompolt, Kígyósér	1994	classical to late ALBK (some Szakálhát and Bükk type finds), Sarmatian and Avar Periods	flat settlement	(Domboróczki 2003)
Maroslele-Pana	1963	Körös culture		(Trogmayer 1969; Paluch 2011; Farkas 1975, p.59; Trogmayer 1964)
Mezőkeresztes-Cethalom	1994	late classical ALBK, elements of Tiszadob and Szkálhát groups	flat settlement	(Wolf & Simonyi 1995)
Mezőkövesd-Mocsolyás	1994	earliest ALBK/ Szatmár group	flat settlement with longhouses, burials among the settlement features	(Kalicz & Koós 2001; Zoffmann 2014)
Mezőszemere, Kismari-fenék	1995	classical and late ALBK, Bronze Age, Migration period	flat settlement	(Domboróczki 1997; Domboróczki 2003)
Mezőzombor, Községi temető	2000	Tiszadob and Bükk groups, late Neolithic stray finds	flat settlement, burials in adjoining living spaces	(Csengeri 2001; Csengeri 2004)
Polgár, Piócási-dűlő	2006	earliest ALBK/Szatmár group	flat settlement with long houses; burials within the settlement	(Dani & Nagy Emese 2007)
Pusztataskony Ledence, 1.lh.	2010	Szakálhát group, Tisza culture, Tiszapolgár culture (Early Copper Age)	flat settlement, cemetery of the Tiszapolgár culture	(Sebők 2010)

Site	Year of Excavation	Chronology	settlement structure	Ref.
Pusztataskony Ledence 2.lh.	2010	ALBK, Szakálhát group, Tisza culture	flat settlement, cemetery of the Tiszapolgár culture	Unpublished, verbal communication by Zs. Zoffmann, A. Anders
Sajószentpéter, vasúti örház	2008	ALBK, Bükk group	flat settlement	unpublished, P. Csengeri
Szegvár-Tűzköves	1985	Tisza Culture	flat settlement	(Korek 1987)
Tiszabura-Bónishát	2010	late ALBK (phase III-IV), Szakálhát elements	flat settlement	unpublished (A. Anders, Zs.Zoffmann)
Tiszadob-Okenéz	2006-2007	Tiszadob group	flat settlement, burials in adjoining living spaces	(Scholcz 2007)
Tiszaföldvár, Téglagyár	1985	Szakálhát group	flat settlement	(Oravecz 2000; Mende 2000)
Tiszalök-Hajnalos	1985	Tiszadob group	Flat settlement, remains of one house and several pits	(Kurucz 1989)
Tiszaszőlős, Domaháza-puszta, Réti-dűlő	2003	Körös culture, Szakálhát group	flat settlement	(Domboróczki 2010)
Törökszentmiklós-Tiszapüspöki, Karancs háromág, 3. lh.	1999	Körös culture	flat settlement	(Sümegi 2004; Zoffmann 2005)
Vésztő-Mágor	1972-1976	Tisza culture	tell settlement, cemeteryy of the Tiszapolgár culture	(Hegedüs & Makkay 1987)

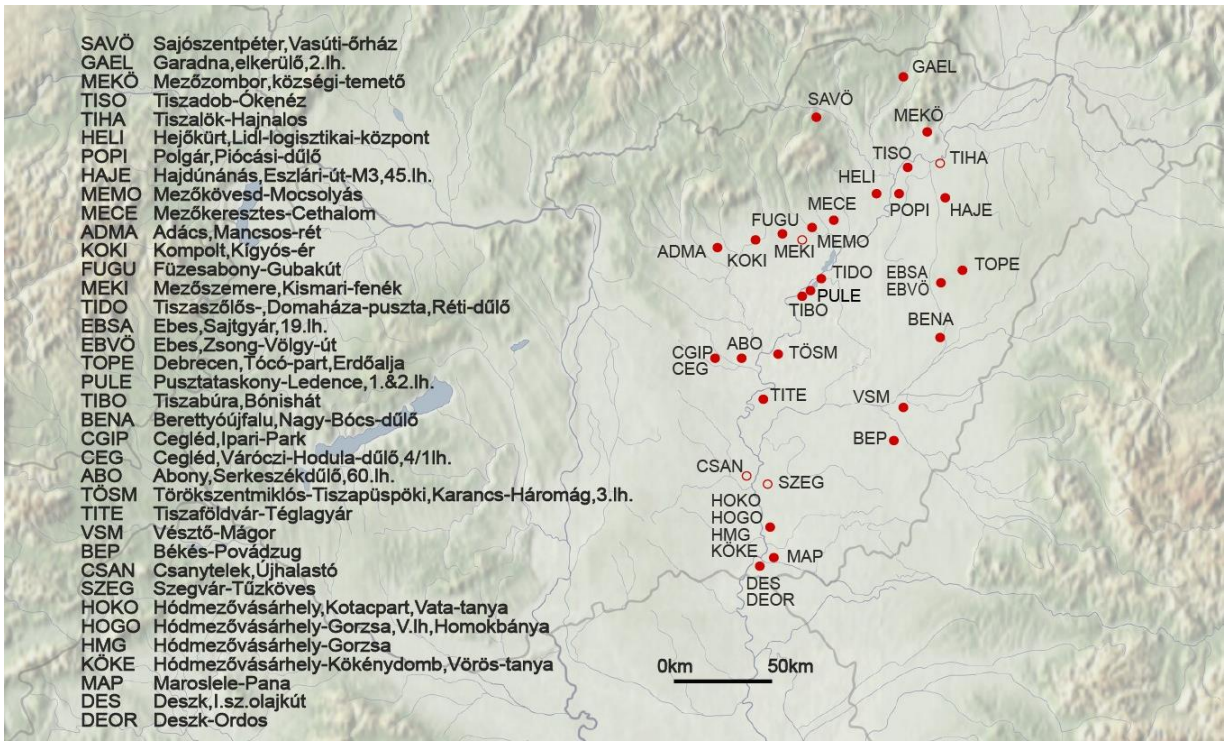

Figure 8: Map of the Neolithic sites on the Alföld that were sampled for this study. Hollow circles indicate sites for which no aDNA data could be obtained.

Sampling strategy

Whenever possible, teeth were preferred over bones for sampling, in particular molars due to their large pulp cavities. Because of a double sampling strategy for aDNA and isotopes, the first and third adult molars were sampled whenever possible. When no intact molars were available, premolars, canines and incisors were taken instead. Fractured teeth, teeth with caries lesions extending into the pulp cavity or those with undeveloped roots were not sampled. When not enough suitable teeth could be collected, pieces of bone were taken from the *compacta* of the major long bones (*Humerus, Femur* or *Tibia*). Rectangular pieces measuring app. 5cm x 3cm were cut from the diaphysis using an electric saw. In cases where only the skull bones were available, the entire *Os temporale* containing the *Pars petrosa* was taken. All surfaces and tools were cleaned with bleach after the sampling of each individual. Disposable gloves, surgical masks and head covers were worn during sampling. The samples were packaged in sealable plastic bags and transported to the aDNA laboratory facilities in Mainz. Since the skeletal remains had been stored at room temperature since their excavation, the samples were not cooled during transport.

2.2 Contamination prevention and authentication of results

The prevention of contamination is the central part of aDNA work, especially when working on ancient human samples. All preparatory and analytical procedures were designed and performed with the objective to minimise all possible types of contamination.

The facilities where the samples were handled prior to PCR were strictly separated from the post-PCR facilities. In Mainz, pre- and post-PCR laboratories are housed in different buildings. The pre-PCR laboratory lies in a building where no other genetic laboratory work is performed. Furthermore, a strict "one-way" system was maintained at all times: samples, chemicals, disposables and workers were only allowed to move from pre- to post-PCR facilities. Researchers and staff entering the pre-PCR laboratory were only allowed to do so wearing freshly laundered clothes. After leaving the pre-PCR laboratory and entering the post-PCR area or the offices, workers had to take a shower and change into clean clothes before reentering the pre-PCR laboratory. This setup minimised the possibility of "carry-over" contamination, where amplified PCR products are reintroduced into the pre-PCR area and contaminate the unprocessed samples.

Further measures were taken to prevent cross-contamination, which can occur when different samples come in contact with each other. This is especially a problem when samples are in powder or liquid form, because of the potential for aerosol or dust dispersal. Cross-contamination was prevented by a) keeping samples separate, working on only one sample at a time and b) avoiding air circulation which could disperse traces of sample material: Powders and liquids were handled in boxes whenever possible, and the time that the samples were exposed to open air was kept at a minimum.

Surface removal, milling, DNA extraction and PCR were each performed in separate rooms (or separate boxes in the case of milling and extraction) in order to minimise the risk of cross contamination (Figure 9).

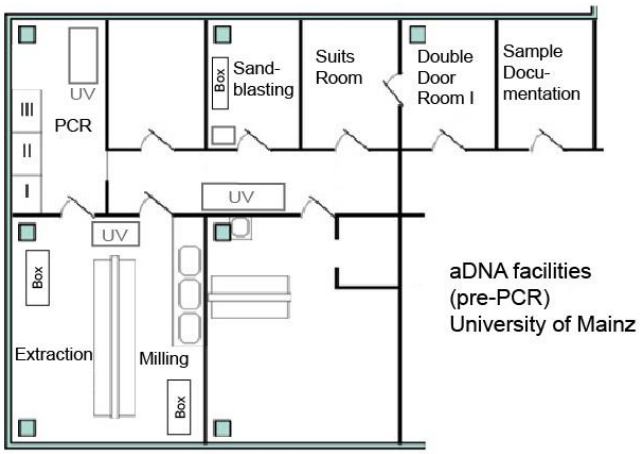

Figure 9: Floor plan of the aDNA laboratoy at the university of Mainz. „UV" denotes UV-cabinets; the PCR-boxes are numbered I-III, refrigerators, freezers and the chemical cabinet are not depicted.

Contamination introduced by chemicals and disposables also posed a risk that had to be mitigated. All items used in the pre-PCR laboratory were cleaned with detergent solution and chlorine bleach (Prince & Andrus 1992) or DNA Exitus upon arrival. Chemicals were then directly transferred into the freezer, refrigerator or the chemical cabinet. All other items were irradiated in UV-cabinets overnight while still in their packaging, before being sorted into cupboards and storage boxes. Tubes and pipette tips,

which came into direct contact with sample material, were taken out of their packaging and irradiated from the inside as well as the outside before use.

Each person working in the laboratory used their own set of labelled aliquots of all chemicals, including water. The lot numbers of the chemicals used were recorded for each extraction and PCR in order to be able to track down contaminated lots.

The water used for the cleaning of intruments and surfaces was drawn from a reverse-osmosis system and UV-irradiated for 24 hours before use. The HPLC- water used for extractions and PCRs was purchased externally. Initially, it was UV-irradiated for 24 hours and then tested for contamination with the medium-length primer system for the HVS-I. After the water consistently proved to be clean, it was eventually aliquoted into irradiated 50ml falcon tubes directly from the bottle, then tested as before. The water was stored at -50°C until further use.

All work surfaces, instruments and boxes were cleaned with detergent and bleach or DNA Exitus after each processing step and at the end of each workday. Additionally, the entire laboratory including floors, walls and the insides of the cabinets was cleaned in three-month intervals. The work benches and the sandblasting machine were irradiated by UV lamps for 7 hours each night. Boxes were UV-irradiated overnight after each use.

Protective clothing was worn at all times. Researchers removed their shoes and overclothes before entering the laboratory and put on clean clothes (usually consisting of a T-Shirt, short pants and a second pair of socks) to go under the coveralls. Long hair was tied back and covered by a bandanna, and a surgical mask and a head cover were put on to further cover the face and hair. The “outer layer” of protective clothing consisted of plastic coveralls, overshoes and three pairs of gloves. Each researcher had their own coverall, and different coveralls were used for each of the different processing steps and stored on different racks, where they were UV-irradiated for 7 hours each night. A plastic face shield was worn at all times to prevent aerosol spray from tears and saliva coming in contact with the samples. The face shields were cleaned and UV-irradiated after each use.

Only one person was working in a room at any given time.

To monitor potential contamination, blanks were included in the milling, DNA extraction and PCR steps. Additionally, the mitochondrial DNA sequence (HVS-I and HVS-II) of each person working in the laboratory facilities was kept in a database in order to be able to identify contaminating lineages. The same was done for archaeologists and archaeological field workers who could have come into contact with the sampled skeletons during the excavation and storage period. It has to be noted, however, that not all persons associated with the skeletal remains could be tracked down to submit a saliva sample.

While contamination prevention was an integral part of the bench work, the sampling and analysis strategy were also designed to ensure the authenticity of results: A and B-samples were processed

independently of each other and then used to establish a consensus profile. In order to be regarded as valid, each nucleotide position needed to be the confirmed in both A and B sample. In the case of HVS-I sequences, a third PCR from either A or B-sample was required for final confirmation. Due to the overlap among the HVS primer pairs, important nucleotide positions were confirmed up to six times. Ambiguous nucleotide positions were examined by cloning the PCR-product in question and assessing the lineages found in the clonal sequences. Because they served a supplementary function to already authenticated HVS-I sequences, HVS-II sequences were only cloned if ambiguous positions were present at phylogenetically relevant positions, and no third PCR was required. For similar reasons, SNP results were checked for consistency in A and B, but did not require further cloning or a third PCR if the results were unambiguous.

In cases where A and B sample showed different profiles, a third sample ("C-sample") was analysed if available. Otherwise, the extraction of either A- or B-sample was repeated.

2.3 General workflow

The samples were documented/photographed upon arrival and given a laboratory number consisting of three to four letters and two digits, e.g. TIDO01. From this point on, they were stored at -20°C. The next step was surface decontamination, where the surface layer of the samples was removed. Afterwards, the decontaminated samples were ground into a powder. DNA was extracted from about 250-300mg of powder, while the remains were stored for future use. A- and B-samples were amplified independently from each other in different PCRs.

The mitochondrial HVS-I sequence was amplified in several overlapping fragments. Additionally, the HVS-II sequence was amplified in some individuals for increased resolution. For further confirmation and increased resolution, additional SNPs situated throughout the entire mt- genome were analysed (see chapter on SNP-multiplexes).

The authentication of HVS-I results was performed by a third PCR of either A or B-sample. PCR amplicons were sequenced using the Sanger-method. Ambiguous nucleotide positions were resolved by cloning of the PCR products.

2.4 Surface removal and milling

The samples were UV-irradiated in a dedicated cabinet for 30 min from each side. Afterwards, the surface-in bone samples the entire porous part- were removed by sandblasting. The samples were then irradiated again for 2x 30 min and stored in the refrigerator until further use. Samples were transferred into fresh sealable plastic bags after each processing step. The sandblasting machine and all work surfaces were cleaned with soap and bleach/ DNA Exitus after each sample.

Prior to milling, the samples were manually broken up into smaller fragments. A piece of enamel was collected from first and third molars for isotope analyses. The fragments were then transferred into

circonium-coated milling cups and milled to a fine powder using a mixer mill. The powder was removed from the cups and weighed inside a dedicated box. Between 250 and 300mg of powder where transferred into a 5ml falcon tube and kept in the refrigerator until the extraction. The remainder was transferred into a second falcon tube and stored at -20°C until further use. After each sample, the inside of the box and all working surfaces were cleaned. The milling cups were cleaned with soap and bleach, then scoured with sterile sea sand before being soaked in bleach for 20min and finally being rinsed with UV-irradiated demineralised water. In each milling session, ca. 250mg of pure synthetic hydroxyapatite- the main component of tooth enamel- were processed to provide a negative control for the milling process.

2.5 DNA extraction

2.5.1 Ancient DNA

Two different extraction methods were used: a) the phenol chloroform method and b) a silica-based method. The initial lysis step was nearly identical for both methods: In order to demineralise the samples and break up remaining cellular structures, the 250-300mg of powdered bone/tooth were incubated overnight on a rotating wheel in a solution containing 0.5M EDTA (pH=8,3) and proteinase K (Table 3). One extraction blank containing only the chemicals of the lysis was included in each extraction.

Table 3: Lysis setup of the two extraction methods.

Reagent	Phenol-Chloroform	Silica-based
Ground sample	230-260mg	250-300mg
EDTA (0.5M)	3ml	3ml
N-Laurylsarkosine (5%)	300µl	-
Proteinase K	30µl	80µl

Phenol-chloroform extraction

In this method, hydrophobic cell debris is trapped in the organic solvent phenol and is subsequently discarded, while the hydrophilic DNA remains in the aqueous phase. For improved lysis, the mix contained 0.5% N-Laurylsarcosine in addition to Proteinase K and EDTA. Overnight incubation was performed at 37°C. The next day, 3ml of phenol/chloroform/isoamylalcohol were added. Both phases were thoroughly mixed, then centrifuged for 10 min at 4000 rpm. The organic phase was then discarded, while the aqueous phase was transferred into a new tube. This was repeated two times, with pure chloroform replacing the phenol/chloroform/isoamylalcohol mixture in the last step. Afterwards, the aquaeous phase of each sample was transferred into Amicon filter tubes and spun down for 7:30 min at 6590 rpm. The filter was washed with 3ml of HPLC- water and centrifuged for 5min at 6590 rpm. If the liquid was clear, 1ml of HPLC- water was added and centrifuged one final time. Then, the clear liquid remaining on the filter – now containing the purified and concentrated

DNA- was transferred into 0.5ml tubes. This extraction method resulted in about 120-200µl of DNA extract, 40µl of which were aliquoted for immediate use. The extracts were stored at -20°C.

Silica-based extraction

This method was adapted from a protocol developed by Brotherton *et al*. (Brotherton et al. 2013). DNA molecules bind to silica particles suspended in an aqueous buffer solution. After purification, the DNA is eluted from the silica by changing the salt concentration. The silica suspension was made by adding 6g of silica to 50ml of HPLC-water. After mixing thoroughly, the suspension was allowed to settle for 1 h, after which the upper 40ml were transferred into a new tube and left at room temperature overnight. The next day, the upper 30ml were discarded, resulting in 10ml of suspension for the subsequent extraction. The silica suspension was used for a maximum of four weeks. The lysis step did not require the addition of N-Laurylsarcosine, but the amount of proteinase K was increased and the incubation temperature was set to 55°C for two hours following the overnight incubation. The tubes were centrifuged for 1 min at 4500 rpm. The supernatant was transferred into tubes containing a binding buffer containing QG buffer, Triton X-100 and Na-Acetate. To this, 125µl of silica suspension were added and the mixture was incubated on a rotating wheel at room temperature for 1 h. Afterwards the tubes were centrifuged for 2 min at 4500 rpm and the supernatant was discarded. The silica pellets at the bottom of the tubes were then dissolved in 900µl of 80% ethanol and transferred into fresh 1.5ml tubes. After centrifuging for 1 min at 13000 rpm, the supernatant was discarded. This washing step was repeated two more times. Afterwards, the tubes were put into a cabinet with the lid left open for 45 min in order for the pellet to dry. The DNA was eluted from the silica by resuspending the pellet in 200µl of Tris-EDTA (TE) buffer that had been heated to 50°C. After incubating for 10 min at room temperature, the mixture was spun down for 1min at 13000 rpm. The pellet was then discarded and the TE-buffer containing the DNA was transferred into fresh 0.5ml tubes.

2.5.2 DNA samples from researchers and other laboratory workers

DNA from laboratory workers, archaeologists and field workers was extracted from buccal cells collected with cheek swabs. The DNA was extracted using a commercial kit according to the manufacturer's instructions. The HVS-I and HVSII were amplified as one fragment each, using the forward primer of the first fragment and the reverse primer of the fourth fragment of the medium-length system. The PCR setup followed the protocol described in section "clone PCR". The sequencing itself followed the protocols used for aDNA samples, outlined in chapter 2.6.

2.6 HVS-I and HVS-II

2.6.1 Polymerase Chain Reaction (PCR)

The PCR is a method to amplify specific segments of DNA and was developed by Karey Mullis *et al.* in 1984 (Saiki et al. 1985). First, the double stranded DNA containing the target region is denatured by heating. Two oligonucleotides (ca. 20-30bp long), the so-called primers, each bind to their respective complementary sequence flanking the target segment. Each primer binds to one strand in such a way that DNA replication occurs across the target region, resulting in its amplification. A heat resistant polymerase- usually a variant of the enzyme first isolated from *Thermus aquaticus*- then elongates the primer sequences and recreates the missing strand. This cycle is repeated several times, with the number of amplified DNA molecules doubling in each cycle.

2.6.2 Primer systems

Table 4: Primer systems used for the amplification of HVS-I and HVS-II.

Primer name	Fragment name	Sequence 5´- 3´	Amplicon length with/ without primers (bp)	Annealing temp. (°C)	Reference
HVS I					
long					
L16045 H16240	1/2	TGTTCTTTCATGGGGAAGCAGATT GGGTGGCTTTGGAGTTGCAGTT	240 / 194	56	(Brandt et al. 2013)
L16212 H16402	2/2	CCCCATGCTTACAAGCAAGTACA GATATTGATTTCACGGAGGATGGT	236 / 189	56	(Adler et al. 2011)
medium					
L15996 H16142	I	CTCCACCATTAGCACCCAAAGC ATGTACTACAGGTGGTCAAG	187 / 145	58	(Endicott et al. 2003; Vigilant et al. 1991) (Stone & Stoneking 1998)
L16117 H16233	II	TACATTACTGCCAGCCACCAT GCTTTGGAGTTGCAGTTGATGTGT	162 / 115	58	(Haak, Forster, et al. 2005)
L16209 H16348	III	CCCCATGCTTACAAGCAAGT ATGGGGACGAGAAGGGATTTG	179 / 138	58	(Handt et al. 1996) (Haak, Forster, et al. 2005)
L16287 H16410	IV	CACTAGGATACCAACAAACC GCGGGATATTGATTTCACGG	162 / 122	58	(Handt et al. 1996) (Haak, Forster, et al. 2005)
H16145	I (alt.)[4]	TTGGGTTTTTATGTACTACAGGTGGTC	150 / 99	56	(Roth 2014 unpublished)
short					
L16018 H16097	1	AGCACCCAAAGCTAAGATTCTAATTTAAACTATT ATATTCATGGTGGCTGGCAGTAATGTA	139 / 78	57	(Knipper et al. 2014)
L16072	2	GGTACCACCCAAGTATTGACTCACC	123 / 74	57	

[4] The -H16145 primer pair was used in conjunction with L16045 as a shorter alternative to fragment I of the medium-length system.

H16144[5]		TGGGTTTTTATGTACTACAGGTGGTCA			
L16122 H16196	3	ATTTCGTACATTACTGCCAGCCACCATGAATA TAGTTGAGGGTTGATTGCTGTACTTGCTTGTAAGC	132 / 76	65	
L16178 H16267	4	AGTACATAAAAACCCAATCCACAT GTAGGTTTGTTGGTATCCTAGTGG	136 / 91	50	(Roth 2014 unpublished)
L16231 H16323	5	GTACAGCAATCAACCCTCAACTAT CTGTAATGTGCTATGTACGGTAAA	139 / 94	50	
L16307 H16402.C	6	GGATACCAACAAACCTACCCACCCTTAACAGTACA TGCGGGATATTGATTTCACGGAGGATGGT	158 / 94 H16402.C	67	
HVS II					
L00034 H00177		TCTATCACCCTATTAACCACTCAC TTAGTAAGTATGTTCGCCTGTAAT	192 / 144	58	
L00144 H00243		CGCAGTATCTGTCTTTGATTCCTG AAAGTGGCTGTGCAGACATTCAAT	148 / 100	58	
L00172 H00327		ATCCTATTATTTATCGCACCTACG TTGGCAGAGATGTGTTTAAGTGCT	204 / 156	58	(Haak et al. 2008)
L00274 H00397		TGTCTGCACAGCCACTTTCCACAC AGTGCATACCGCCAAAAGATAAAA	174 / 124	58	

Because of the fragmented nature of mitochondrial DNA, primer systems for HVS-I and HVS-II were designed to cover the target sequence in several overlapping fragments between 100 and 200 bp in length. For the HVS-I, systems with two, four and six fragments were used (Table 4). The overlapping regions of the HVS-I primers were designed in a way that they contained multiple phylogenetically relevant nucleotide positions. That way, important nucleotide positions were confirmed by more than 3 PCRs.

The HVS-II was amplified with a four-fragment system.

2.6.3 PCR of HVS-I and HVS-II

PCR reactions were carried out in 25µl volumes (Table 5). A mastermix containing all reaction chemicals was prepared and aliquoted into the PCR-tubes. Then, between 2 and 5µl of DNA extract were added to each tube. At least 25% of samples in each PCR reaction were blanks.

To prevent unspecific crosslinks that could inhibit PCR, bovine serum albumin (BSA) was included in the reaction mix.

Because of the low initial number of target molecules, the cycle number in aDNA PCRs is higher than the customary PCR with ca.30 cycles. PCR conditions were as follows:

6min 95°C

15s 95°C

15s 58°C (depending on primer pair, see Table 4) x 45-50

[5] Hwas also used in combination with L15997

20s 72°C

10min 72°C

During the final elongation phase consisting of 10 min at 72°C, the polymerase adenylates the 5' ends of the PCR products, thus creating the "sticky ends" that are necessary for ligating the fragment and the vector during clongin.

Table 5: Standard PCR for HVS-I and HVS-II.

Reagents	Final Concentration	Amount [µl]
10x Buffer	1x	2.5
$MgCl_2$	2.5 mM	2.5
dNTP Mix	0.2 mM	0.5
Primer L (10µM)	0.2 µM	0.5
Primer H (10µM)	0.2 µM	0.5
BSA (40µg/µl)	0.8µg/µl	0.5
Taq (10 U/µl)	2.5 U (0.1U/µl)	0.25
HPLC-H_2O		14.75
Target DNA		3
TOTAL		**25**

The products were screened for successful amplification on a 2% TBE-agarose gel containing ethidiumbromide. A size standard for fragments between 50 and 1000bp long was run on a separate lane. The run time was set to 20min at 130V. After examining the results under an UV lamp, the PCR products were purified on a filter plate and eluted in HPLC- water. The purified PCR products were stored at -20°C until further use.

2.6.4 Sanger sequencing and electrophoresis

The HVS-I and HVS-II were sequenced with the Sanger method, which was developed in the 1970's (Sanger & Nicklen 1977). The sequencing reaction is similar to a PCR, but in addition to the customary deoxynucleotides, the reaction mix also contains labelled dideoxynucleotides (ddNTP). Elongation stops once a ddNTP is incorporated into the growing DNA strand. Fluorescent labelling makes each ddNTP identifiable. Stochastically, after a certain amount of cycles each nucleotide position in a given sequence has been replaced by a ddNTP at least once. The result is a solution containing DNA fragments of varying lengths. These fragments are then separated by length using electrophoresis.
Sequencing primers were the same as the respective PCR primers. Usually, each product was only sequenced in one direction. If that was not sufficient, such as in the case of C-stretch mutations (np16189C), the fragments were sequenced in reverse as well.

Table 6: The setup of the sequencing PCR.

Reagent	Final Concentration	Amount (µl)
5x BigDye Terminator v3.1 Sequencing Buffer	~ 0.7x	1.5
Big Dye Terminator v3.1 Ready Reaction mix		1
Primer (10 µM)	0.9µM	1
HPLC-H20		5.5
Purified PCR-product		2
TOTAL		11

The conditions for the cycle sequencing reaction were as follows:

92°C 30s
58°C 15s x 25 cycles
60°C 2:30min

Leftover chemicals and primer fragments were removed by treatment with Shrimp Alkaline Phosphatase (SAP). 1 µl of a mix of SAP and buffer (ratio 1:3) were added to each tube and incubated at 37°C for 45 min, followed by an inactivation step of 80°C for 15 min. In some instances, a slightly different AP was used, which required reduced incubation and inactivation times of 10 and 5min, respectively. Alkaline phosphatase removes the terminal phosphate groups from RNA and DNA, i.e. sequencing products and leftover oligonucleotides. Afterwards, the sequencing products were purified on a filter plate for 10min to remove dye and other chemical remains before being resuspended in 12µl of formamide.
The electrophoresis was carried out on a capillary sequencer with four capillaries.

2.6.5 Cloning

The double stranded PCR-amplicons were ligated into plasmid vectors and transferred into *E.coli*, where they were multiplied. Since each vector can only incorporate only a single DNA-molecule, the PCR product was „split up" into single lineages and could be subsequently examined for signs of contamination or degradation.

Ligation

The PCR products were cloned into pUC 18 vectors. The vector conveys resistance to the antibiotic ampicillin and contains part of the *lac* operon for the detection of inserts. Successful insertion of a DNA fragment at the Multiple Cloning Site disrupts the reading frame of the lacZ gene, which codes for β-galactosidase. Without this enzyme, the bacteria cannot metabolise the indicator substance X-gal (5-bromo-4-chloro-3-indolyl-beta-D-galactopyranoside), which turns bright blue when cleaved. The ligation setup consisted of 4µl of PCR-product, 4 units of T4 DNA-Ligase, 1x Ligation Buffer, and 50ng/µl linearised pUC18 vector (Table 7). It was incubated at 16°C overnight, followed by vigorous shaking in

a thermal mixer for 1 h at 450 rpm. The ligase was inactivated at 72°C for 15 min. One volume each of chloroform and HPLC-water were added and centrifuged. The DNA was then precipitated from the chloroform by adding 1µl of 3 M sodium acetate (pH 4.6) and 50µl of ethanol (100%). The resulting pellet was dried and re-suspended in 10µl of HPLC water.

Table 7: The setup for ligation.

Reagents	Final Concentration	Amount [µl]
10x Ligase Puffer	1x	1
Linearised pUC18 vector (500ng/µl)	50ng/ µl	1
T4 DNA-Ligase (1U/µl)	0.4U/µl	4
PCR-Product		4
TOTAL		10

Transformation

The 10µl of ligation product were mixed with 50µl of a suspension containing the electrocompetent *E.coli* RRI strain (Haak 2006, p.93). Transformation by electroporation was performed at 2500 V. Afterwards, the bacteria were suspended in 1ml of sterilized LB medium and plated out on LB-agar plates containing ampicillin, the inductor IPTG (isopropyl β-D-1-thiogalactopyranoside) and X-Gal. After growing on the LB-agar overnight at 37°C, the plates were screened for white colonies.

Colony PCR

An average of 8 white colonies were picked and directly subjected to a PCR without prior DNA extraction (Table 8).

Table 8: Setup of the colony PCR. The M13 primers (forward GTAAAACGACGGCCAGT; reverse CAGGAAACAGCTATGAC) targeted the insert.

Reagent	Final Concentration	Volume [µl]
10x PCR Buffer	1x	5
MgCl2	2.5mM	5
dNTP	0.2mM	5
M13 forward primer	0.2µM	1
M13 reverse primer	0.2µM	1
Polymerase (5U/µl)	2.5U	0.2
H20		32.8
TOTAL		50

PCR conditions were as follows:

94°C 15min
94°C 30s
58°C 30s x 30cycles
72°C 30
4°C ∞

The PCR products were then screened for the expected insert length on a 2% agarose gel. The products with the desired length were purified with 2 U Exo I and 0.5 U SAP, added directly to the PCR tube. Incubation conditions were 37°C for 45 min, followed by an inactivation step at 80°C for 15 min. The sequencing of the purified products was performed according to the cycle sequencing protocol described in the PCR-section, with the M13 primers as sequencing primers.

2.7 Multiplexes

2.7.1 PCR primer systems

The multiplex PCR reactions contained multiple primer pairs, each targeting a specific SNP of the mitochondrial genome (Table 9). Three multiplexes were used:

1) GenoCoRe22, a set of 22 markers coding for the most common Eurasian haplogroups (Haak et al. 2010)
2) The HPLEX17, a set of 17 markers resolving the most common subhaplogroups of H in present-day populations (Martínez-Cruz et al. 2012)
3) The U-Plex, which was designed as a supplement to the GenoCoRe22. It resolves haplogroup U as detected by GenoCoRe22 into its most common European subclades: U2, U3, U4, U5, U5a, U5b and U8.

A “diplex” system consisting of two markers distinguishing T1 and T2 was also designed. However, in this study T1 and T2 could be unambiguously resolved by HVS-I in all cases. Therefore, this test was performed on only a selection of samples and with the main purpose of testing the accuracy and specificity of the T1/T2 diplex.

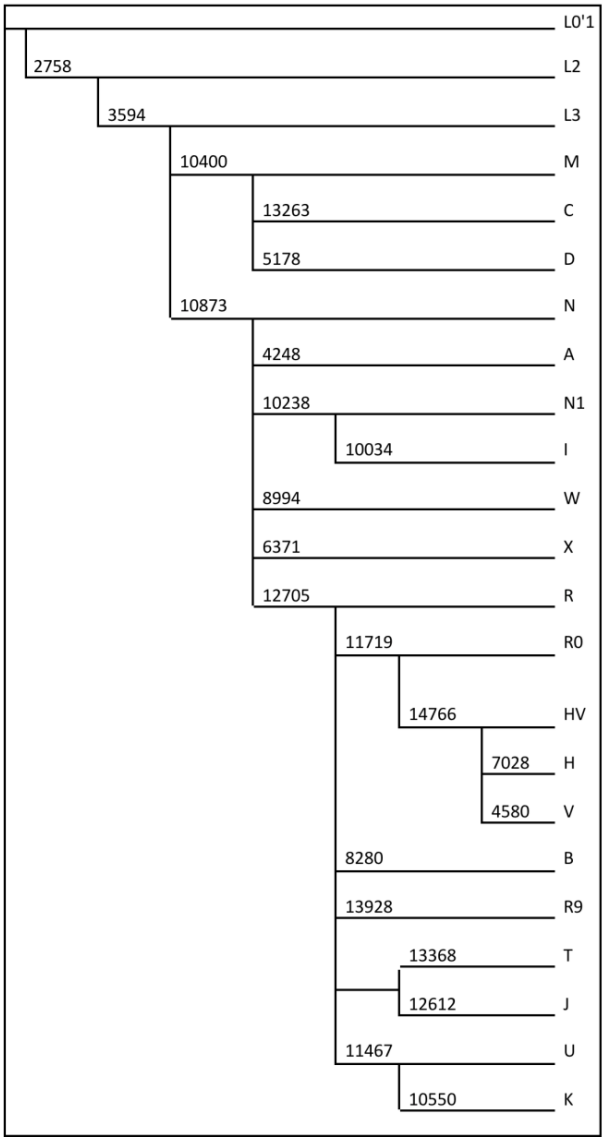

Figure 10: The SNPs of the GenoCoRe22 Multiplex and their phylogenetic structure. The numbers denote the nucleotide positions of the haplogroup-defining SNPs, while the letters denote the haplogroups that can be distinguished with the multiplex.

The GenoCoRe22 is constructed hierarchically, starting with haplogroup L3, separating macrohaplogroups M, N and R (which is nested within N). The remaining markers differentiate the main subclades of macrohaplogroup N, thus targeting the major European haplgroups. Using this system, the haplogroup results given by the "terminal" SNPs can be checked for internal consistency and possible contaminations.

2.7.2 Design of the U-Plex and T-plex, and adaptation of the HPLEX17

The target SNPs for the major European subclades of U (U2, U3, U4, U5, U5a, U5b, U8) and the two clades of T were identified using Phylotree build 15 (Van Oven & Kayser 2009). Wherever possible, SNPs lying outside the HVS-I and II were preferred, to maximise the amount of information gained in cases where the HVS-I was available. Most SNPs were specific for the targeted haplogroup, and the additional use of GenoCoRe allowed for unambiguous haplogroup assignment even for SNPs where this was not the case.

PCR-Primer design for the U-Plex and the T-Plex were performed using the SeqEdit and PrimerSelect programs of the Lasergene suite v.9.04 (DNASTAR Inc., Madison, USA), a software package for editing, aligning and designing nucleotide sequences. The preferred fragment length was set to 80-110bp, mirroring the fragment lengths from the GenoCoRe22 and HPLEX17. The PrimerSelect program evaluates the efficiency of each primer pair, their chemical parameters (annealing temp. etc.) and their tendency to form secondary structures (hairpins, duplexes) within themselves or each other. When designing primers for mtDNA, the presence of mitochondrial inserts in the nuclear genome (numts) is

an issue (Zhang & Hewitt 1996). This poses less of of a problem in ancient DNA than in modern DNA because most nuclear DNA in ancient samples is too far degraded to be amplified. However, in order to further test for specificity of the primers for mtDNA, a primer BLAST (Basic Local Alignment Search Tool) was performed using the web based platform offered by the NCBI[6]. The primers for the single base extension (SBE) were designed by examining 20-25 bp long regions directly adjacent to the target SNP and chosing those with the lowest tendency to form secondary structures or interact with the other SNaPshot primers. To generate length differences between the different SBE primers, TC-tails were added as needed. Chemical concentrations and cycling parameters were based on those of the HPLEX17 system.

The primer pairs were first tested for function in singleplex reactions on 1µl extract of modern DNA. The products were then sequenced in their entirety with the Sanger method to ensure the specificity of the primer pairs. The PCR-products were then subjected to the SBE. The SBE-primers were also tested in singleplex reactions first.

After a functioning system had been established, the U-Plex and T-Plex were tested on ancient samples known to belong to different subhaplogroups of U and T based on their HVS-I sequence.

Since the phylogeny of H is complex and prone to changes, some adaptations had to be made to the HPLEX17 based on Phylotree build 15 (published on 30.09.2012). The marker for haplogroup H1 (3010 G/A) was not specific for H1 alone, but was also found to also occur in H30b. Since these two clades could not be distinguished based on the remaining H-Plex SNPs or their HVS-I sequence, a primer pair targeting the H30-specific SNP 8200 T/C was designed, to be used on the samples carrying a derived H1-allele. The subclade H19, targeted by 14869 G/A is nowadays subsumed under clade H22, the diagnostic SNPs for which lie in the HVS-I. Since the primer pair for np14869 also amplified the marker for H13 (14872 C/T), it was kept in the multiplex.

Table 9: PCR primers for the GenoCoRe22, HPLEX17 and U-Plex.

Target SNP	Primer	Primer sequence 5'-3'	Amplicon (bp)
GenoCoRe22			
R9_13928	L13923	TTTCTCCAACATACTCGGATTCTAC	66/17
	H13942	AGAAGGCCTAGATAGGGGATTGT	
L3'4_3594	L03556	AGCTCTCACCATCGCTCTTC	60/14
	H03597	AAATAGGAGGCCTAGGTTGAGG	
K_10550	L10548	GAATACTAGTATATCGCTCACACCTCA	66/8
	H10558	GCGATAGTATTATTCCTTCTAGGCATAGTA	
U_11467	L11454	ATCGCTGGGTCAATAGTACTTGC	73/23
	H11479	TGAGTGTGAGGCGTATTATACCATAG	
A_4248	L04237	TGATATGTCTCCATACCCATTACAA	70/14
	H04253	CTTTTATCAGACATATTTCTTAGGTTTGAG	
W_8994	L08970	CATACTAGTTATTATCGAAACCATCAGC	83/31

[6] http://www.ncbi.nlm.nih.gov/tools/primer-blast/

Target SNP	Primer	Primer sequence 5'-3'	Amplicon (bp)
	H09003	CTGCAGTAATGTTAGCGGTTAGG	
C_13263	L13258	ATCGTAGCCTTCTCCACTTCAA	80/35
	H13295	AGGAATGCTAGGTGTGGTTGGT	
T_13368	L13350	CACGCCTTCTTCAAAGCCATA	67/20
	H13372	GTTCATTGTTAAGGTTGTGGATGAT	
R0/preHV_11719	L11710	GGCGCAGTCATTCTCATAATC	70/23
	H11735	AGTTTGAGTTTGCTAGGCAGAATAG	
B_8280	L08268	AATAGGGCCCGTATTTACCCTATA	78/25
	H08295	AGGTTAATGCTAAGTTAGCTTTACAGTG	
V,M3_4580	L04578	TTACCTGAGTAGGCCTAGAAATAAACA	85/38
	H04618	GCAGCTTCTGTGGAACGAG	
X_6371	L06363	ACCATCTTCTCCTTACACCTAGCAG	60/13
	H06378	GATGAAATTGATGGCCCCTAA	
N1_10238	L10228	TCCCTTTCTCCATAAAATTCTTCTT	70/ 19
	H10249	AGGAGGGCAATTTCTAGATCAAATA	
H_7028	L07003	GCAAACTCATCACTAGACATCGTACT	77/24
	H07029	CCTATTGATAGGACATAGTGGAAGTG	
I_10034	L10025	CTTTTAGTATAAATAGTACCGTTAACTTCCAA	73/10
	H10037	AAGTTTATTACTCTTTTTTGAATGTTGTCA	
D_5178	L05171	ACCCTACTACTATCTCGCACCTGA	76/31
	H05204	CTAGGGAGAGGAGGGTGGAT	
HV_14766	L14759	AGAACACCAATGACCCCAATAC	78/38
	H14799	GGTGGGGAGGTCGATGA	
R_12705	L12689	CAGACCCAAACATTAATCAGTTCTT	78/24
	H12715	TGTTAGCGGTAACTAAGATTAGTATGGT	
N_10873	L10870	CCACAGCCTAATTATTAGCATCATC	67/16
	H10888	GCTAAATAGGTTGTTGTTGATTTGG	
J_12612	L12611	CTACTTCTCCATAATATTCATCCCTGT	60/8
	H12621	AATTCTATGATGGACCATGTAACG	
L2'6_2758	L02727	AACACAGCAAGACGAGAAGACC	75/31
	H02760	GGACCTGTGGGTTTGTTAGGT	
M_10400	L10382	AAGTCTGGCCTATGAGTGACTACAA	85/37
	H10421	TGAGTCGAAATCATTCGTTTTG	
HPLEX17 (incl. H30)			
H1_3010	L03005	ACGACCTCGATGTTGGATCAGGACA	100/50
	H03056	CCGGTCTGAACTCAGATCACGTAGG	
H2_1438	L01432	AGGGTCGAAGGTGGATTTAGCAGT	88/44
	H01477	AGGGTGACGGGCGGTGTGTA	
H3_6776	L06744	GGCTTCCTAGGGTTTATCGTGTGAGC	83/32
	H06802	GCGGAGGTGAAATATGCTCGTGTGT	
H4_3992	L03965	GAATACGCCGCAGGCCCCTT	89/44
	H04010	AGGAAGATTGTAGTGGTGAGGGTGT	
H7_4793	L04735	TCTCCGGACAATGAACCATAACCAATAC	110/59
	H04795	TGGGACTCAGAAGTGAAAGGGGG	
H9_13020	L13013	AGCAGCAGGCAAATCAGCCCA	77/36
	H13050	CTGAGACTGGGGTGGGGCCT	
H10_14470a	L14466	ACTCCTCAATAGCCATCGCTGTAGT	104/51
	H14518	TCTGAATTTTGGGGGAGGTTATATGGGT	
H11_8448	L08411	TGGCCCACCATAATTACCCCCA	95/49

Target SNP	Primer	Primer sequence 5'-3'	Amplicon (bp)
	H08461	TTTGGTGAGGGAGGTAGGTGGTAG	
H12_3936	L03911	ACCCCCTTCGACCTTGCCGA	71/31
	H03943	GGGCCTGCGGCGTATTCGAT	
H14_7645	L07608	GGCACATGCAGCGCAAGTAGG	83/38
	H07647	TGAGGGCGTGATCATGAAAGGTGA	
H15_6253	L06244	CCCTCTCTCCTACTCCTGCTCGC	57/14
	H06259	ACCTGTTCCTGCTCCGGCCT	
H16_10394	L10382	AAGTCTGGCCTATGAGTGACTACAA	85/38
	H10421	TGAGTCGAAATCATTCGTTTTG	
H18_14364	L14348	ACCACAACCACCACCCCATCAT	67/22
	H14371	TGGGGTTAGCGATGGAGGTAGGA	
H19/13_14869	L14865	GGCTCACTCCTTGGCGCCTG	87/47
	H14913	GGCGGTTGAGGCGTCTGGTG	
H23_10211	L10202	ACCCTATATCCCCCGCCCGC	104/61
	H10264	TGGTAGGGGTAAAAGGAGGGCAA	
H25_9620	L09590	AGTCCCACTCCTAAACACATCCGT	107/56
	H09670	GCAGTGCTTGAATTATTTGGTTTCGGT	
H30_8200	L08177	TATACTACGGTCAATGCTCTG	101/63
	H08241	TACGGGCCCTATTTCAA	
U-Plex			
U2_16051	L16047	TCATGGGGAAGCAGATTTG	60/41
	H16071	ATAGCGGTTGTTGATGGG	
U3_16343	L16340	AAGCCATTTACCGTACATAGCACA	50/5
	H16346	GGGGACGAGAAGGGATTTGAC	
U4_4646	L04634	AAAAATAAACCCTCGTTCCACAGAAGCT	79/24
	H04659	TATTAGAAGGATTATGGATGCGGTTGC	
U5_3197	L03182	GCCTTCCCCCGTAAATGATA	61/22
	H03205	TGTTCTTGGGTGGGTGTGG	
U5a_14793	L14766	CACCAATGACCCCAATACGCAAAAC	76/27
	H14794	GGGGTGGGGAGGTCGATGAATGAG	
U5b_14182	L14179	CCCCCGAGCAATCTCAATTACAATA	82/29
	H14209	TGATTATGGGCGTTGATTAGTAGTAGTT	
U8_9698	L09684	TAGAAAACAACCGAAACCAAATAA	82/34
	H09719	GAGGCTTGTAGGAGGGTAAAATAG	
T1/T2			
T1_12633	L12623	CATCCCTGTAGCATTGTTCGT	82/37
	H12661	CTGATTAATGTTTGGGTCTGAGTT	
T2_11812	L11793	TCACAGTCGCATCATAATCCTCTC	81/33
	H11827	AGGCTTGCTAGAAGTCATCAAAAA	

2.7.3 PCR setup

The PCR reaction for the multiplex contained the same chemicals as the HVS-I PCR, but at slightly different concentrations (Table 10). Since multiplex PCRs were always used in conjunction with HVS-PCRs, less blanks were included in the multiplex PCR than in the HVS- PCR.

Table 10: PCR- setup for the GenoCoRe22, HPLEX17 and U-Plex.

Reagent	GenoCoRe22 Final Concentration	(µl)	HPLEX17/U-Plex Final Concentration	(µl)
Puffer	1x	2.5	1x	2.5
$MgCl_2$	6.5mM	6	8mM	7.4
dNTPs	600µM	1.25	500 µM	1.04
Primer Mix	0.013 -0.06µM each	5.5	~ 0.016 µM each	5.5
BSA	0.2µg/µl	1.00	0,4µg/µl	0.5
Taq	1.25 U	0.25	2U	0.4
HPLC-H_2O		6,5		5.5
Target DNA		2		3
TOTAL		**25**		**24.84**

The primer mix was prepared fresh from stock solutions and for multiple PCRs at once. PCR conditions for the GenoCoRe22 were as follows:

10min 95°C

30s 95°C

45s 60°C x35 cycles

30s 65°C

6min 65°C

The PCR-conditions for the HPLEX17 and the U-Plex were identical, except for the lower annealing temperature chosen for the latter.

6min 95°C

30s 95°C

30s 59°C (HPLEX17)/ 56°C (U-Plex) x 32 cycles

30s 65°C

10min 65°C

The PCR products were purified with a mixture of exonuclease I (ExoI)- which degrades single-stranded DNA- and SAP. 2µl of ExoI were added to 50µl of SAP and mixed thoroughly. 1µl of the enzyme mix was added to 5µl reaction product and incubated at 37°C for 45 min, followed by inactivation at 7°C for 10 min. The purified PCR products were kept at 4°C until further use.

2.7.4 Single base extension sequencing (SBE)

The SBE is a modified variant of the Sanger Cycle Sequencing reaction. The sequencing primers directly flank the target SNPs, and the reaction mix contains *only* ddNTPs, so that elongation stops immediately with the target SNP (Table 11). Poly-TC tails of varying lengths on each SBE primer allow the different SNPs to be separated by length during electrophoresis (Table 12). The SBE was carried out using the commercially available SNaPshot Multiplex Kit (Applied Biosystems). The markers H30, T1 and T2 were sequenced directly with the Sanger method.

Table 11: Setup of the SBE reaction.

Reagent	Final Concentration	Amount (µl)
Ready Reaction Mix		2.5
SBE primer mix		0.5
HPLC-H20		1
Purified PCR-Product		2.5
TOTAL		6.5

Sequencing conditions were as follows:

96°C 10s
55°C 5s x 35 cycles
60°C 30s

The setup and protocol of the SBE Reaction was the same for all multiplexes. The SNaPshot products were purified with SAP treatment (see section sequencing products). 2 µl of purified product was then pipetted into the wells of a 96-well sequencing plate each containing 11.8 µl of formamide and 0.2 µl of size standard. The products were then sequenced on the capillary sequencer.

Table 12: SBE primer sequences for the GenoCoRe22, HPLEX17 and U-plex.

Name	Orientation	Sequence	Target SNP (a/d)
GenoCoRe22			
R9_13928	reverse	tctctctctctctGATTGTGCGGTGTGTGATG	C/ G or T
L3'4_3594	reverse	ctctctctctctctctctGAGGCCTAGGTTGAGGTT	A/G
K_10550	reverse	ctctctctctctctctTCTAGGCATAGTAGGGAGGA	T/C
U_11467	forward	ctctctctctctctctctctGTACTTGCCGCAGTACTCTT	A/G
A_4248	forward	tctctctctctctctctATACCCATTACAATCTCCAGCAT	T/C
W_8994	forward	ctctctctctctctctctctTACTCATTCAACCAATAGCCCT	G/A
C_13263	reverse	ctctctctctctctctctCCGATTGTAACTATTATGAGTCCTAG	T/C
T_13368	forward	ctctctctctctctctctctctctCCATACTATTTATGTGCTCCGG	G/A
R0/preHV_11			
719	reverse	tctctctctctctctctctctTAGGCAGAATAGTAATGAGGATGTAAG	T/C
B_8280	reverse	tctctctctctctctctctctctctCTTTACAGTGGGCTCTAGAGGGGGT	A/G
V,M3_4580	reverse	ctctctctctctctctctctctTTTTGGTTAGAACTGGAATAAAAGCTAG	C/T
X_6371	reverse	tctctctctctctctctctctctctctctctctAAATTGATGGCCCCTAAGATAGA	G/A
N1_10238	forward	tctctctctctctctctctctctCTTTCTCCATAAAATTCTTCTTAGTAGCTAT	T/C
H_7028	reverse	tctctctctctctctctctctctctctctctctCTATTGATAGGACATAGTGGAAGTG	A/G
I_10034	forward	ctctctctctctctctctctctctGTATAAATAGTACCGTTAACTTCCAATTAACTAG	T/C

D_5178	reverse	tctctctctctctctctctctctctctctctctctctctGGAATTAAGGGTGTTAGTCATGTTA	G/T
HV_14766	reverse	ctctctctctctctctctctctctctctctctctctctGAGTGGTTAATTAATTTTATTAGGGGGTTA	A/G
R_12705	reverse	ctctctctctctctctctctctctctctctctctctctctctGGTAACTAAGATTAGTATGGTAATTAGGAA	A/G
N_10873	reverse	ctctctctctctctctctctctctctctctctctctctctctctGTTGTTGTTGATTTGGTTAAAAAATAGTAG	G/A
J_12612	forward	ctctctctctctctctctctctctctctctctctctctctctctctctctCTACTTCTCCATAATATTCATCCCTGT	A/G
L2’6_2758	forward	ctctctctctctctctctctctctctctctctctctctctctctctctctCTATGGAGCTTTAATTTATTAATGCAAACA	A/G
M_10400	reverse	ctctctctctctctctctctctctctctctctctctctctctctctctAAATCATTCGTTTTGTTTAAACTATATACCAATTC	G/A
HPLEX17			
H10_14470	reverse	tctctctctctctctctctctctctctctctctctctctctctctctGGGAATGATGGTTGTCTTTGG	A/T
H7_4793	reverse	tctctctctctctCTCAGAAGTGAAAGGGGGC	T/C
H1_3010	reverse	ctctctctctctctctTTAATAGCGGCTGCACCAT	C/T
H18_14364	reverse	ctctctctctctctctctCGATGGAGGTAGGATTGGTG	C/T
H4_3992	forward	ctctctctctctctctctctCCCTATTCTTCATAGCCGAATACA	C/T
H11_8448	forward	tctctctctctctctctctctctCTATTCCTCATCACCCAACTAAAAA	T/C
H2_1438	reverse	ctctctctctctctctctctctctctCCCTGTTCAACTAAGCACTCTACTCT	C/T
H16_10394	forward	ctctctctctctctctctctctctctctCCTATGAGTGACTACAAAAAGGATTAGA	C/T
H15_6253	reverse	ctctctctctctctctTGCTCCGGCCTCCACT	A/G
H9_13020	reverse	tctctctctctctctctctGGGAGTCAGGGGTGGAG	A/G
H12_3936	reverse	tctctctctctctctctCGGCGTATTCGATGTTGAA	G/A
H14_7645	reverse	ctctctctctctctctctctctctGCGTGATCATGAAAGGTGAT	A/G
H19_14869	forward	tctctctctctctctctctctctctctctctctctCCTTGGCGCCTGCCT	G/A
H13_14872	reverse	tctctctctctctctctctctctctctctAATAGTCCTGTGGTGATTTGGAG	G/A
H25_9620	reverse	tctctctctctctctctctctctctctctctctCAGGTGATTGATACTCCTGATGC	G/A
H23_10211	reverse	ctctctctctctctctctctctctctctctGGTAATAGCTACTAAGAAGAATTTTATGGA	G/A
H3_6776	reverse	tctctctctctctctctctctctctctctctctGTGTGTCTACGTCTATTCCTACTGTAAATAT	A/G
U-Plex			
U2_16051	forward	tctctctctctctctTGGGGAAGCAGATTTGGGT	A/G
U3_16343	reverse	GGACGAGAAGGGATTTGACTG	T/C
U4_4646	reverse	GGATGCGGTTGCTTGCGTGAGGAA	A/G
U5_3197	reverse	tctcTTGGGTGGGTGTGGGTATAAT	A/G
U5a_14793	reverse	ctctcGGGGTGGGGAGGTCGATGAATGAG	T/C
U5b_14182	forward	tctctCGAGCAATCTCAATTACAATATA	T/C
U8_9698	reverse	ctctctctctAGAGACCCAGTAAAATTGTAAT	A/G

2.8. Alignments and software

2.8.1 HVS-I and HVS-II

The electropherograms of each sequence were first viewed and edited with the Applied Biosystems sequencing analysis software. Further editing took place using the SeqMan program of the Lasergene suite. The fragments were aligned against the rCRS and mislabelling of bases caused by the base- calling algorithm of the software was corrected manually. Transitions and transversions were labelled according to the Nucleotide Ambiguity Code proposed by the International Union of Biochemistry (IUB, see Table 13) (Cornish-Bowden 1985).

Table 13: IUB nucleotide codes. Not included are the codes for adenine, thymine, guanine and cytosine, which are abbreviated as A, C, T and G.

Nucleotide	Symbol
A or G	R
C or T	Y
G or T	K
A or C	M
G or C	S
A or T	W
C or G or T	B
A or G or T	D
A or C or T	H
A or C or G	V
A or C or G or T	N

Double peaks were called whenever the lower of the two peaks was at least 30% as large as the higher one. The entire HVS-I (and HVS-II) was assembled and aligned against the rCRS with the MegAlign program using the Clustal V algorithm for multiple alignments (Higgins & Sharp 1988; Higgins et al. 1992). Nucleotide positions were labelled according to the rCRS.

The final consensus sequences were reported in reference to the rCRS.

Phylogenetic assignments were performed based on Phylotree build 15. The web-based tool Haplogrep[7] (Kloss-Brandstätter et al. 2011) was used for the initial haplogroup assignation, which was then checked manually.

2.8.2 Multiplexes

The multiplex data was analysed with the GeneMapper software from Applied Biosystems. This program has an automated base calling function based on "panels" The panels contained the name, possible alleles and fragment lengths of the markers in the multiplex PCR. Peaks below 50 Relative Fluorescence Units (RFU) were not counted. Panels were constructed manually based on the expected fragment lengths and calibrated on the observed actual fragment lengths. The allele calling was then proofread and the results were recorded.

2.9 Statistical analyses

2.9.1 The dataset

The dataset incorporated the SNP and HVS-I sequence data. Only nine individuals were typed for the HVS-II region, and the HVS-II data were not considered in the population genetic analyses. In order to track trends chronologically from the early to the late Neolithic, the Alföld samples were divided into four major groups: *Körös, earliest ALBK/Szatmár* (also referred to as *ALBK early*), *ALBK later* and *Tisza*.

[7] http://haplogrep.uibk.ac.at/

The two samples dating to the early Chalcolithic Tiszapolgár culture were not included in the statistical analyses.

In a second set of analyses the *ALBK later* and *Tisza* sets were subdivided based on the archaeological and geographical data available. The Szakálhát group of the ALBK was broken down further in two subgroups based on geography. Because the different chronological periods and subgroups were not equally represented among the sampled individuals, the size of the datasets varied between groups by as much as a factor of 9 (Table 14).

In order to examine the distribution of the subhaplogroups of H in the Alföld Neolithic and compare it to other prehistoric European cultures, a dataset containing only the individuals belonging to haplogroup H and subgroups thereof was assembled.

The chronological dataset

The *Körös* set contained all samples belonging to the early Neolithic Körös culture. The *ALBK early* set contained the individuals from the earliest Alföld LBK/ Szatmár group, thus representing the transition phase from the early to the middle Neolithic. The samples from the classical and late phase of the ALBK, including those belonging to the regional subgroups, make up the *ALBK later* set. This set also included one published ALBK- individual from Ecsegfalva (Haak, Forster, et al. 2005), which fits into this set based on radiocarbon dating. The samples from the *Tisza* culture formed the fourth group, representing the late Neolithic of the ALföld. This subdivision was also used for the comparisons with the European Neolithic cultures, since a division into regional groups did not make sense in a continent-wide context.

Table 14: The subdivisions of the dataset according to chronology, cultural affiliation and geographic location. n_{seq} denotes the number of individuals included in sequence-based analyses (for which a fully reproduced HVS-I sequence was required), n_{freq} denotes the number of individuals included in the frequency-based analyses, where fully reproduced SNP profiles were sufficient for haplogroup assignation. Note: not all indvididuals from the ALBK could be assigned to a particular subgroup based on chronology or cultural context. Furthermore, while a total of 320 individuals were sampled, DNA could not be obtained from all of them (see appendix for total size of all sampled groups).

Culture	n_{seq}/ n_{freq}
Körös	**16/16**
ALBK early	**33/35**
ALBK later	**143/144**
Szakálhát	51/51
North	*14/14*
South	*37/37*
Tiszadob/Bükk	44/44
Esztár	20/20
Tisza	**45/48**
East	*25/26*
River	*20/22*
TOTAL	**237/243**

The regional datasets

The *ALBK later* set was divided into following groups: Esztár, Szakálhát and Tiszadob/Bükk. The Tiszadob and Bükk individuals were combined into a single group because the Bükk group immediately succeeded the Tiszadob group in the northern Alföld and both groups occupied the same territory. Samples from sites that could not be assigned to a specific regional subgroup, e.g. Hajdúnánás- Eszlári út, where Tiszadob, Bükk and Esztár elements were all present, were excluded from the analyses.

To further test for geographical differentiation, the Szakálhát group and the Tisza culture- which spanned the largest geographic area among the Neolithic cultural groups in this study- were also divided into geographical groups. The Szakálhát group was divided into a southern and a northern Group. The northern group encompassed the sites Adács (ADMA), Pusztataksony Ledence (PULE) and Tiszaszőlős-Domaháza (TIDO), while the southern group contained Cegléd (CEG), Abony (ABO), Cegléd Iparipark (CGIP) and Tiszaföldvar-Teglagyár (TITE) (Figure 11).

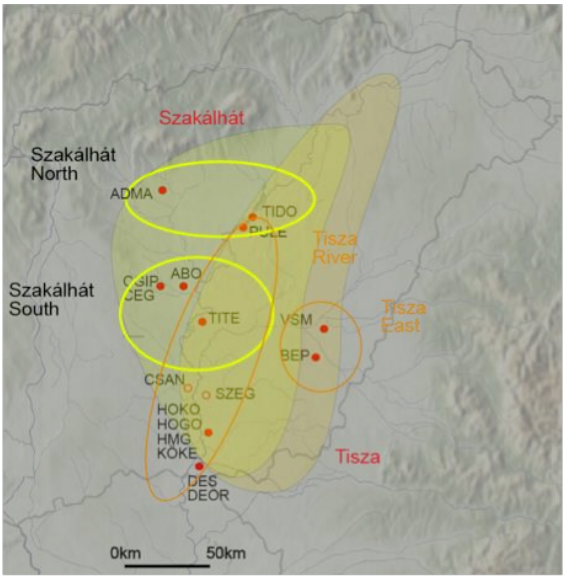

Figure 11 The regional subdivision of the Szakálhát group of the ALBK and the Tisza culture mapped onto their total distribution area. The yellow and orange circles denote the subgroups.

The Tisza culture was originally divided into a northern, southern and eastern group. This subdivision was modified after preliminary testing (Table 15, Table 16). With p-values close to or above 0.5, all Tisza subgroups were found to be highly similar to each other. However, Tisza North and South only contained 10 individuals each, which may made them vulnerable to statistical artefacts. Furthermore, with a p-value of 1, the haplogroup composition of the northern and southern Tisza groups was practically identical. The extremely low F_{ST} value of the north/south pairing showed that this similarity also extended to the sequence level. Possible ways of combining the regional groups were tested with Fisher's exact test with the following result:

Table 15: Fisher's exact test of the regional groups of the Tisza culture.

		Tisza North	Tisza South	Tisza East
Fisher Test	**Tisza North**	*	1	0.7521
	Tisza South	1	*	0.4771
	Tisza East	0.7521	0.4771	*
F_{ST}-values	**Tisza North**	*	-0.06387	0.00115
	Tisza South	-0.06387	*	0.00323
	Tisza East	0.00115	0.00323	*

The combination of the northern and southern group produced a considerably lower p-value than all other combinations including the single-group-comparisons (Table 15Table 16). Although the results did not approach statistical significance, there is a strong support for a grouping of northern and southern Tisza group versus the eastern group. Based on these results, the northern and southern Tisza groups were combined to form the *river* group, so called because the sites within it (Pusztataksony-Ledence, Hódmezővásárhely-Gorzsa, Hódmezővásárhely-Kökenydomb and Deszk-Ordos) are all adjacent to the Tisza, as opposed to the *eastern* Tisza sites.

Table 16: Fisher's exact test of different combinations of the regional groups of the Tisza culture.

Combinations	p-values
(Tisza_north+Tisza_south)+Tisza_east	0.1464
(Tisza_north + Tisza_east)+Tisza_south	0.6841
(Tisza_south+Tisza_east)+Tisza_north	0.9613

The H-dataset

This dataset contained the 40 individuals from the Alföld cultures that belonged to haplogroup H and was subdivided into three chronological groups. The "early Neolithic Hungary" set (ENH, n=11) contained the H-individuals from the Körös cultures and the earliest ALBK/Szatmár group. The two were pooled because the Körös dataset only contained 3 individuals belonging to H. The "middle Neolithic Hungary" (MNH, n=24) set contained the individuals from the *ALBK later* set, and the H-individuals from the Tisza culture comprised the " late Neolithic Hungary" dataset (LNH, n=5). Since the resolution of H was based on the HPLEX17 and the samples were largely indistinguishable by their HVS-I, only frequency-based statistical analyses, specifically cluster analysis and PCA, were performed on the H-dataset.

2.9.2 Amplification success and contamination rates

Amplification success rates for the individuals were based on the number of individuals for which reliable haplogroup information could be obtained by a fully reproduced HVS-I sequence and/or SNP

profile compared to the total number of individuals analysed. The amplification success of the HVS-II was not evaluated due to the low number of individuals typed for this region.

Amplification success rates for the HVS-I primer systems were based on the 239 individuals for which a reproducible HVS-I profile could be obtained.

Contamination rates of the multiplex primer systems (GenoCore22, HPlex17, U-Plex, T1/T2 Diplex) were based on the 245 individuals with a reliable haplogroup assignation (including those individuals where only SNPs yielded results).

Contamination rates of the controls were based on the total number of controls included in all millings, extractions and PCRs.

Contamination rates of the individuals were based on the 245 individuals for which reliable haplogroup information could be obtained.

The evaluation of contamination by primer system was based on a) for the HVS-I primer systems: the total number of successful HVS-I PCRs among the 239 individuals with a reproduced HVS-I sequence and b) for the SNP multiplex systems: the total number of successful SNP PCRs among the 245 individuals with a reliable haplogroup assignation.

2.9.3 Prehistoric comparison data

In order to analyse the Alföld Neolithic in a wider geographical context, a dataset containing data from prehistoric cultures from various regions of Europe was assembled (

Table 17). This comparison dataset contained three preneolithic hunter-gatherer metapopulations from Central, southwestern and Eastern Europe as well as cultures that were contemporaneous to the Alföld Neolithic (6000 BC to 4500 BC).

A modified European comparison dataset was used to analyse the distribution of haplogroup H (Table 18).

Hunter-gatherer metapopulations

The preneolithic (hunter-gatherer/ HG) set contained individuals from the Palaeo- and Mesolithic (Figure 7). The distinction between preneolithic and Neolithic cultures was based on both chronological and cultural data. The preneolithic dataset was split into three metapopulations based on geographical distribution: southwestern, Central and Eastern Europe. The latter also included the individual from Mal'ta, which was found in Central Asia, but whose DNA indicates a genetic affiliation towards (preneolithic) European populations (Raghavan et al. 2014).

The Central European hunter-gatherer group was furthermore used as a proxy for the presumed Mesolithic population background of the Carpathian Basin.

Comparison data Neolithic Europe

The comparison with contemporaneous Neolithic data from Europe was perfomed on two levels: Carpathian Basin and Europe. Comparison data for the former included aDNA from the early to late Neolithic cultures of Transdanubia (Szécsényi-Nagy 2014 unpublished; Szécsényi-Nagy et al. 2014).

In the wider context, Neolithic cultures from Eastern Europe, Central Europe and the Iberian peninsula were included in the dataset (Figure 8).

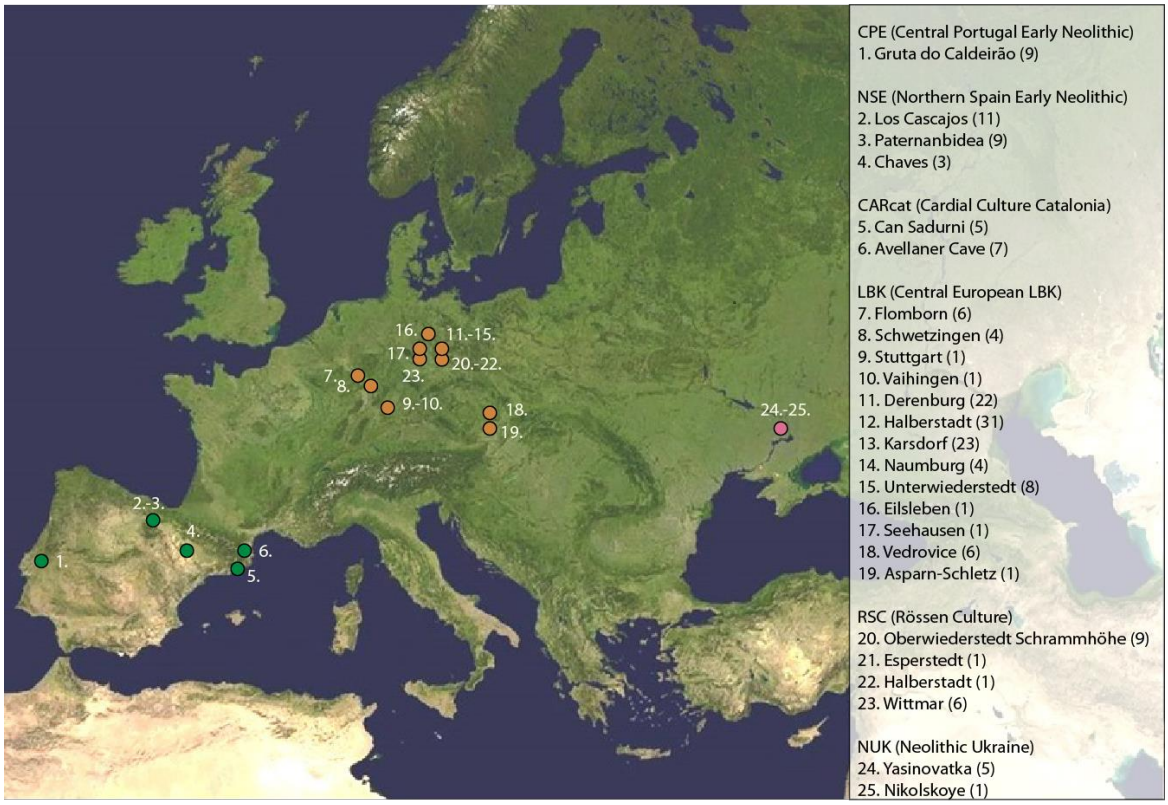

Figure 12: Location of sites included in the European Neolithic comparison dataset. Colours indicate the geographic regions: Iberian Peninsula (Green), Central Europe (orange), Eastern Europe/Ukraine (pink). The numbers in brackets after each site state the number of individuals considered for the analyses.

Table 17: Chronology and cultural affiliations of the prehistoric comparative data. The column with the header "n" contains the number of individuals included in the dataset. The numbers after the slash indicate the number of individuals used for the frequency-based methods, if different from the number of individuals for which HVS-I sequence data was available. Note: some individuals from the original studies were not included in the comparison datasets (see appendix for details).

Culture	Age [cal BC]	Abbr.	n	References
Starčevo	5800-5400	STA	44	(Szécsényi-Nagy et al. 2014)
Transdanubian LBK	5400-4900	TLBK	39/52	(Szécsényi-Nagy et al. 2014)
Sopot	5000-4800	SOP	37	(Szécsényi-Nagy 2014 unpublished)
Lengyel	5000-4300	LGY	82	(Szécsényi-Nagy, 2014 unpublished)
Vinča (Transdanubia)	ca 5400 /5300	VIN	31	(Szécsényi-Nagy, 2014 unpublished)
Central European LBK	5500-4750	LBK	109	(Haak, Forster, et al. 2005; Brandt et al. 2013; Bramanti et al. 2009; Bramanti 2008; Lazaridis et al. 2013)
Rössen Culture	4625-4250	RSC	17	(Brandt et al. 2013; Lee et al. 2013)
Neolithic Ukraine (Dniepr-Donetsk cultural complex)	5557-4792[8]	NUK	6	(Nikitin et al. 2012; Newton 2011)
Central Portugal early Neolithic	5480-4843	CPE	9	(Chandler et al. 2005)
Northern Spain early Neolithic	5350-4555	NSE	23	(Hervella et al. 2012; Gamba et al. 2012)
Cardial culture Catalonia[9]	5475-4460	CARcat	12	(Gamba et al. 2012; Lacan, Keyser, Ricaut, Brucato, Duranthon, et al. 2011)
Hunter-gatherers Central Europe	*31000-2250*[10]	HGC	27/28	(Bramanti et al. 2009; Lazaridis et al. 2013; Fu et al. 2013; Bollongino et al. 2013; Szécsényi-Nagy et al. 2014)
Hunter- gatherers south(western) Europe	*21000-4700*	HGS	17/18	(Chandler et al. 2005; Sánchez-Quinto et al. 2012; Hervella et al. 2012; Mannino et al. 2012; Caramelli et al. 2003)
Hunter-gatherers Eastern Europe	*31000-5000*	HGE	15	(Raghavan et al. 2014; Der Sarkissian et al. 2013; Bramanti et al. 2009; Krause, Briggs, et al. 2010)

European comparison data for haplogroup H

A modified European comparison dataset was used for analyzing the distribution of haplogroup H. It contained exclusively individuals belonging to haplogroup H from European populations from the

[8] The C14 dates for the six individuals were given as uncalibrated BP and converted to cal BC dates using the OxCal online platform.
[9] The three Iberian datasets were assembled based on the information in the original papers and personal communication by C. Roth.
[10] Not all of the data given for the individuals in the three hunter-gatherer metapopulations are calibrated C-14 dates. For details see appendix

Neolithic to the Bronze Age where haplogroup H had been resolved. Unfortunately, the Transdanubian samples had not been resolved to this level and were therefore not included in the comparison dataset. Furthermore, the scarcity of aDNA studies where haplogroup H was resolved made it necessary to widen the chronological scope and include late Neolithic and Chalcolithic populations in the dataset.

Table 18: The prehistoric European H-dataset.

Group	Abbr.	Chronology [BC]	Cultures	n	References
Early Neolithic central Europe	ENC	5500-3950	Central European LBK, Rössen Culture, Schöningen Group	16	(Brandt et al. 2013; Brotherton et al. 2013)
Middle Neolithic Central Europe	MNC	3950-3100/3025	Baalberge culture, Salzmünde Culture	9	(Brandt et al. 2013; Brotherton et al. 2013)
Late Neolithic Central Europe	BBC	2500-2200/2050	Bell Beaker Culture	10	(Brandt et al. 2013; Brotherton et al. 2013)
Bronze Age Central Europe	UC	2200-1550	Unetice culture	7	(Brandt et al. 2013; Brotherton et al. 2013)
Neolithic Iberia	NEOI	2943-3101		11	(Hervella et al. 2012; Roth 2014 unpublished; Lacan, Keyser, Ricaut, Brucato, Duranthon, et al. 2011)
Neolithic France	TRE	3030-2890	Treilles culture	6	(Lacan et al. 2011)
Chalcolithic Iberia	CHI	~3340-2420		31	(Chandler et al. 2005; Roth 2014 unpublished)
Bronze Age Iberia	BAI	~2200-1700 (estimate)		8	(Roth 2014 unpublished)

2.9.4 Fisher's exact test (Fisher test)

Fisher's exact test is a nonparametric test for statistical significance in multivariate datasets based on contingency tables (Fisher 1922; Bärlocher 1999). The probability of obtaining the observed data if the null hypothesis H_0 is true is given by the hypergeometric distribution of the values in the tables. Fisher's exact test is suitable even for small sample sizes, which makes it applicable to aDNA studies. The test was performed with absolute frequencies of the haplogroups which were observed in the data: **C**, **N***, N1a, N1b, **I**, W, X, R1, HV, V, H, T1, T2, J, U, U2, U3, U4, U5, U5a, U5b, U8, and K (haplogroups that were only considered in the pan-European analyses are marked in bold). In the tests involving only the Alföld samples, haplogroup H was split into H1, H7, H5 and "other H".

The test was performed as a series of pairwise comparisons of subgroups using the *fisher.test* function in R v.3.0.3 (R Core Team 2014). The H_0 for each test was that the subgroups belonged to the same population; the resulting p-value thus described the probability of obtaining the observed haplogroup compositions if both groups were part of the same metapopulation.

2.9.5 Principal Component Analysis (PCA)

The Principal Component Analysis (PCA) is a method to reduce the dimensionality of a multivariate dataset, which is useful when looking for underlying structures in complex datasets. A set of possibly correlated variables is converted into a set of linearly uncorrelated principal components by orthogonal transformation (Hotelling 1933). The number of principal components is equal to or lesser than the number of the original variables, thereby reducing the complexity of the dataset while maintaining an accurate representation of its variability. The principal components are organised in such a way that the first principal component contains the largest possible proportion of the variance. The PCA was performed with the relative frequencies of the same haplogroups used for Fisher's exact test. For the PCA of the H-dataset, the haplogroup categories were based on the haplogroups of the HPLEX17, since the Alföld samples and parts of the comparison data were analysed with this system. The haplogroups considered were: H1, H2, H3, H4, H5, H7, H10, H11, H13, H14, H16, H23 and "other H".

The results of the PCA were plotted in two -dimensional graphs, with the axes representing the first and second principal component. The PCA was run in R using the *prcomp* function for categorical PCA from the *stats* package (R Core Team 2014).

2.9.6 Cluster analysis

Cluster analysis consists of grouping a set of objects into groups in such a way that the objects in a given group are more similar to each other than to those of other groups. Algorithms used for cluster analyses operate under several different principles; in this study, a hierarchical, agglomerative approach was used. Hierarchical clustering constructs the clusters based on distances between objects, usually resulting in a dendrogram. The dendrogram depicts a hierarchy of clusters along the branching points, hence the name "hierarchical" clustering. Agglomerative hierarchical clustering methods start with each object forming its own cluster, which are then merged in a stepwise fashion. Like the PCA, the cluster analysis was based on relative haplogroup frequencies. Clusters were assembled using the Ward clustering algorithm, which employs a criterion of minimal variance between objects in a cluster, and the Manhattan distance metric (Brandt et al. 2013; Ward Jr 1963). The p-values for each branching point were computed by multiscale bootstrap resampling ($n_{resampling}$= 1000). To correct for possible selection bias in the bootstrap probability, an approximately unbiased (AU) test was performed. The AU p-values and the bootstrap probability (BP) values were displayed in the resulting dendrogram (Shimodaira 2002). The clustering was performed in R using the *pvclust* function of the *pvclust* package for hierarchical cluster analysis (Suzuki & Shimodaira 2011).

2.9.7 Test of Population Continuity (TPC)

The TPC was performed to test for continuity between a) the Central European hunter-gatherer metapopulation and the Alföld Neolithic including its subgroups and b) among the four chronological groups of the Alföld dataset (*Körös, ALBK early, ALBK later, Tisza*).

The test shows whether genetic differences between two populations from different timepoints can be adequately explained by genetic drift alone or whether a discontinuity has to be assumed. A model of genetic drift is defined *a priori* based on the presumed number of generations separating the two populations and the effective population size N_e. The fit of the model to the observed data is then evaluated with the Markov-Chain-Monte-Carlo method (for further information see (Brandt et al. 2013 supplement). The result is a p-value which gives the probability of obtaining the observed data if the assumed model of drift is true; a low p-value therefore means that the observed genetic differences cannot be explained by drift alone. As with Fisher's exact test, absolute haplogroup frequencies were used and the populations were tested against each other in pairs. The prior on the drift parameter was set for each population pair based on a presumed generation time of 20 years, an effective population size N_e of 10 000 individuals and the terminal dates of the cultural groups (Table 19).

Table 19: Terminal dates of the Alföld Neolithic cultures used for the TPC. The end date of the earliest ALBK was extended to 5300 BC in order to allow for a minimum of genetic drift to occur.

Culture	Terminal date
Central European hunter-gatherers	6000 BC
Körös culture	5500 BC
ALBK early	5300 BC
ALBK later (*and regional subgroups)*	5000 BC
Tisza culture (*and regional subgroups)*	4500 BC

The TPC script was run in R using the packages *mvtnorm* for the analysis of multivariate normal and t-distributions (Genz et al. 2014) and *MCMCpack* for the MCMC simulation of the posterior distribution (Martin et al. 2011).The Markov Chain was run for 50 000 iterations with a burn-in of 2000 iterations. The code for the TPC is available online at *https://github.com/joepickrell/tpc*.

2.9.8 (Ancestral) Shared Haplotype Analysis (ASHA)

The shared haplotype analysis (Excoffier & Lischer 2010) examines the occurrence of identical lineages (presumed to be identical by descent) in different populations. The approach can either be lineage-based, where purely the number of lineages and the proportion of shared lineages are evaluated, or individual-based, where the number of individuals sharing a given lineage is also taken into account. In this study, the latter approach was chosen to reflect the strong prevalence of a limited number of basal lineages in the dataset, which cannot be solely explained by direct maternal kinship.

For the ancestral shared haplotype analysis (ASHA), the approach was modified to incorporate the relative chronology of the studied groups. The objective was to track lineages through time, i.e. their first appearance and transmission to later populations. The SHA included the Central European hunter-

gatherer population (as a possible contributing population to the Alföld Neolithic), the Alföld Neolithic cultures (in total and divided into the regional subgroups) and the Transdanubian Neolithic Cultures, due to their presumed shared origin with the Alföld Neolithic. The ASHA was performed on the Alföld cultures with the Central European hunter-gatherers as a presumed ancestral population. The Transdanbuian cultures were not included, since the Transdanubian and Alföld Neolithic developed in parallel and are thus not expected to be ancestral to each other. The only exception was the Starčevo culture, which was included to supplement the small Körös dataset as a proxy for the early Neolithic maternal gene pool of the (eastern) Carpathian Basin.

2.9.9 F_{ST}-values and MDS

The F_{ST}, also referred to as "fixation index", is a measure for the amount of genetic structuring in populations. It measures which proportion of the observed genetic variation observed in populations is due to inter- vs. intrapopulation differences. An F_{ST} value of 1 between two populations means that they are genetically completely distinct, or in other words, that 100% of the observed genetic variation are due to population structure. An F_{ST} value of 0 on the other hand indicates perfect panmixia. Therefore, F_{ST} values can also be understood as a measure of genetic distance between populations.
F_{ST} values were computed using the Arlequin v.3.5.software (Excoffier & Lischer 2010) using the Tamura & Nei substitution model (Tamura & Nei 1993); The associated gamma-values (Table 20) were determined by using jModelTest (Guindon & Gascuel 2003; Posada 2008; Darriba et al. 2012) , a free software that is available online (*https://code.google.com/p/jmodeltest2/)*. The p-values of the F_{ST}'s were estimated by 10 000 permutations.

Table 20: Gamma values used for the different datasets.

Dataset	Gamma-value
Alföld cultures and HGC	0.182
Carpathian Basin cultures and HGC	0.236
Prehistoric Europe (incl. Carpathian Basin and all hunter-gatherer metapopulations)	0.246

In order to display the genetic distances between the tested populations, Slatkin's linearised F_{ST} values (Slatkin 1995) were generated in Arlequin and plotted in a two-dimensional space using nonmetric Multidimensional Scaling (MDS). Similar to the PCA, MDS translates the distances/dissimilarities between multidimensional objects into spatial (usually Euclidean) distances and plots them in a lower-dimensional space. The MDS was implemented in R using the *metaMDS* function from the *vegan* package for ordination methods and diversity analysis (Oksanen et al. 2010). Vegan depends on the *permute* (Simpson 2014) and *lattice* (Sarkar 2008) packages.

2.9.10 Analysis of Molecular Variance (AMOVA)

The Analysis of Molecular Variance (AMOVA) is a method to test for genetic structuring in a dataset (Excoffier et al. 1992). It takes both haplotype frequencies and the sequence data itself into account.

The genetic structure of the dataset is predefined by the user. Using a matrix of Euclidean squared distances between the haplotypes in the dataset, the total genetic variance in the dataset is divided into covariance components representing the percentage of genetic variance on different levels of the population structure: intra-individual, within populations, within groups of populations and among groups. The variance components are then tested for significance by a nonmetric permutation method (Excoffier & Lischer 2010 manual, p.85). The AMOVA was performed using the standard AMOVA function in Arlequin v. 3.5. with 10 000 permutations, under the Tamura and Nei substitution model ((Tamura & Nei 1993) and an associated gamma value of 0.243. The AMOVA was only performed for the cultural and regional subgroups of the Alföld Neolithic cultures. The starting point was a three-group model based on chronology: ("early Neolithic") + ("middle Neolithic") + ("late Neolithic). The subgroups were then shifted around between groups to maximise the genetic variance among groups. Based on the best three-group-model, the same was repeated for a model involving four groups in order to reveal finer substructures.

3 Results

3.1 Samples

3.1.1 Amplification success

Individuals

Of the 320 processed samples, a fully reproduced HVS-I sequence could be obtained from 239 individuals, equalling a success rate of 74.7%. By using diagnostic SNPs, the mitochondrial haplogroup of further six individuals could be determined in spite of incomplete HVS-I sequences, leading to a final success rate of 245 individuals out of 320 (76.6%).

Table 21: Results of all fully authenticated Alföld samples. Asterisks denote the individuals which were typed for the HVS-II region (see appendix for results). The HPLEX17 results incorporate the results of the H30 singleplex. The final haplogroup assignment was based on Phylotree build 15.

Cultural affiliation	Site	Lab. name	HVS-I	Range HVS I	GenoCoRe 22	HPLEX 17	U-Plex	T1/T2	Haplo-group
Körös	Tiszaszőlős, Domaháza-puszta, Réti-dűlő	TIDO02	16174T 16224C 16311C	16046-16401	K				K
		TIDO03	16069T 16126C	16046-16401	J				J
	Maroslele-Pana	MAP01	16093C 16126C 16294T 16296T 16304C	15997-16409	T			T2	T2b
		MAP02	16093C 16126C 16294T 16296T 16304C	15997-16409	T			T2	T2b
		MAP03	16126C 16189C 16294T 16296T	15997-16409	T				T2f
	Deszk -1. olajkút	DES06*	16298C	15997-16409	V				V
	Törökszentmiklós-Tiszapüspöki, Karancs háromág 3. lh.	TÖSM01*	16093C	15999-16409	H				H
		TÖSM03*	16093C 16224C 16311C	16046-16401	K				K
		TÖSM04*	16093C 16224C 16311C	15999-16401	K				K
		TÖSM05*	16093C 16224C 16311C	15999-16401	K				K1a1
		TÖSM06*	16093C 16224C 16311C	16047-16409	K				K
		TÖSM07*	16179T 16189C 16223T 16278T 16362C	15997-16401	X				X2
	Berettyóújfalu, Nagy-Bócs dűlő	BENA01	CRS	16019-16409	H	H1			H1
		BENA03	16093C 16224C 16311C	15997-16401	K				K
	Hódmezővásárhely -Kotacpart	HOKO01	CRS	16020-16407	H				H
		HOKO02	16126C 16294T 16296T 16304C	16046-16401	T				T2b
Early ALBK/ Szatmár (II)	Füzesabony-Gubakút	FUGU03	16147A 16172C 16223T 16248T	16020-16397	N1				N1a1a1
		FUGU04	16126C 16292T 16294T	16019-16400	T			T2	T2c1
		FUGU05	CRS	16019-16401	H				H
		FUGU08	16147A 16172C 16223T 16248T 16320T 16355T	16019-16400	N1				N1a1a1a
		FUGU09	16126C 16292T 16294T 16296T	16019-16401	T			T2	T2c1
		FUGU10	16304C 16335G	16019-16395	H				H5
		FUGU11	16129A 16224C 16311C	16019-16401	K				K
		FUGU12	16126C 16147T 16294T 16296T 16297C 16304C	16001-16401	T2				T2b23
earliest ALBK/ Szatmár group	Polgár, Piócasi-dűlő	POPI02	16093C 16189C 16224C 16311C	16019-16401	K				K

Cultural affiliation	Site	Lab. name	HVS-I	Range HVS I	Geno CoRe 22	HPLEX 17	U-Plex	T1/T2	Haplo-group
Szatmár	Mezőkövesd-Mocsolyás	POPI03	16147A 16172C 16223T 16248T 16355T	16022-16401	N1				N1a1a1
		POPI04	16126C 16294T 16296T 16304C	15999-16404	T				T2b
		POPI05	16093C 16189C 16224C 16311C	15999-16404	K				K
		POPI06	16224C 16311C	16020-16403	K				K
		MEMO01	16311C	15999-16406	HV				HV
		MEMO02	16093C 16224C 16239T 16311C	15999-16404	K				K
		MEMO03	16192T 16256T 16270T	15998-16404	U		U5a		U5a
		MEMO04	n.d.		H	H7			H7
		MEMO05	16069T 16126C	16019-16403	J				J
		MEMO06	16153A 16298C	15999-16404	V				V7a
		MEMO07	16311C	16022-16404	HV				HV
		MEMO08	CRS	16019-16403	H				H
		MEMO09	16304C	15998-16405	H				H5
		MEMO12	n.d.		U		U5a		U5a
		MEMO13	16189C	15998-16404	H	H7			H7
		MEMO14	16356C	15998-16401	U		U4		U4
		MEMO15	16311C	15998-16401	R				R1
		MEMO16	CRS	16021-16401	H				H
		MEMO17	16134T 16356C	16019-16401	U		U4		U4a1
		MEMO18	16093C 16224C 16311C	16019-16401	K				K
		MEMO19	16093C 16224C 16311C	16019-16403	K				K
		MEMO20	16224C 16311C	16001-16404	K				K
		MEMO21	16304C	16019-16403	H				H5
		MEMO22	16183C 16189C 16223T 16278T	16022-16401	X				X
		MEMO23	16270T 16274A 16311C 16362C	15997-16401	U		U5b		U5b
		MEMO24	16182C 16183C 16189C 16234T 16324C	15997-16401	U		U8		U8b1b
Late classical ALBK (phase II-III)	Mezőkeresztes-Cethalom	MECE01	16304C	16019-16401	H				H5
		MECE08	16304C	16019-16401	H				H5
		MECE10	CRS	15999-16401	H				H
		MECE12	16147A 16154C 16172C 16223T 16248T 16320T 16355T	15998-16402	N1				N1a1a1a3
		MECE14	16069T 16126C	15998-16395	J				J
late ALBK (phase III-IV)	Tiszabura-Bónishát	TIBO 1	CRS	16001-16401	H				H
		TIBO 2	CRS	15999-16401	H				H
		TIBO 3	16092C 16189C 16270T	15999-16401	U		U5b		U5b
		TIBO 4	n.d.		K				K

Cultural affiliation	Site	Lab. name	HVS-I	Range HVS I	GenoCoRe 22	HPLEX 17	U-Plex	T1/T2	Haplo-group
late ALBK (phase III-IV)	Hajdunanas, Eszlári út, M3-45	TIBO 5	16126C 16163G 16186T 16189C 16294T	16046-16401	T		T1		T1a
		HAJE01	16126C 16147T 16294T 16296T 16297C 16304C	15997-16401	T				T2b23
		HAJE02	16093C 16224C 16311C	16046-16401	K				K
		HAJE03	16093C 16224C 16224.1C 16311C	15997-16409	K				K
		HAJE04	16069T 16126C 16193T 16311C	16046-16409	J				J
		HAJE06	16311C	16003-16409	HV				HV
		HAJE07	16093C 16224C 16284G 16311C	16006-16401	K				K
		HAJE08	16147A 16154C 16172C 16223T 16248T 16320T 16355T	16019-16409	N1				N1a1a1a3
		HAJE09	16126C 16189C 16294T 16296T	15997-16409	T			T2	T2f
		HAJE10	16069T 16126C 16193T 16311C	16003-16401	J				J
		HAJE11	16134T 16356C	16006-16409	U		U4		U4a1
		HAJE12	16147A 16172C 16223T 16248T 16320T 16355T	16019-16409	N1				N1a1a1a
		HAJE15	16224C 16311C	15999-16409	K				K
		HAJE18	16224C 16311C	16019-16396	K				K
		HAJE20	16126C 16153A 16189C 16294T 16296T	15999-16409	T				T2e
ALBK	Kompolt, Kígyos-ér	KOKI01	16051G 16192T 16256T 16270T 16399G	16047-16401	U		U5a		U5a1
		KOKI02	16069T 16126C	16020-16401	J				J
		KOKI05	16129A 16224C 16311C	16020-16401	K				K
ALBK	Tiszaszőlős, Domaháza-puszta, Réti-dűlő	TIDO05	CRS	16046-16401	H				H
Szakálhát	Pusztataskony-Ledence, 1. lh.	PULE1.2	CRS	16021-16402	H	H7			H7
		PULE1.4	16126C 16294T 16296T 16304C	15997-16401	T				T2b
		PULE1.15	16298C	15999-16401	V				V
		PULE1.18	16126C 16292T 16294T	16000-16402	T			T2	T2c1
		PULE1.20	16093C 16126C 16294T 16296T 16304C	15997-16402	T				T2b
		PULE1.21	16126C 16163G 16186T 16189C 16294T	15998-16409	T				T1a
		PULE1.23	16189C	15997-16409	H	H1			H1
Szakálhát	Pusztataksony-Ledence, 2.lh.	PULE2.2	16298C	15997-16404	V				V

Cultural affiliation	Site	Lab. name	HVS-I	Range HVS I	GenoCoRe 22	HPLEX 17	U-Plex	T1/T2	Haplo-group
Szakálhát	Abony, Serkeszék-dűlő , 60.lh	ABO03	CRS	16019-16401	H	H1/H30[11]			H
		ABO05	16069T 16126C	15999-16409	J				J
		ABO06	16069T 16126C	16046-16401	J				J
		ABO08	16069T 16126C 16193T	16046-16401	J				J
		ABO10	16069T 16126C	15999-16396	J				J
		ABO11	16126C 16147T 16294T 16296T 16297C 16304C	16046-16401	T			T2	T2b23
		ABO12	16270T	16019-16398	U		U5b		U5b
		ABO13	16069T 16126C	16020-16401	J				J
		ABO15	16069T 16126C	16019-16404	J				J
		ABO16	16069T 16126C 16193T 16278T	15999-16409	J				J2b1a
		ABO17	16126C 16147T 16294T 16296T 16297C 16304C	16021-16401	T				T2b23
		ABO19	16192T 16270T	15998-16409	U		U5b		U5b
Szakálhát	Deszk -1. olajkút	DES05	16304C	15997-16409	H				H5
Szakálhát	Tiszaföldvár-Téglagyár	TITÉ01	16224C 16311C 16319A	15999-16401	K				K1b1a
		TITÉ02*	16069T 16126C 16193T	16046-16409	J				J2b
		TITÉ03	16147A 16172C 16189C 16209C 16223T 16248T	16019-16401	N1				N1a1a1
		TITÉ04	16274A 16355T CRS	15999-16409	H	H7			H7
		TITÉ06	16069T 16126C 16193T	16046-16409	J				J
Szakálhát	Cegléd, Ipari- Park	CGIP01	16093C 16224C 16311C	16019-16409	K				K
		CGIP02	16126C 16294T 16296T 16304C	15997-16401	T				T2b
		CGIP03	16093C 16224C 16311C	16046-16401	K				K
		CGIP06	16224C 16311C 16319A	16046-16401	K				K1b1a
		CGIP09	16147A 16172C 16223T 16248T	16046-16401	N1				N1a1a1
Szakálhát	Tiszaszőlős, Domaháza-puszta, Réti-dűlő	TIDO01	16126C 16153A 16294T 16296T	16046-16409	T				T2e
		TIDO04	16093C 16224C 16311C	15997-16401	K				K
Szakálhát	Adács, Mancsos-rét	ADMA01	16298C	15997-16401	HV				HV0
		ADMA02	16069T 16126C 16193T 16278T	16019-16401	J				J2b1a
		ADMA03	CRS	16019-16408	H				H
		ADMA04	CRS	15997-16409	H	H7			H7
Szakálhát	Cegléd, Váróczi-Hodula-dűlő, 4/1 lh.	CEG01	16134T 16356C	15999-16409	U		U4		U4a1

[11] The HPLEX17 indicated H1, but the results of the H30-singleplex were inconclusive.

Cultural affiliation	Site	Lab. name	HVS-I	Range HVS I	GenoCoRe 22	HPLEX 17	U-Plex	T1/T2	Haplo-group
		CEG02	16223T 16292T	15999-16401	W				W
		CEG03	16093C	15999-16409	H				H
		CEG04	16126C 16163G 16186T 16189C 16294T	15997-16405	T			T1	T1a
		CEG05	16126C 16189C 16294T 16296T	15997-16405	T				T2f
		CEG06	16304C	16046-16401	H				H5
		CEG07	16069T 16126C 16193T	16047-16409	J				J
		CEG08	16069T 16126C	16047-16401	J				J
		CEG10	16069T 16126C 16193T	15999-16401	J				J
		CEG11	16126C 16294T 16296T 16304C	15999-16401	T				T2b
		CEG12	16126C 16294T 16296T 16304C	15999-16404	n.d.				T2b
		CEG13	16126C 16147T 16294T 16296T 16297C 16304C	15999-16404	T				T2b23
		CEG14	16069T 16126C 16304C	16019-16403	J				J
		CEG15	16129A 16224C 16311C	16019-16401	K				K
Tiszadob	Tiszadob-Okenéz	TISO01	CRS	16001-16401	H	H7			H7
		TISO02	16192T 16270T	16046-16401	U		U5b		U5b
		TISO03	16270T 16274A 16311C 16362C	16046-16401	U		U5b		U5b
		TISO04	16189C 16223T 16278T 16362C	16046-16401	X				X
		TISO05	16179T 16189C 16223T 16278T 16291T	16046-16401	X				X
		TISO06	16126C 16163G 16186T 16189C 16294T	16019-16401	T				T1a
		TISO07	16224C 16311C	16019-16401	K				K
		TISO08	16093C 16224C 16311C 16320T	16019-16401	K				K
		TISO09	CRS	15999-16406	H	H7			H7
		TISO10	16126C 16292T 16294T	16019-16401	T			T2	T2c1
		TISO11	16298C	15997-16401	HV				HV0
		TISO12	16069T 16126C 16261T	16019-16401	J				J1c
		TISO13	16069T 16126C 16287T	16001-16401	J				J
		TISO14	16111G 16126C 16163G 16186T 16189C 16294T	16019-16401	T				T1a
		TISO15	16298C	16019-16401	V				V
		TISO16	16093C 16189C 16224C 16311C	16073-16399	K				K
		TISO17	CRS	16019-16400	H				H
Tiszadob	Mezőzombor, Községi temetö	MEKÖ01	CRS	16047-16401	H				H
		MEKÖ02	16134T 16356C	16012-16409	U		U4		U4a1

Cultural affiliation	Site	Lab. name	HVS-I	Range HVS I	Geno CoRe 22	HPLEX 17	U-Plex	T1/T2	Haplo-group
		MEKÖ03[12]	16126C 16292T 16294T	16019-16401	T			T2	T2c1
Bükk		MEKÖ04	16092C 16129A 16147A 16154C 16172C 16223T 16248T 16320T 16355T	16019-16401	N1				N1a1a1a3
Tiszadob		MEKÖ07	16147A 16172C 16189C 16223T 16248T 16274A 16355T	16046-16401	N1				N1a1a1
Bükk	Garadna, Elkerülő 2.lh	GAEL01	16192T 16256T 16270T	15997-16401	U		U5a		U5a
		GAEL02	16126C 16294T 16296T 16304C	16019-16401	T				T2b
		GAEL04	16126C 16294T 16296T	15999-16409	T				T2
		GAEL06	CRS	16019-16409	H				H
		GAEL07	16319A 16343G	16020-16398	U		U3		U3
		GAEL08	16069T 16126C	16019-16401	J				J
		GAEL10	16183C 16189C 16209C 16223T 16278T	15999-16409	X				X
		GAEL12	16069T 16126C	15997-16409	J				J
		GAEL13	16069T 16126C 16193T	16019-16409	J				J
Tiszadob	Hejőkürt, Lidl logisztikai központ	HELI01	16192T 16256T 16270T 16362C	16022-16401	U		U5a		U5a
		HELI02	16183C 16189C 16234T 16290T 16324C	15999-16396	U		U8		U8b1b
		HELI03	16179T 16189C 16223T 16278T	15999-16404	X				X
		HELI05	16126C 16294T 16296T 16304C	15999-16403	T				T2b
		HELI07	16224C 16311C	15998-16402	K				K
		HELI08	16126C 16294T 16296T 16304C	15998-16404	T				T2b
		HELI09	16192T 16256T 16270T	16003-16404	U		U5a		U5a
		HELI10	16179T 16189C 16223T 16278T	15997-16409	X				X
		HELI11	16147A 16172C 16189C 16223T 16248T 16274A 16355T	15998-16409	N1				N1a1a1a1a
		HELI12	16069T 16126C	16019-16404	J				J
		HELI13	16183C 16189C 16223T 16278T	16007-16407	X				X
		HELI14	16147A 16172C 16189C 16223T 16248T 16274A 16355T	16003-16403	N1				N1a1a1a1a

[12] Most of the material found at the site belongs to the Tiszadob group of the ALBK, but there were some late Neolithic stray finds. The individuals MEKÖ01-03 lack distinct finds assigning them to either phase. Based on the predominance of Tiszadob materials at the site, the individuals were included in the Tiszadob/Bükk sample set.

Cultural affiliation	Site	Lab. name	HVS-I	Range HVS I	GenoCoRe 22	HPLEX 17	U-Plex	T1/T2	Haplo-group
		HELI15	16126C 16294T 16296T 16304C	16003-16406	T				T2b
Esztár	Ebes, Zsong-Völgy út	EBVÖ02	16093C 16224C 16311C	16001-16409	K				K1a
		EBVÖ05	16298C	16046-16401	V				V
Esztár	Debrecen, Tócópart Erdőalja	TOPE01	16126C 16217C 16292T 16294T 16296T	15999-16409	T				T2c1
		TOPE02	16298C	15999-16401	HV				HV0
		TOPE03	16069T 16126C	16019-16401	J				J
		TOPE04	16311C	15999-16409	R				R1
		TOPE06	16298C	15999-16405	V				V
		TOPE07	CRS	15999-16404	H				H
		TOPE08	16192T 16256T 16270T	15999-16409	U		U5a		U5a
		TOPE09	16304C	15998-16404	H				H5
		TOPE11	16266T	15997-16404	H				H
		TOPE12	16182C 16183C 16189C 16234T	15997-16403	U		U8		U8b1
		TOPE13	16093C 16183C 16189C 16224C 16311C	15997-16404	K				K
Esztár	Berettyóújfalu, Nagy Bócs-dűlő	BENA02	CRS	16019-16401	H				H
		BENA06	16311C	15999-16409	HV				HV
		BENA08	16224C 16311C	16019-16401	K				K
Esztár	Ebes, Sajtgyár 19. lh.	EBSA01	16224C 16311C	16019-16405	K				K
		EBSA02	16224C 16311C	15997-16404	K				K
		EBSA03	16069T 16126C	16019-16397	J				J
		EBSA04	16129A 16224C 16311C	16019-16404	K				K
Tisza	Vésztő-Mágor	VSM01	16069T 16126C	16047-16401	J				J
		VSM02	16069T 16126C	15997-16409	J				J
		VSM03	16259T	16000-16409	H				H
		VSM04	16069T 16126C	15997-16406	J				J
		VSM06	16145A 16176A 16223T 16390A	16118-16409	N1				N1b
		VSM07	16189C 16223T 16278T	15999-16409	X				X
		VSM08	16311C	15997-16409	HV				HV
		VSM09	16126C 16153A 16294T 16296T	16019-16409	T				T2e
		VSM10	16126C 16294T 16304C	15997-16409	T				T2b
		VSM11	16086C	16047-16401	H	H1			H1
		VSM13	CRS	16047-16396	H	H1			H1
		VSM14	16069T 16126C 16261T	16047-16401	J				J1c
		VSM15	CRS	16019-16401	H	H1			H1
		VSM16	16126C 16163G 16186T 16189C 16294T	16019-16401	T			T1	T1a

Cultural affiliation	Site	Lab. name	HVS-I	Range HVS I	GenoCoRe 22	HPLEX 17	U-Plex	T1/T2	Haplo-group
		VSM17	n.d.		U		U8		U8
		VSM18	16182C 16183C 16189C 16234T	16022-16401	U		U8		U8b1
		VSM19	16182C 16183C 16189C 16234T	16019-16400	U		U8		U8b1
		VSM21	CRS	15999-16401	H				H
		VSM22	16093C 16224C 16311C	15999-16403	K				K1a
Tisza	Békés-Povádzug	BÉP01	16234T 16311C	15997-16409	HV				HV15
		BÉP03	16147A 16154C 16172C 16223T 16248T 16320T 16355T	16019-16409	N1				N1a1a1a3
		BÉP04	16126C 16292T 16294T	16019-16409	T			T2	T2c1
		BÉP05	16147A 16154C 16172C 16223T 16248T 16320T 16355T	16019-16409	N1				N1a1a1a3
		BÉP06	16224C 16311C	16019-16409	K				K
		BÉP07	16069T 16126C 16261T	16001-16406	J				J1c
		BÉP08*	16069T 16126C	15998-16409	J				J
Tisza	Hódmezővásárhely -Gorzsa	HMG01	16126C 16189C 16294T 16296T	16019-16408	T			T2	T2f
		HMG02	n.d.		U		U5b		U5b
		HMG03	16093C 16224C 16311C	16025-16401	K				K1a
		HMG05	16069T 16126C	16019-16401	J				J
		HMG06	16126C 16292T 16294T	16019-16401	T			T2	T2c1
		HMG07	16126C 16259A 16294T 16304C	16019-16401	T			T2	T2b
		HMG10	16069T 16126C	16019-16409	J				J
Tisza	Pusztataskony-Ledence, 1.lh.	PULE1.1	16069T 16126C	15997-16409	J				J
		PULE1.3	16069T 16126C	15997-16409	J				J
		PULE1.7	n.d.		J				J
		PULE1.14	16126C 16189C 16294T 16296T	16000-16407	T				T2f
		PULE1.16	16069T 16126C	16000-16407	J				J
		PULE1.17	16172C 16183C 16189C 16234T 16311C 16352C	15999-16407	U		U8		U8b1
		PULE1.24	16093C 16224C 16311C	15997-16409	K				K
		PULE1.25	16093C 16224C 16311C	15997-16409	K				K
		PULE1.26	16126C 16189C 16294T 16296T	15997-16409	T				T2f
Tisza	Deszk -Ordos	DEOR01	16298C	16000-16400	HV				HV0
Tisza	Hódmezővásárhely -Kökénydomb	KÖKE01	16069T 16126C	15999-16409	J				J

Cultural affiliation	Site	Lab. name	HVS-I	Range HVS I	Geno CoRe 22	HPLEX 17	U-Plex	T1/ T2	Haplo-group
Tisza	Hódmezővásárhely -Kökénydomb, Vörös tanya	KÖKE02	16069T 16126C	16019-16401	J				J
		KÖKE03	16093C 16224C 16311C 16319A	15999-16409	K				K
	Pusztataskony Ledence, 2.lh.	PULE2.1	16126C 16294T 16296T 16304C	16047-16401	T				T2b
		PULE2.3	16298C	15999-16405	HV				HV0
Tiszapolgár	Pusztataskony-Ledence, 1.lh.	PULE1.8	16221T 16284G 16291T	15997-16409	HV				HV4a1
		PULE1.10	16126C 16292T 16294T 16296T	15997-16404	T				T2c1
Unclear[13]	Mezőkeresztes-Cethalom	MECE11	16069T 16126C 16193T 16274A 16278T	15998-16400	J				J
TOTAL	**245**	**HVS-I**	**239**						

Primer systems

The success rates for the different HVS-I primer systems ranged between 40% and 82% (Figure 13). Among the HVS-I sequence primer systems, the mean amplification success was lowest for the long-fragment primer system (52.7%). In the medium-length system, the average amplification success was 69.7%, closely followed by the short fragment-system with 67.5%.

The two primers of the long-fragment system showed nearly equal efficacy. In the medium-length system, fragment I (np 15997-16142) was the least effective. fragment II (np 16117-16233) showed the highest success rate, followed by fragment IV (np 16287-16419) and III (np 16209-16348).

In the short-fragment system, fragments 1 and 2 (np 16018-16097, np 16072-16144) yielded the highest amplification success -in the case of fragment 2, even the highest success among all HVS-I primer pairs. Fragments 3 through 5 were equally effective at 64%, while fragment 6 showed the lowest success rate with 52%.

The SNP multiplex systems had amplification success rates between 88% (U-Plex)-and 93% (GenoCore22), and were thus more effective than the HVS-I primer systems. The multiplexes for the subhaplogroups of H, U and T1 each had close to a 100% success rate – however, it has to be noted that they were only performed on samples where a HVS-I sequence and/or a GeneCoRe22 SNP profile had already been successfully obtained.

[13] This individual was sampled alongside the Neolithic individuals from the Mezőkeresztes-Cethalom site, but was not found in the archaeological documentation. Since it is unclear whether this individual actually belongs to the Neolithic series from this site, it was left out in further analyses

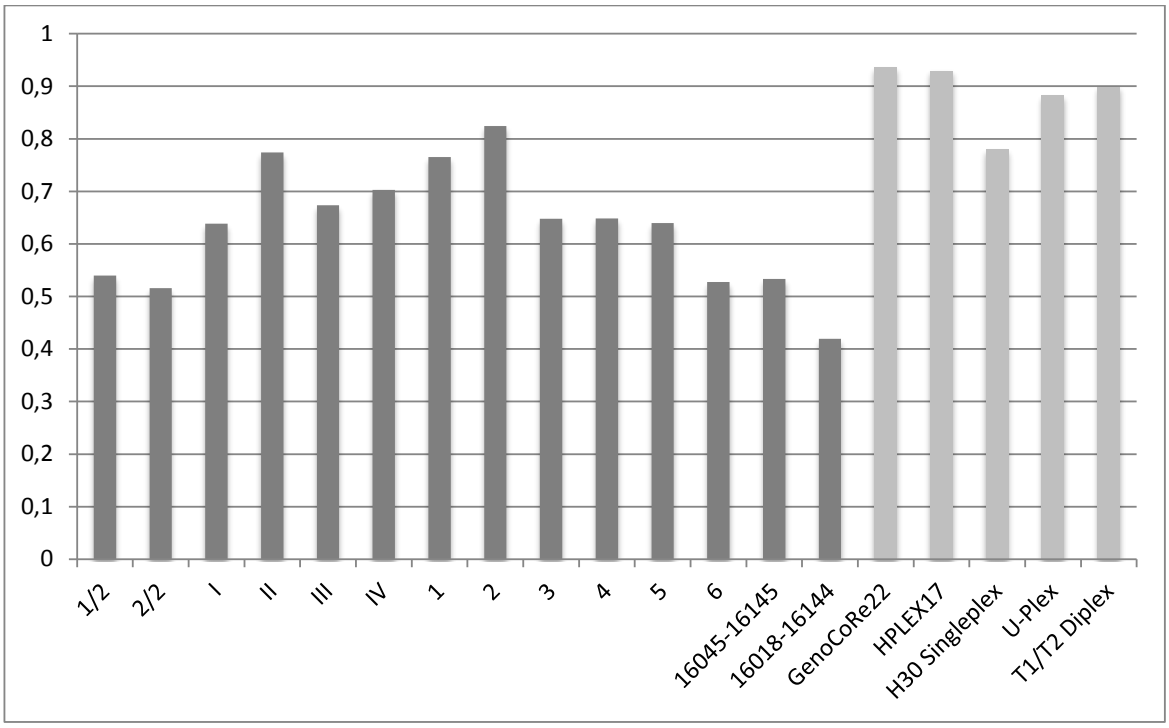

Figure 13: Amplification success rates of the different primer systems.

3.1.2 Contamination rates

Controls

Of a total of 2155 controls (1796 PCR blanks, 189 milling blanks and 170 extraction blanks), 3.9% were contaminated (Figure 14).

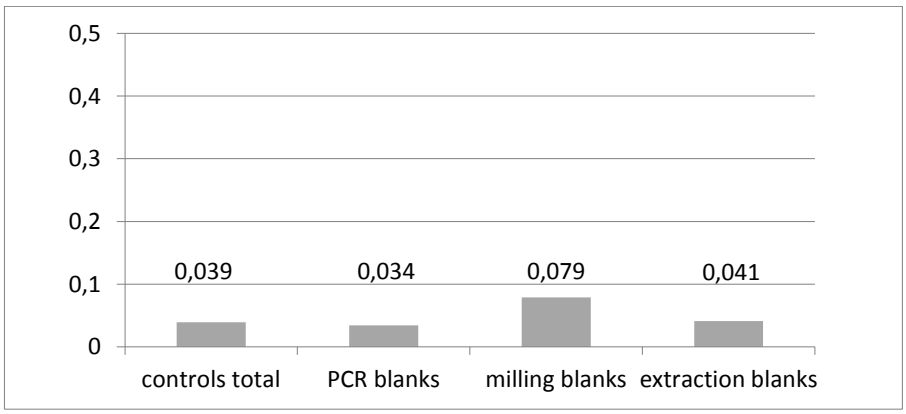

Figure 14: Contamination rates by control type.

The highest contamination rate was observed in the milling blanks, where a total of 15 out of 189 blanks showed contaminations. However, only one of these could be reproduced in a second, independent PCR. The contamination rate of the extraction blanks lay at 4.1%. None of the contaminations in the extraction blanks could be reproduced in a second, independent PCR.

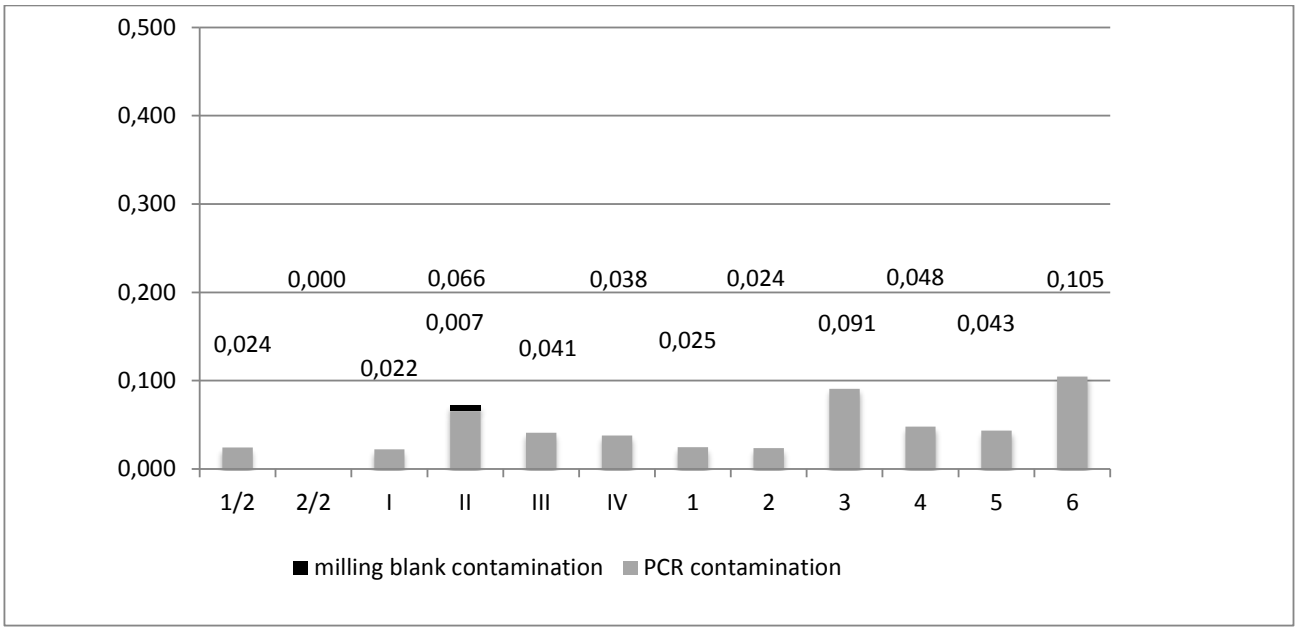

Figure 15: Contamination rates of controls by primer system. The SNP multiplex systems, the fragments amplified with the HVS-II primers and those amplified with the HVS-I primers for np 16045-16145 and 16018-16144 showed no contamination and are not shown. The depicted rates are given as proportions of the total number of controls and are differentiaded by source (PCR contamination, milling contamination and extraction blank contamination). Thus, the contamination rates in fragment II include the contamination in PCR blanks (0.066) and the one confirmed case of milling blank contamination (0.007). Since all contaminations in extraction blanks were proven to be PCR contaminations, they are not depicted.

The highest contamination rates were observed in controls of fragment II of the medium-length system and the fragments 3 and 6 of the short-fragment system, with the latter approaching 10.5%. The controls of the multiplexes and singleplexes showed no contamination.

One milling blank (Extraction No. VD10) out of a total of 44 showed a reproducible contamination in fragment II of the medium-length system (np 16117-16233). The fragment amplified from the milling blank carried the mutation 16126C. This mutation is part of the HVS-I motifs of haplogroups J and T, which were common in the dataset. The other samples in the VD extraction showed no signs of contamination matching that found in the milling blank (Table 22). The HVS-I of MAP05 could not be fully reproduced, therefore the “true” haplotype could not be established. However, none of the fragments amplified from MAP05 exhibited the 16126C-mutation. Five further samples of extraction VD carried 16126C as part of their fully reproduced haplotype.

Table 22: Samples from extraction VD, which contained the contaminated milling blank VD10. The "haplotype" column contains the reproduced (in A and B-sample) haplotype of the individuals. Where 16126C is part of the reproduced haplotype, it is marked in bold. The column "16126C present as contamination" shows whether the sample showed contamination with 16126C. The "-" indicates the cases where a contamination with 16126C in fragment II would not have been detected because it matched the consensus haplotype of the sample.

Extraction No.	Sample	Haplotype HVS-I [np 16045-16400]	16126C present as contamination
VD1	VSM08 B	16311C	no
VD2	VSM09 B	**16126C** 16153A 16294T 16296T	no
VD3	VSM10 B	**16126C** 16294T 16304C	-
VD4	MAP01 B	16093C **16126C** 16294T 16296T 16304C	-
VD5	MAP02 B	16093C **16126C** 16294T 16296T 16304C	-
VD6	MAP03 B	**16126C** 16189C 16294T 16296T	no
VD7	*MAP05 B*	*n.d.*	*[no]*
VD8	DES05 B	16304C	no
VD9	DES06 C	16298C	no
VD11	Extraction blank	No positive PCR results	no

None of the contaminations occurring in the several extraction blanks could be reproduced in a second PCR. This indicates contamination during the PCR itself as the most likely cause.

Table 23: Mitochondrial haplotypes (HVS-I) of researchers who came in contact with the samples during sampling and processing.

ID	HVS-I [16045-16400]	Haplogroup
1	16209C 16311C	H
2	CRS	H
	16145A 16176G 16223T 16244A	N1b
3	16390A	
	16126C 16163G 16186T 16189C	
4	16294T	T1
	16126C 16163G 16186T 16189C	
4	16264T T16294T	T1
5	16223T 16257T 16292T	W
6	16260T 16327T	n.d.
7	16319A	H
8	16240G 16298C	V
9	16051G 16126C 16129C 16182C	U2e
	16183C 16189C 16362C	
10	16080G 16189C 16356C	H
11	16126C 16294T 16304C	T2b
12	16265G	H
	16129A 16189C 16223T 16249C	M1a1
13	16311C 16359C	
14	CRS	H
15	16256T 16270T 16399G	U5a1a
16	16126C 16294T 16296T 16362C	T
17	16304C	H5
	16223T 16234T 16288C 16298C	
18	16327T 16359C	C5
19	16051G 16162G 16304C	H

Individuals

About one third (36.4%) of all individuals with a reproduced HVS-I sequence showed some signs of contamination in the HVS-I, either in the direct sequencing results or the clones.

Of a total of 3270 PCR products obtained from these 239 individuals, 143 (4.4%) were found to contain lineages that deviated from the consensus haplotype. Of these, 6 sequences (4.2%) could be deaminated endogenous sequences. Further 33 sequences (23.1%) contained parts of the consensus haplotype combined with unusual mutation patterns and made no phylogenetic sense, which is typical for a jumping-PCR event. In 14 of the non-consensus PCR products (9.8%), identical non-endogenous lineages were found in other- independent- PCRs from the same extract (see Table 25).

Contaminations from five of the contaminated PCR products (3.5%) were found to partially match the contaminated blanks from the same PCR (Table 24).

Table 24: Contamination in individuals matching contamination from blanks.

Contaminated PCR (fragment)	Sample	Haplotype of contaminated PCR	Contaminated blank	Haplotype of contaminated blank
VK59.7 (4)	HMG07 B	CRS	VK59.10	CRS
VK128.5 (4)	TISO04 A	16209C	VK128.17	16209C 16239T
VK292.17 (II)	MEMO15 B	16224C	VK292.20 (ExLK)[14]	16126C 16224C
VK333.7 (4)	MEKÖ07 B	CRS	VK333.22	CRS
VK466.2 (IV)	HMG01 B	16298C	VK466.23	16298C

Not all of the contaminating lineages could be assigned to a mitochondrial haplogroup, due to the short fragment length and the multiple occcurrence of certain mitochondrial mutations across different clades, e.g. 16311C. One lineage, which appeared repeatedly in five individuals from four different sites, is notable for its unusual motif: *16129A 16189a 16218T 16230G* (see Table 26). Only fragment II of the medium-length system was affected. The lineage only appeared in the form of ambiguous positions in the direct sequences of the affected PCR products, becoming “fully visible” only in clonal sequences. The lineage could not be conclusively identified, but exhibits the highest similarity to mitochondrial haplogroup L0f, which has a sub-Saharan origin. This lineage did not appear in any of the negative controls and does not match the haplotypes of the known researchers/ field workers associated with these samples.

[14] The contamination was not reproduced in a second PCR, therefore it was regarded as a PCR contamination in the contamination statistics.

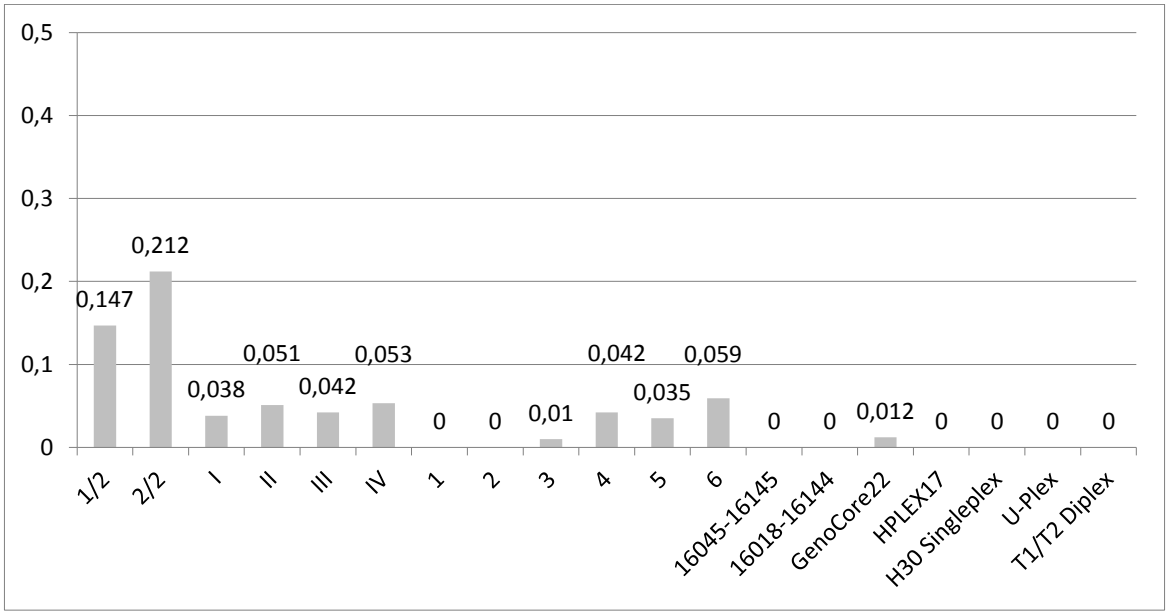

Figure 16: Contamination rates of individuals by fragments. No contamination was noted in the HVS-II sequences of the fewindividuals that were typed for HVS-II.

When the contaminations in individuals were divided by primer system, the contamination rates in the HVS-I sequence primer systems averaged 17.95% in the long-fragment system, 4.6% in the medium-length system and 2.4% in the short-fragment system. The long-fragment system therefore was considerably more prone to contamination than the other two systems, with fragment 2/2 showing a higher contamination rate than fragment 1/2 (see also Figure 16). Contamination rates in the medium-length system ranged between 3.8% and 5.3%, with fragments II and IV showing slightly elevated contamination rates. In the short-fragment system, the differences between fragments were more pronounced: fragments 1 and 2 showed no contamination, whereas fragments 4 and 6 showed comparatively high rates between 4% and 6%.

In the multiplex primer systems, contaminations in individuals only occurred in the GenoCoRe22 system. Here, 7 individuals out of 245 showed contaminations (2.86%), equating to 8 of 649 amplifications (1.23%).

Table 25: Contaminating lineages in DNA extracts.

Extraction	Sample	Haplotype of contamination	Sequence limits	Affected PCRs	Haplogroup
VC9	DES06 B	16311C	16209-16409	VK12.9, VK87.3	undeterminable
VE5	BEP05 A	16140C 16183C 16189C 16217C	15997-16233	VK21.1, VK22.5	B4 or B5
VF12	HMG04 B	CRS (16126C)[15]	16209-16348	VK26.12, VK33.12, VK447.4	undeterminable

[15] The 16126C SNP was found in one PCR of fragment I (15997-16144). Because there is no overlap between fragment I and III (16209-16348) and therefore no shared polymorphisms, it cannot be determined whether the contaminations are all due to the same lineage.

VH11	TITE02 B	16294T 16296T 16298C	16209-16348	VK386.1, VK419.2,	T2f
VJ2	VSM06 A2	16126C	15997-16144	VK64.2, VK494.1	T
VU9	CEG02 A	16266T 16304C	16209-16409	VK163.4, VK307.7, VK514.4	R5

Table 26: The L0f- lineage sporadically occurring in fragment II. Bold positions indicate a position that is part of the consensus haplotype, question marks indicate positions unknown to Phylotree build 15 and brackets indicate possible C-T transitions/ deaminations. Transversions are written in lower case letters.

Sample	Extraction	PCR	Fragment	Haplotype HVS-I (np 16117-16233)
BEP04 A	VE4	VK22.1	II	16129A 16189a 16218T 16230G
		VK22.1	II	**16126C** (16155G?) 16189a 16218T 16230G
TITE01 A	VG13	VK40.13	II	16129A 16189a 16218T 16230G
		VK40.13	II	16189A 16218T (16220G) 16230G
TISO03 A	VO14	VK105.14	II	16218T 16230G
		VK105.14	II	16189a 16218T 16230G
ABO12 B	WB18	VK219.18	II	16129A 16189a 16218T 16230G
ABO13 A	WC1	VK223.1	II	16129A 16189a 16218T 16230G
		VK223.1	II	16129A (16147T 16150T) 16189a (16192T) 16218T 16230G

3.2 General Diversity indices

The *Körös* sample set contained only 16 individuals; therefore the spectrum of observed haplogroups is predictably small. The predominance of K (37.5%) is mainly caused by the results from Törökszentmiklós-Tiszapüspöki (TÖSM), where five of seven individuals belonged to this haplogroup. The second-most frequent haplogroup is T2, followed by H including one instance of H1. X, V and J are represented by one individual each.

The *ALBK early* set contains 35 individuals belonging to the earliest ALBK/ Szatmár group. As in the Körös sample, haplogroups K, T2 and H (including subclades H5 and H7, but not H1) are the most frequent. The haplgroup N1a (8.57%) and several subclades of U appear in this dataset for the first time. The combined U-clades, namely U4, U5a, U5b and U8, constituted 17.14% of all haplogroups in this sample set. Notably, the U-clades in the *ALBK early* set were all found in individuals from the Mezőkövesd-Mocsolyás (MEMO) site. Further haplogroups in this sample are X, HV, V, J and R1, the latter being rare in the entire Alföld dataset.

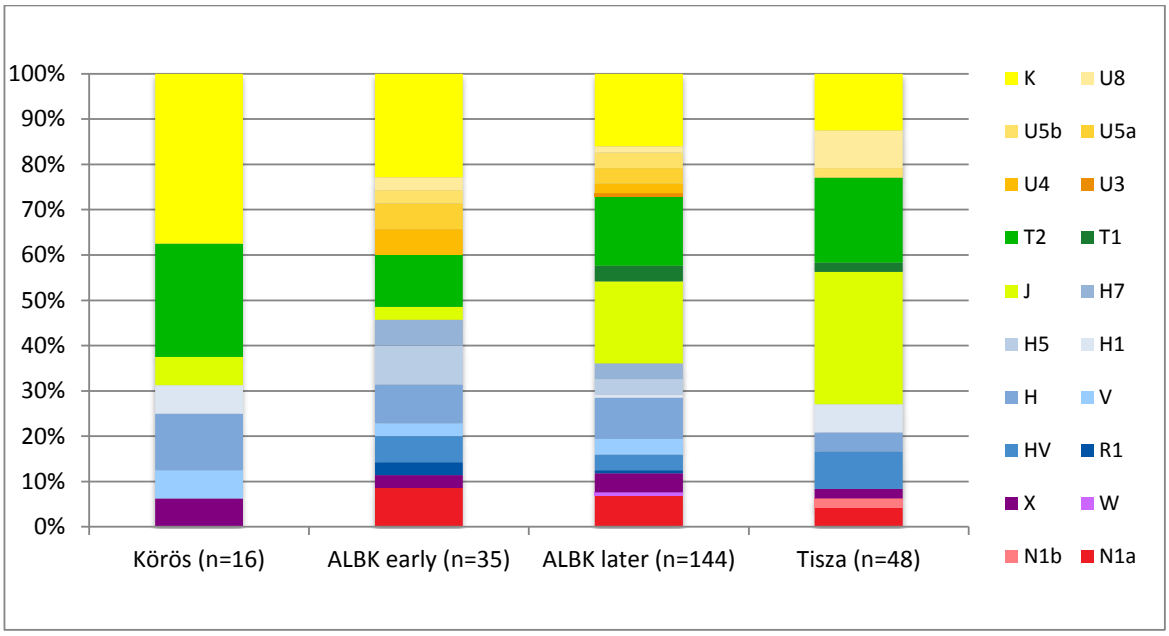

Figure 17: Haplogroup composition of the early, middle and late Alföld Neolithic.

With 144 individuals, the *ALBK later* set was the largest group studied. It contained individuals from the Szakálhát, Esztár and Tiszadob/Bükk groups as well as individuals from the classical and late phase of the ALBK who could not be assigned to a specific subgroup. As in the *Körös* and *ALBK early* datasets, haplgroups K, T2 and H (incl. H1, H5 and H7) play dominant roles at about 15% each. Haplgroup J is more frequent in this dataset (18%) than in the preceding groups. The proportion of U clades is smaller than in the ALBK early set, but still amounts to 11%. Besides U4, U5a, U5b and U8, the *ALBK later* set contains one individual belonging to U3, the only observed occurrence of this haplogroup in the Alföld Neolithic. A number of haplogroups are present at frequencies lower than 10%, such as N1a, R1, X, W, T1, HV and V.

The *Tisza* culture dataset is dominated by K, T2 and J. Compared to the *ALBK later* set, the frequency of J has increased even further to 29.1%. Except for one instance of U5b, the U clade is represented exclusively by U8. The high frequency of U8 is partly due to three individuals from the site of Vésztö, for whom maternal kinship cannot be excluded. A substantial portion of the haplogroups belongs to the HV- branch, which could already be observed in the early and later ALBK datasets. A previously undetected haplogroup was N1b, which was found in one individual from Vésztő -Mágor (VSM).

Regional groups

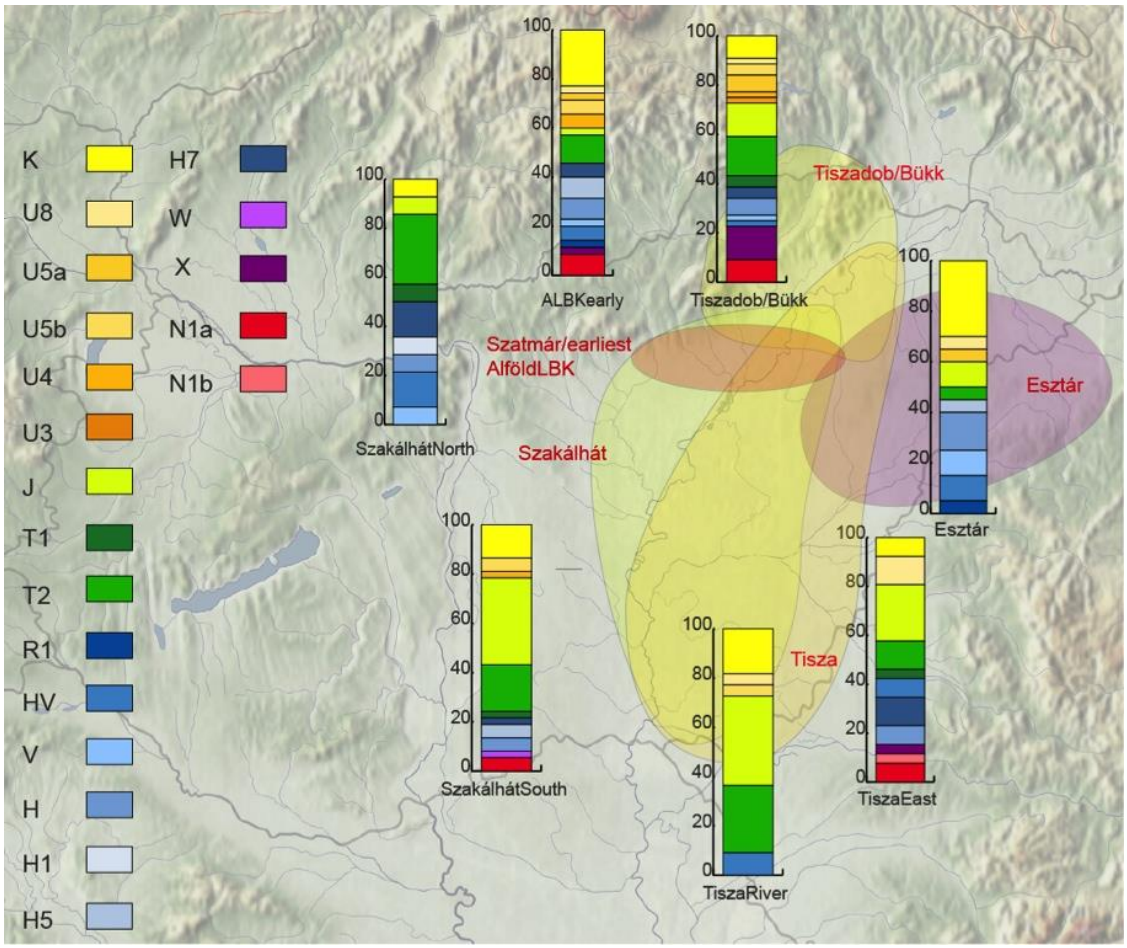

Figure 18: Haplogroup compositions of the middle and late Neolithic regional groups on the Alföld mapped according to their distribution areas.

Haplogroups K, T2 and J are present in all regional groups. Furthermore, all groups contain one or more subgroups of the R0 branch, i.e. HV, V and H (incl. H1, H5 and H7). Other common haplogroups are U8, U5b, T1 and N1a. The southerly groups (Szakálhát South, Tisza River and Tisza East) have higher frequencies of J than the more northerly groups (Szakálhát North, Tiszadob/Bükk, earliest ALBK and Esztár). Subclades of U, on the other hand, are more frequent in the northeastern groups (ALBK early, Tiszadob/Bükk, Esztár). Other than that, there is little regional patterning observable. The haplotype diversity ranges between 0.908 in the *Körös* set and 0.985 in the *ALBK early* set (

Table 27). Among the regional subgroups, haplotype diversity is highest in the Tiszadob/Bükk and Esztár groups of the ALBK and lowest for the river group of the Tisza culture. Haplogroup diversity is lower than the haplotype diversity in all instances, reflecting the fact that at the haplogroup resolution used for the analyses, a haplogroup could be represented by different haplotypes.

Table 27: Haplogroup and haplotype diversity of the Alföld Neolithic Cultures and their subgroups.

	Haplotype diversity	Haplogroup diversity
Körös	0.908	0.817
ALBK early	0.985	0.921
ALBK later	0.974	0.901
Szakálhát	0.965	0.865
North	0.978	0.912
South	0.949	0.83
Tiszadob/Bükk	0.979	0.924
Esztár	0.976	0.889
Tisza	0.929	0.859
River	0.853	0.784
East	0.967	0.914

3.3 Fisher's exact test

3.3.1 Alföld

Table 28: Fisher Test values of the Alföld Cultures. HGC: hunter-gatherers Central Europe. Grey fields indicate statistically significant values ($p < 0.05$)

	HGC	Körös	ALBK early	ALBK later	Szakálhát	*North*	*South*	Tiszadob/ Bükk	Esztár	**Tisza**	*River*	*East*
HGC	*	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$
Körös	$9.99*10^{-5}$	*	0.7516	0.7031	0.2771	0.446	0.07199	0.404	0.6217	0.1287	0.0438	0.154
ALBK early	$9.99*10^{-5}$	0.7516	*	0.5022	0.0412	0.3748	0.0269	0.3781	0.8993	0.0041	0.0236	0.05449
ALBK later	$9.99*10^{-5}$	0.7031	0.5022	*	*	*	*	*	*	0.09879	0.6242	0.1022
Szakálhát	$9.99*10^{-5}$	0.2771	0.0412	*	*	*	*	0.1799	0.0448	0.2941	0.7806	0.1418
North	$9.99*10^{-5}$	0.446	0.3748	*	*	*	0.0494	0.4222	0.2436	0.07309	0.048	0.3194
South	$9.99*10^{-5}$	0.07199	0.0269	*	*	0.0494	*	0.1597	0.0136	0.2624	0.6694	0.09129
Tiszadob/ Bükk	$9.99*10^{-5}$	0.404	0.3781	*	0.1799	0.4222	0.1597	*	0.07959	0.05079	0.1476	0.3088
Esztár	$9.99*10^{-5}$	0.6217	0.8993	*	0.0448	0.2436	0.0136	0.07959	*	0.0261	0.0327	0.1501
Tisza	$9.99*10^{-5}$	0.1287	0.0041	0.09879	0.2941	0.07309	0.2624	0.05079	0.0261	*	*	*
River	$9.99*10^{-5}$	0.0438	0.0236	0.6242	0.7806	0.048	0.6694	0.1476	0.0327	*	*	0.2678
East	$9.99*10^{-5}$	0.154	0.05449	0.1022	0.1418	0.3194	0.09129	0.3088	0.1501	*	0.2678	*

All Alföld Neolithic cultures and their regional subgroups differ significantly in their haplogroup composition from the Central European hunter-gatherer group. The differences among the Alföld cultures and their regional groups, on the other hand, reach statistical significance (p-value < 0.05) much less frequently. With p-values above 0.5, the *Körös* culture, the *ALBK early* and the *ALBK later* sets are highly similar to each other. The haplogroup composition of the *Tisza* culture deviates somewhat from that of the early and middle Neolithic groups, as indicated by low p-values, but the differences are rarely statistically significant.

At the level of the regional groups, some pairings are significantly different in their haplogroup composition: “ALBK early – Szakálhát (South)”, “ALBK early- Tisza River”, “Esztár- Szakálhát (South)”, “Esztár-Tisza (River)” and “Tisza River- Szakálhát North”.

3.3.2 Carpathian Basin

Table 29: Fisher test results of the comparison between Alföld and Transdanubian Neolithic.

	Starčevo	TLBK	Vinča	Sopot	Lengyel
Körös	0.9704	0.7011	0.284	0.3525	0.3238
ALBK early	0.2148	0.3033	0.1732	0.7296	0.3868
ALBK later	0.3661	0.5113	0.05609	0.5469	0.0464
Szakálhát	0.1197	0.3146	0.005999	0.1174	0.007099
North	0.3368	0.6529	0.0244	0.4318	0.118
South	0.08949	0.06019	0.018	0.07539	0.008099
Tiszadob/Bükk	0.3326	0.034	0.1724	0.4211	0.0101
Esztár	0.2085	0.2075	0.06999	0.403	0.08409
Tisza	0.0293	0.0114	0.0117	0.3392	0.05079
River	0.1591	0.007599	0.1168	0.05739	0.0284
East	0.05709	0.07529	0.0177	0.8484	0.2209

With p-values of 0.97 and 0.7 respectively, the haplogroup composition of the *Körös* culture is extremely similar to that of the Starčevo culture and Transdanubian LBK. The values decline towards the late Transdanubian Neolithic represented by the Sopot and Lengyel cultures, but remain statistically non-significant. The *ALBK early* set is significantly different to none of the Transdanubian cultures, while the *ALBK later* set only shows differences to the late Neolithic Lengyel culture. The *Tisza* culture differs significantly from the early and middle Neolithic of Transdanubia, but not the late Neolithic Lengyel and Sopot cultures. The eastern and river groups of the Tisza culture behave differently in the pairwise comparisons: the river group differs significantly from the TLBK and Sopot cultures, whereas the eastern group only shows differences to the Vinča culture.

None of the Alföld regional groups show significant differences in haplogroup composition to the Starčevo culture. Most statistically significant differences are observed in pairings of the Alföld Neolithic regional groups and the Vinča and Lengyel cultures.

3.3.3 Europe

Table 30: Fisher Test values of the Alföld Cultures in comparison to European (pre-) Neolithic cultures.

	HGE	HGS	HGC	LBK	RSC	CPE	CARcat	NSE	NUK
Körös	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$	0.6412	0.4773	0.0118	0.7393	0.0007999	0.0131
ALBK early	$9.99*10^{-5}$	0.0026	$9.99*10^{-5}$	0.06749	0.8103	0.2103	0.6314	0.007699	0.1024
ALBK later	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$	0.1317	0.1589	0.0191	0.1095	$9.99*10^{-5}$	0.0019
Tisza	$9.99*10^{-5}$	$9.99*10^{-5}$	$9.99*10^{-5}$	0.005499	0.0325	0.0006999	0.0268	$9.99*10^{-5}$	0.0008999

The low p-values show that the haplogroup composition of the Alföld Neolithic cultures differs significantly from the three European hunter-gatherer populations and the early Neolithic of northern Spain. The *Körös* culture and *ALBK later* sets also differ from the early Neolithic of Central Portugal and Neolithic Ukraine, while the *ALBK early* does not. The *Tisza* culture shows significant differences in haplogroup composition from all studied Euroepan cultural groups. The p-values of the pairings of the early and middle Neolithic Alföld cultures with the Central European LBK and Rössen cultures are quite high, indicating high similarities.

3.4 PCA and cluster analysis

3.4.1 Alföld

The first component of the PCA represents nearly 42% of the total variance observed in the dataset, and it clearly separates the Alföld Neolithic cultures from the Central European hunter-gatherer-metapopulation, which is characterised by its high frequencies of U-subclades (Figure 19). About 24% of the variance separates the Alföld Cultures from each other, with the early ALBK and Tisza culture occupying the outermost positions. The cluster analysis confirms the deep split between the hunter-gatherers and the Alföld cultures. It groups the early and later ALBK close together, which is also reflected in the PCA. However, cluster analysis and PCA differ in the placement of the Körös culture. In the PCA, it is closest to the later ALBK, whereas in the cluster analysis it occupies a different branch than the other three Alföld groups.

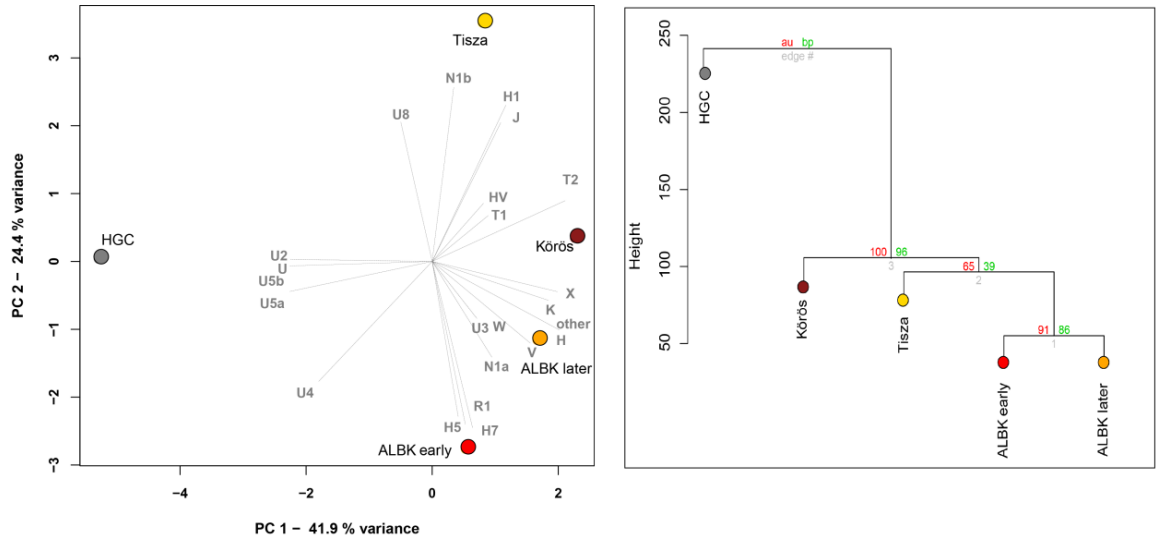

Figure 19: PCA and cluster analysis of the Alföld Neolithic cultures. The red and green numbers on the branches in the cluster dendrogram show the approximately unbiased (au) and bootstrap probability (bp) values, respectively.

Regional

When the Alföld LBK is split into regional groups, the separation of preneolithic and Neolithic groups along the first component remains Figure 20). As in fig. 19, the Alföld Neolithic groups separate along the second component: In the upper right quadrant, the Körös, earliest ALBK and the Esztár groups are loosely associated (defined by R1, V, K, H5 and HV). In the lower right quadrant the Tiszadob/Bükk group and the eastern Tisza group are characterised by T1, H1, N1b and U3. The two Szakálhát groups and the river group of the Tisza region occupy intermediate positions along the second component. The cluster analysis only reflects the close proximity of the southern Szakálhát group and the river group of the Tisza culture, while the other clusters differ from the affinities displayed in the PCA: The Körös and Esztár groups appear much closer to each other in the cluster analysis, as do the earliest ALBK and the Tiszadob/Bükk group. The positioning of the northern Szakálhát and eastern Tisza group in the dendrogram is also not apparent from the PCA.

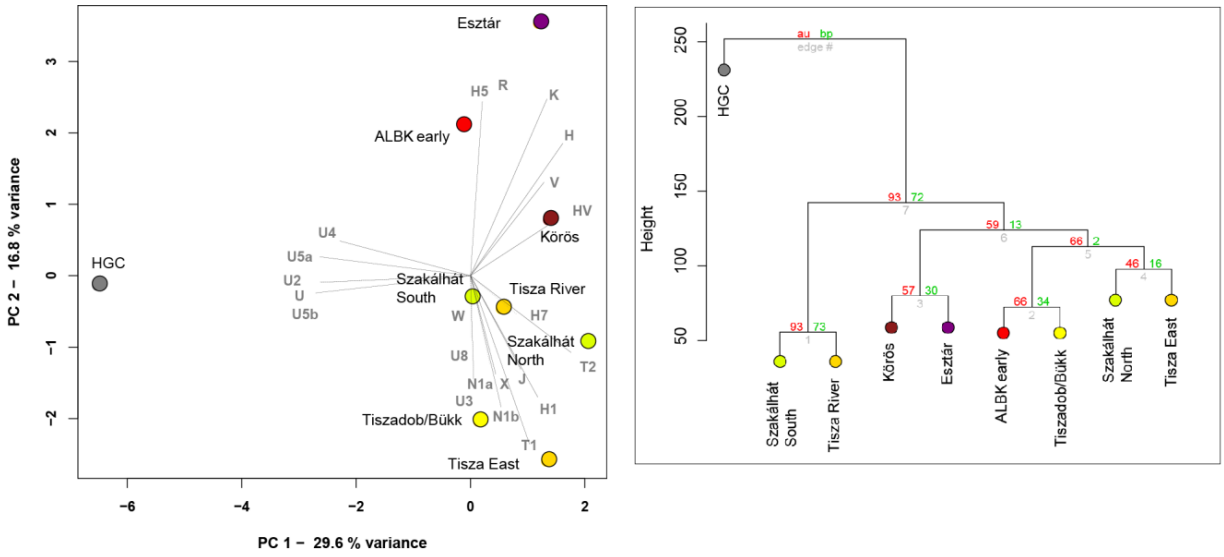

Figure 20: PCA and cluster analysis of the Alföld Neolithic Cultures (regional subgroups).

3.4.2 Carpathian Basin

The first component represents 37% of the variance within the dataset and separates the Neolithic from the Central European hunter-gatherer metapopulation (Figure 21). The second component represents a lower proportion of the total variance (19.7%) and shows a split between early, middle and late Neolithic cultures of the Carpathian Basin. The vectors defining the early Neolithic cultures are X, K, W and V. The middle Neolithic is associated with the vectors of R, T1 and U2, whereas the late Neolithic is characterized by J, HV and U8.The cluster analysis also shows a clear separation between hunter-gatherers and the Neolithic cultures. The early Neolithic cultures are clustered together, as are the ALBK and the Transdanubian LBK. The positioning of the Vinča and Tisza cultures differs between PCA and cluster analysis: Vinča clusters with the early Neolithic cultures rather than with the other middle Neolithic cultures, while the Tisza culture forms a separate branch apart from the other late (and middle) Neolithic groups.

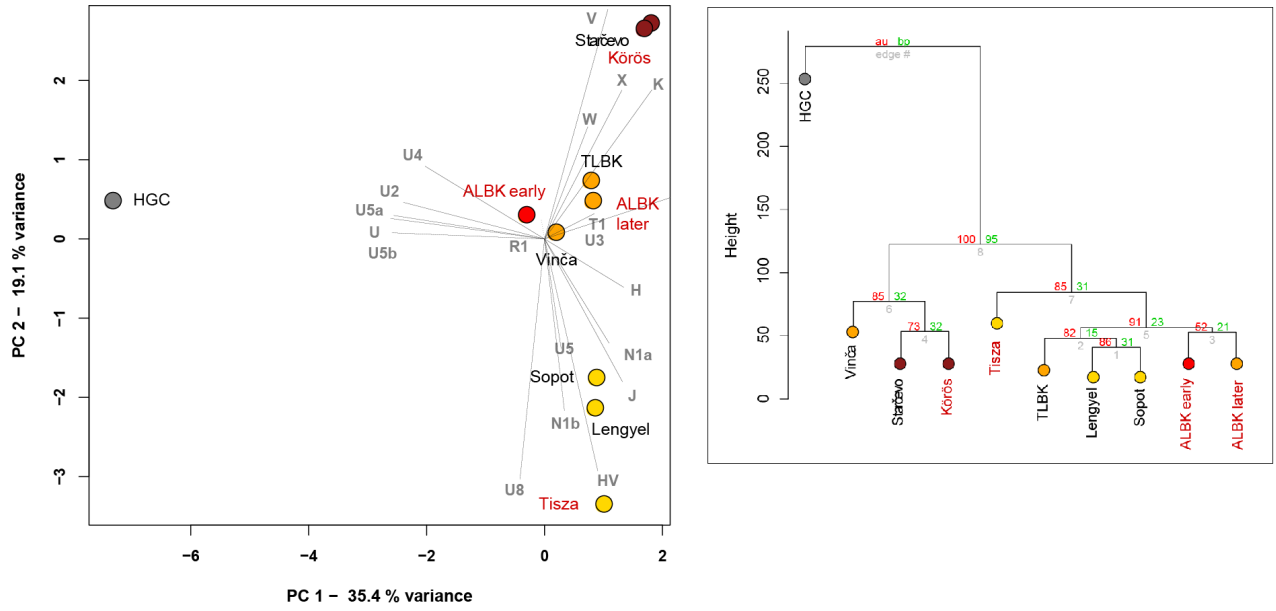

Figure 21: PCA and cluster analysis of the Carpathian Basin Neolithic.

Regional

When splitting the Alföld LBK and Tisza culture into subgroups, the biggest percentage (29.3%) of the variance is contained within the preneolithic/Neolithic split, whereas approximately half that percentage is observed among the Neolithic cultures (Figure 22). Compared to Figure 21, the separation between early, middle and late Neolithic culture becomes less defined. The early Neolithic Körös and Starčevo cultures lie close to the Vinča culture in the lower left quadrant of the plot, a configuration that is also visible in the cluster dendrogram. Lengyel, Sopot and the river group of the Tisza region lie closest to the Esztár group and the early ALBK. The Szakálhát groups, the Tiszadob/Bükk group and the Transdanubian LBK are loosely associated with each other in the lower left quadrant of the PCA plot. Cluster analysis assigns these groups to different positions in the dendrogram: The Tiszadob/Bükk group and the eastern Tisza group are clustered together, as are the southern Szakálhát group and the river group of the Tisza culture- both arrangements are not visible in the PCA plot. Sopot and Lengyel are as close to each other in the dendrogram as in the PCA plot, but unlike in the PCA plot, their nearest neighbours in the dendrogram are the TLBK and the early ALBK.

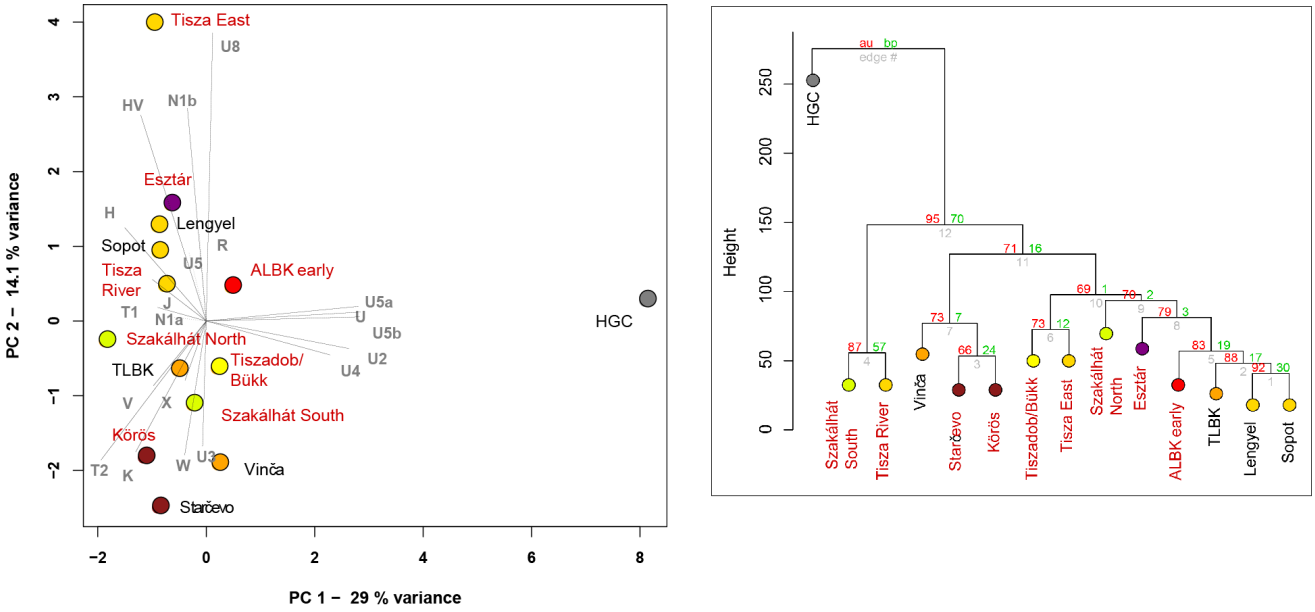

Figure 22: PCA and cluster analysis of the Carpathian Basin Neolithic with Alföld middle and late Neolithic split into regionl subgroups.

3.4.3 Europe

The first component represents 24.6% of the variance and sets the hunter-gatherers and the Iberian Neolithic apart from the Carpathian Basin and Central European Neolithic. The second component (13.5% of the variance) separates the hunter-gatherers from the Iberian Neolithic. The Central European and Carpathian Basin cultures form a rather uniform group, with the Tisza, Starčevo, Körös and Rössen cultures at the periphery. The latter two appear to have a higher affinitiy with the Cardial culture of Catalonia than with the Carpathian Basin groups. The cluster analysis shows two main branches: one contains all Central European and Carpathian Basin Neolithic cultures, the other branch is split into two sub- branches: one contains the Neolithic cultures of northern Spain and Portugal and the southwestern European hunter-gatherers, while the second branch contains the Central and Eastern European hunter-gatherers and the Ukrainian Neolithic group. The proximity of the Catalonian Cardial population to the Carpathian Basin and Central European Neolithic is also apparent in the cluster analysis.

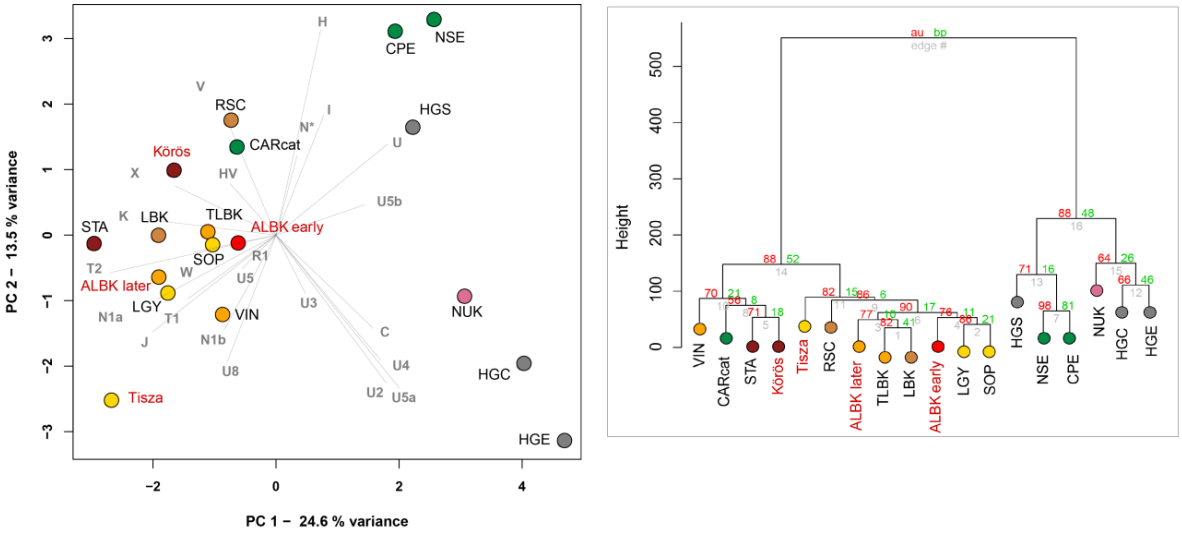

Figure 23: PCA and Cluster analysis of the European Neolithic cultures. STA=Starčevo, TLBK= Transdanubian LBK, VIN= Vinča LGY= Lengyel, SOP= Sopot, LBK= Central European LBK, RSC= Rössen Culture, CPE= Central Portugal early Neolithic, NSE= Northern Spain early Neolithic CARcat= Catalonian Cardial, NUK= Neolithic Ukraine, HGC= Central European hunter-gatherers, HGS= Southwestern European hunter-gatherers, HGE = Eastern European hunter-gatherers.

Subhaplogroups of H in the European context

When a pan-European PCA is performed using only the individuals belonging to haplogroup H, the groups from southwestern Europe fall close together (Figure 24). They are characterised by high frequencies of H1 and the presence of H3, which is totally absent in the Alföld Neolithic and rare in the Central European cultures. The early and middle Neolithic groups of the Alföld Neolithic are very close to each other, with H5 as a defining subclade. The late Neolithic Tisza culture with its high proportion of H1, on the other hand, is closer to the southwestern European groups than to its Alföld predecessors. The middle and late Neolithic Cultures of Central Europe occupy an intermediate position between the Alföld groups and those of southwestern Europe, while the early Neolithic Central European group lies isolated in the lower right quadrant and is closest to the Hungarian early and middle Neolithic than to the other Central European cultures. The Unetice Culture in the lower left quadrant is closest to the Alföld early and middle Neolithic, but still occupies a somewhat distant position characterised by H2 and H11. The cluster analysis confirms the close proximity of early and middle Neolithc Alföld groups and the affinity of the late Neolithic Alföld to southwestern Europe. It differs from the PCA in its sorting of the Central European cultures: the Bronze Age Unetice Culture is grouped together with the middle Neolithic of Central Europe, while the early and late Neolithic of Central Europe form their own cluster.

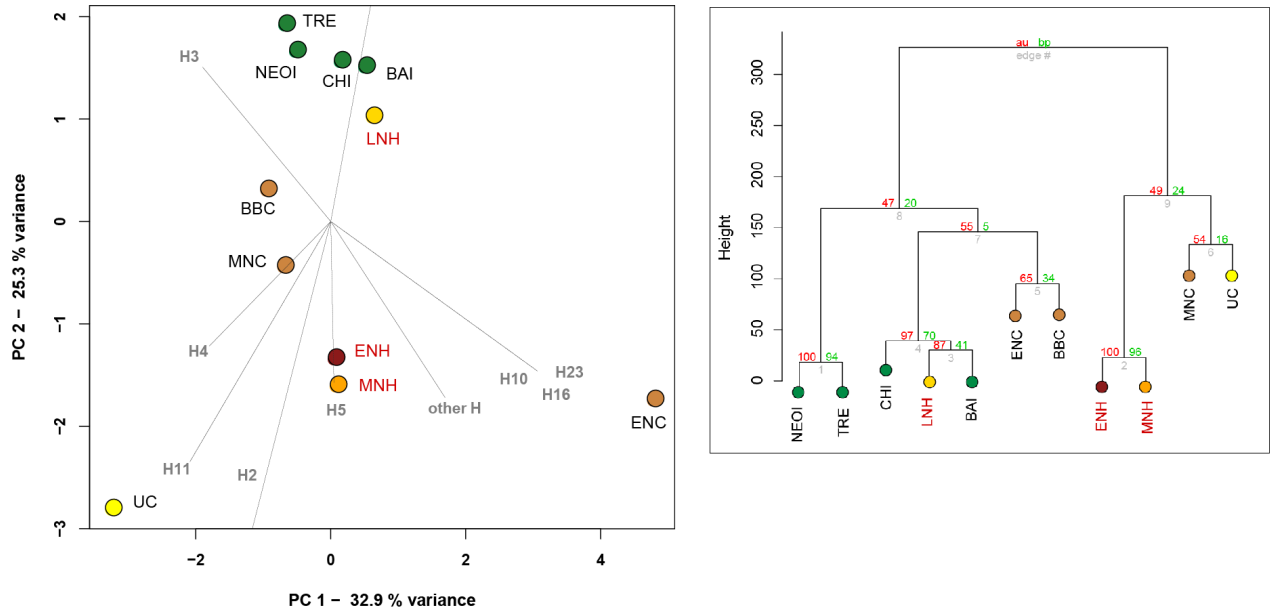

Figure 24: PCA of the European prehistoric populations (Neolithic to Bronze Age) where H could be resolved into subclades. TRE= Treilles Culture, BAI= Bronze Age Iberia, CHI= Chalcolithic Iberia, NEOI= Neolithic Iberia, ENH= early Neolithic Hungary, MNH= Middle Neolithic Hungary, LNH= Late Neolithic Hungary, ENC= Early Neolithic Central Europe, MNC= Middle Neolithic Central Europe, BBC= Late Neolithic Central Europe (Bell Beaker Culture), UC= Bronze Age Central Europe (Unetice Culture).

3.5 Test of Population Continuity

The Alföld Neolithic cultures and their subgroups were tested against the Central European hunter-gatherer population. Furthermore, the four main chronological groups (*Körös, ALBK early, ALBK later* and *Tisza*) were tested against each other. The regional groups of the Alföld were not tested against each other, because only few of the subgroups showed significant differences in haplogroup composition in Fisher's exact test, thus not warranting a further test for possible population continuity. Furthermore, in the case of those pairings that did show significant differences, e.g. "Esztár-Tisza River", it did not make much sense to simulate population continuity without taking into account that these populations were surrounded by contemporaneous groups which could have influenced either one. More succinctly: in the described case, a TPC would only make sense if there was reason to assume that the river group of the Tisza culture developed directly from the Esztár group of the ALBK.

Table 31: TPC of the Alföld Neolithic Cultures and the Central European hunter-gatherer metapopulation.

	HGC	**Körös**	**ALBK early**	**ALBK later**	**Tisza**
HGC	*	$7.791989*10^{-7}$	$7.791989*10^{-7}$	$7.791989*10^{-7}$	$7.791989*10^{-7}$
Körös	$7.791989*10^{-7}$	*	0.1580082	0.1717959	0.1806243
ALBK early	$7.791989*10^{-7}$	0.1580082	*	0.9452283	0.2234653
ALBK later	$7.791989*10^{-7}$	0.1717959	0.9452283	*	0.2485217
Szakálhát	$7.791989*10^{-7}$	*	*	*	*
North	$7.791989*10^{-7}$	*	*	*	*
South	$7.791989*10^{-7}$	*	*	*	*
Esztár	$7.791989*10^{-7}$	*	*	*	*
Tiszadob/Bükk	$7.791989*10^{-7}$	*	*	*	*
Tisza	$7.791989*10^{-7}$	0.1806243	0.2234653	0.2485217	*
River	$9.92493*10^{-6}$	*	*	*	*
East	$7.791989*10^{-7}$	*	*	*	*

The posterior p-values are statistically significant for each pairing involving the Central European hunter-gatherers, meaning that genetic drift cannot account for the observed differences in haplogroup frequencies between the hunter-gatherers and the Neolithic population of the Alföld.
In contrast to this, population continuity can be presumed from the early through to the late Neolithic on the Alföld.

3.6 (Ancestral) Shared Haplotype Analysis

3.6.1 Shared Haplotype Analysis

Alföld

Throughout the Alföld Neolithic, very few individuals share lineages with the Central European hunter-gatherer metapopulation (Figure 25). More than half (56%) of the Körös individuals share haplotypes with those of the earliest ALBK, 87.5% share lineages with the later ALBK and 62.5% with the late Neolithic Tisza Culture. Only 20-36% of early ALBK individuals share haplotypes with the Körös and Tisza cultures, while a substantially higher proportion (75.7%) share lineages with the later ALBK. In the *ALBK later* set (the largest of the datasets) between 30 and 50% of individuals share lineages with the other Alföld cultures. Most of the Tisza individuals (80%) share lineages with the later ALBK, and only half as much share lineages with the Körös culture and early ALBK.

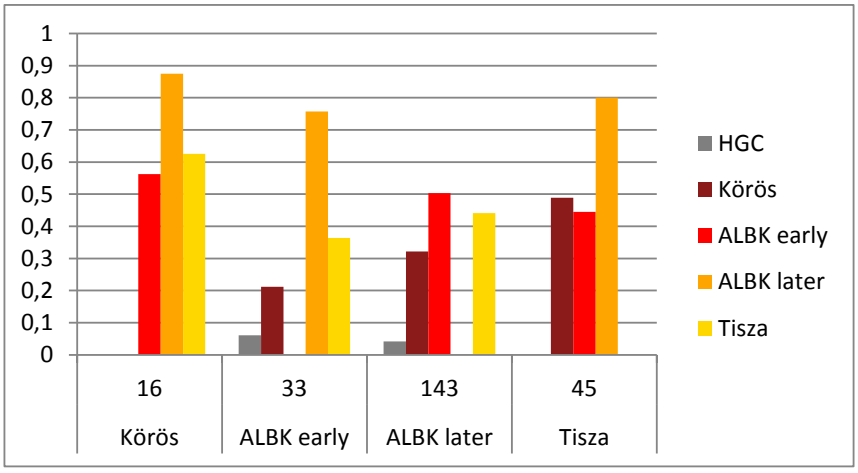

Figure 25: Shared Haplotype Analysis of the early, middle and late Neolithic of the Alföld. The numbers denote the number of individuals in each dataset.

Lineages shared with Central European hunter-gatherers, although rare, are widespread in the regional groups of the later ALBK (Figure 26).
There is a strong overlap among the regional groups of the Alföld Neolithic- at least 20% and up to 70% of individuals in any given group share haplotypes with all other groups.

Although the sample sets are roughly the same size, there is a pronounced difference between the two groups of the Tisza region as far as individuals sharing lineages with other Alföld cultural groups is concerned. The river group shares most of its lineages with the Körös culture and the two Szakálhát groups. The eastern group, on the other hand, seems to be composed largely of individuals carrying haplotypes which do not match those from the other Alföld groups: no more than 32% of individuals share lineages with any given group.

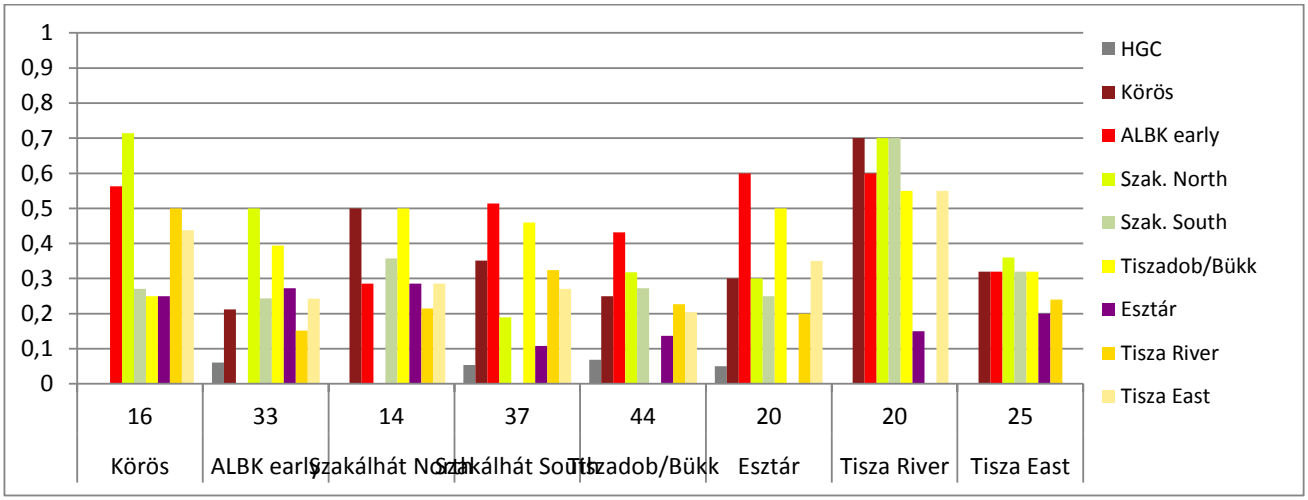

Figure 26: Shared Haplotype Analyses of the Alföld Neolithic, middle and late Neolithic divided into regional subgroups.

Carpathian Basin

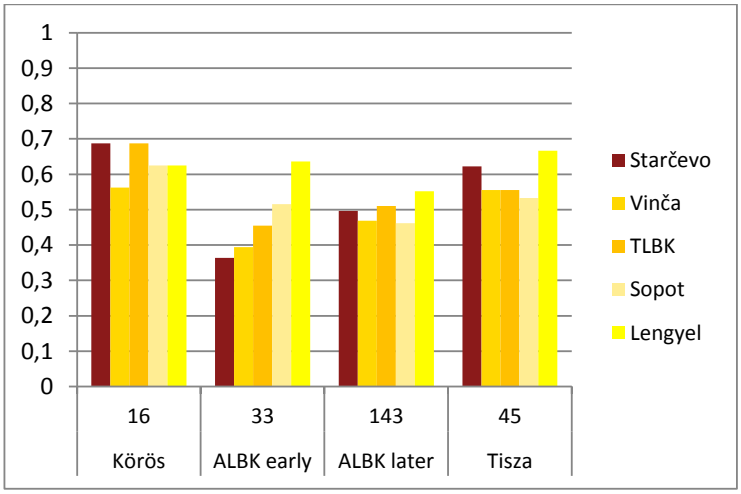

Figure 27: Shared Haplotypes between the Alföld and Transdanubian Neolithic cultures.

The percentage of individuals sharing lineages with the Transdanubian cultures is generally high. In the early Neolithic Körös culture, 70% of the individuals share lineages with the early Neolithic Starčevo culture and the middle Neolithic Transdanubian LBK. In the earliest Alföld LBK, the commonalities with the Starčevo are decreased by half (36%), before they increase again in the middle and late Neolithic. The proportion of individuals sharing lineages with the Transdanubian LBK remains fairly constant

throughout the middle and late Neolithic, ranging between 45% and 55%. The individuals sharing lineages with the Vinča culture show a slight upwards trend from the early middle Neolithic onwards. The proportion of individuals sharing lineages with the late Neolithic Lengyel and Sopot cultures remains stable throughout.

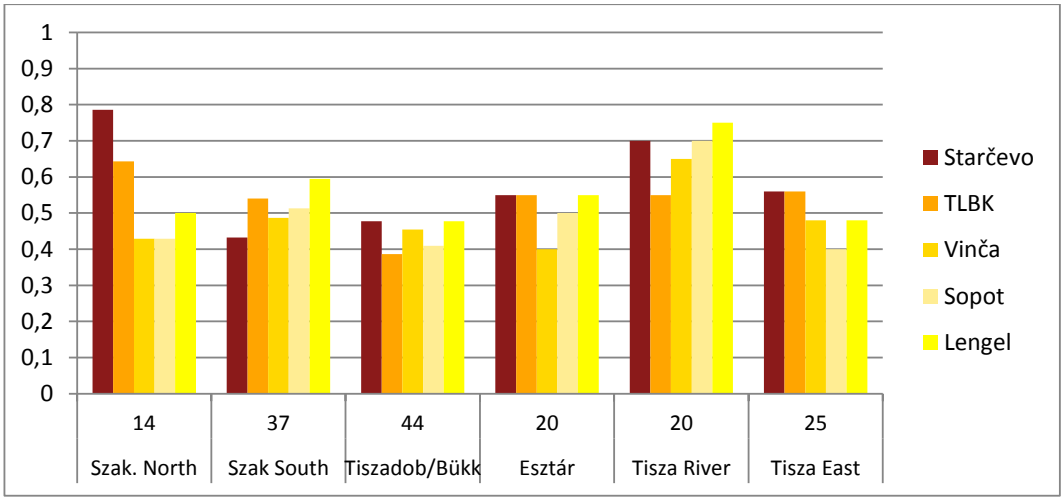

Figure 28: Shared Haplotypes between the regional groups of the middle and late Alföld Neolithic and the Transdanubian Neolithic cultures.

When looking at the regional subgroups of the ALBK, the picture does not change much. It is notable that the northern Szakálhát group and the river group of the Tisza culture both show very high proportions of individuals sharing Starčevo lineages (78% and 70%, respectively).

3.6.2 Ancestral Shared Haplotype Analysis

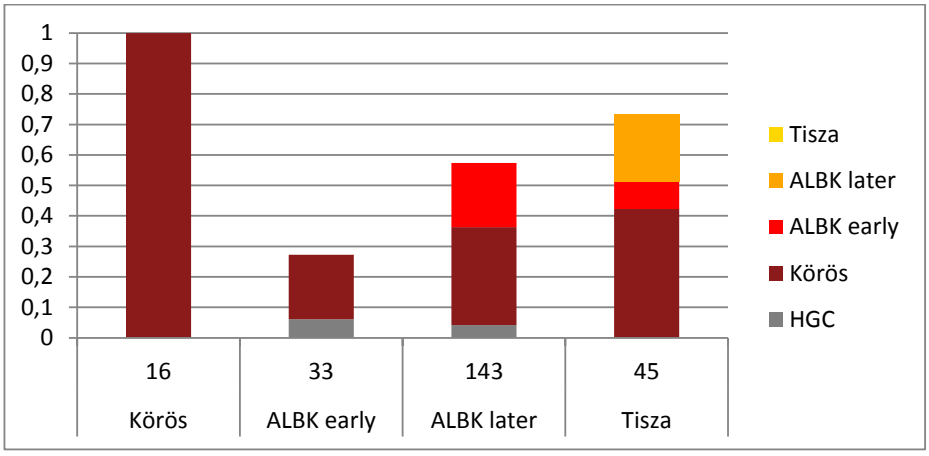

Figure 29: ASHA of the Alföld Neolithic.

The proportion of individuals carrying early Neolithic/Körös lineages doubles from 21% in the earliest Alföld LBK to 42% in the late Neolithic (Figure 29). Meanwhile, the influence of the earliest Alföld LBK decreases from formerly 20% to 8% in the late Neolithic.

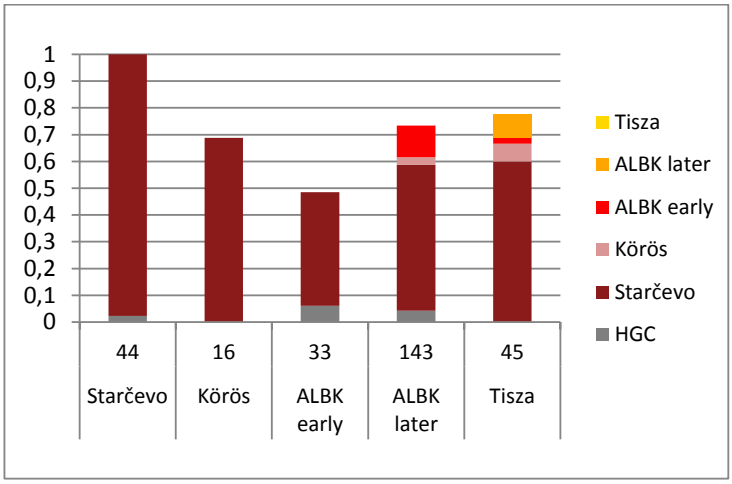

Figure 30: ASHA of Alföld Cultures including the Starčevo culture.

When the Transdanubian Starčevo culture is included in the analysis as a proxy for the early Neolithic gene pool of the Carpathian Basin (Figure 30), the proportion of individuals carrying early Neolithic lineages nearly doubles in the Alföld cultures. Interestingly, the basic trends remain the same: an increase of early Neolithic lineages and a decrease of "early middle" Neolithic lineages towards the late Neolithic.

Regional

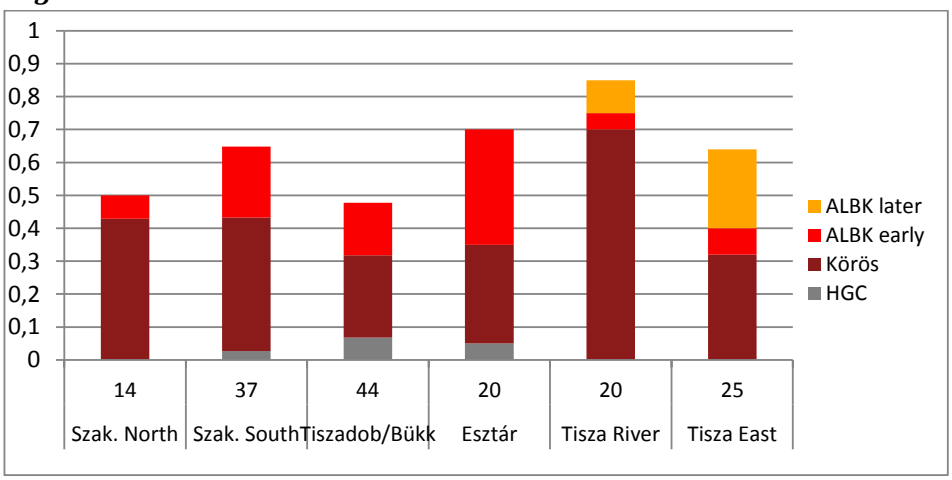

Figure 31: ASHA of the regional groups of the middle and later Alföld Neolithic.

The largest contributor to all regional groups except the Esztár group is the Körös culture (Figure 31). The percentage of individuals carrying early ALBK lineages is highest in the Esztár group (35%) and southern Szakálhát group. The eastern and river Tisza group differ in the ancestry of their lineages: the eastern Tisza group shows a lower Körös influence, but a higher proportion of lineages from the later

ALBK than the river group.

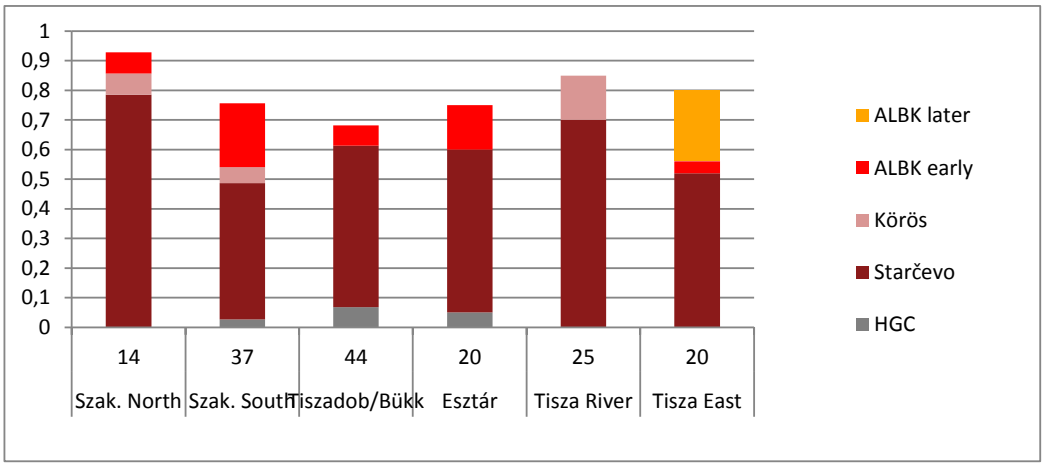

Figure 32: ASHA of regional groups of Alföld LBK, Starčevo culture included.

When the Starčevo culture is included in the ASHA (Figure 32), its influence reveals to be substantial. Genuine Körös lineages that have not already appeared in the Starčevo culture can only be observed in the Szakálhát groups and the river group of the Tisza region. In the Esztár group, the proportion of lineages derived from the early ALBK decreases by 20%.

In the river group of the Tisza culture, nearly 90% of the individuals have haplotypes that can be traced back to the early Starčevo and Körös cultures. *ALBK early*-derived lineages are only found in the eastern group.

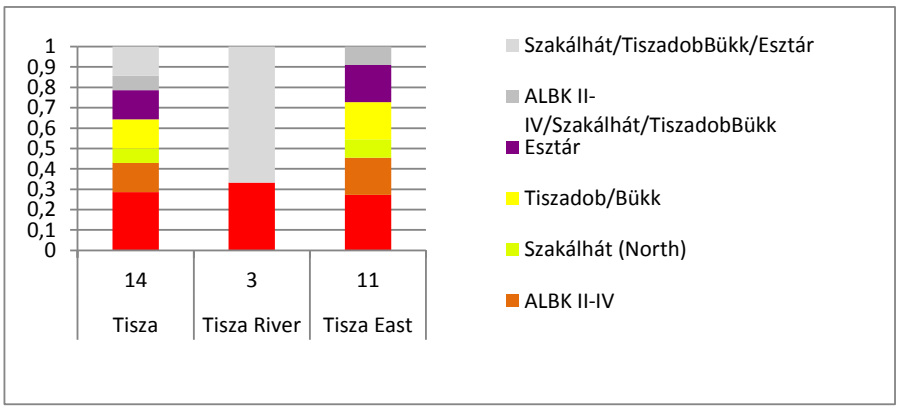

Figure 33: Lineages from the *ALBK later* set that are present in the Tisza divided by regional group.

When dividing the "ALBK later lineages" in the Tisza culture by chronology and the regional subgroup (Figure 33), it becomes apparent that every regional group of the Alföld LBK has contributed to the Tisza culture.

3.6.3 Unique lineages

From the early to the middle Neolithic, the percentage of individuals carrying unique lineages- lineages that occurred only once or within the same group- steadily rises to 32% in the middle Neolithic, but

then declines by about 10% during the later Neolithic (Figure 34). When the scope is widened to the entire Carpathian Basin by looking for haplotype matches in the Transdanubian cultures as well as within the Alföld cultures, it becomes apparent that a substantial portion of lineages that are unique in the Alföld are present in Transdanubia. However, the same pattern (steady increase until the middle Neolithic, then a decline) can be observed.

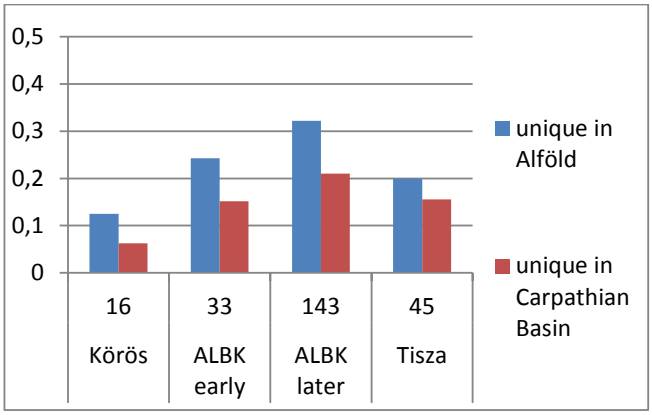

Figure 34: Proportion of individuals carrying unique lineages in the Alföld Neolithic Cultures. A lineage was regarded as "unique" if it appeared only in the studied group, but it could be shared by two or more individuals within that group.

A percentage of 32% individuals with unique lineages in the *ALBK later* appears large, but many of the lineages observed in this dataset appeared at several sites within the ALBK later set. Therefore, the analysis was also performed for each regional group. Among the regional groups of the Alföld Neolithic, the middle Neolithic Tiszadob/Bükk and the eastern Tisza group show the highest percentage of individuals with unique haplotypes, while the southern Szakálhát group shows the lowest (Figure 35). The proportion of "unique" individuals declines when the Transdanubian Cultures are included in the analysis, an effect which is most strongly pronounced for the Tiszadob/Bükk group, but also the eastern Tisza group and thus the two groups with the highest percentage of "unique" lineages to begin with.

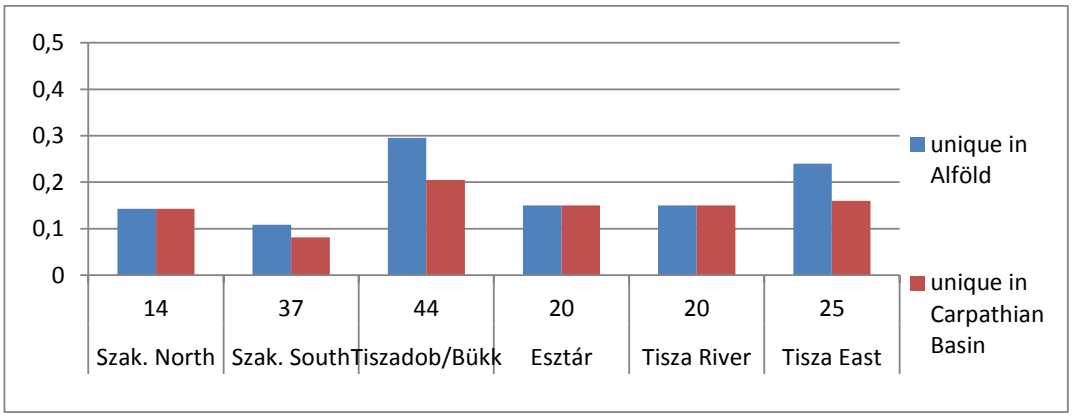

Figure 35: Unique lineages in middle and late Alföld Neolithic, divided by regional subgroups.

3.7 F_{ST}-values and MDS

3.7.1 Alföld

Table 32: F_{ST}-values for Neolithic cultures of the Alföld (including regional groups) Statistically significant FST values (p > 0.05) are marked grey. For exact p-values see appendix.

	HGC	**Körös**	**ALBK early**	**ALBK later**	Szakálhát	*North*	*South*	**Tiszadob/Bükk**	**Esztár**	**Tisza Total**	*Tisza East*	*Tisza River*
Körös	0.32269	*										
ALBK early	0.2134	0.01777	*									
ALBK later	0.18772	0.04005	0.01049	*								
Szakálhát	0.27003	0.06221	0.05982	*	*							
North	0.29706	0.03169	0.04257	*	*	*						
South	0.2812	0.07418	0.06729	*	*	0.00167	*					
Tiszadob/Bükk	0.15934	0.0618	0.01799	*	0.02796	0.00445	0.03387	*				
Esztár	0.25265	0.03404	-0.01497	*	0.07351	0.06806	0.08482	0.03609	*			
Tisza Total	0.26721	0.05181	0.03891	-0.00038	0.00259	-0.00314	0.00564	0.01217	0.04267	*		
Tisza East	0.25242	0.07409	0.02421	-0.00539	0.01635	0.01484	0.01837	-0.00651	0.04093	*	*	
Tisza River	0.32823	0.03343	0.06655	0.01231	-0.00497	-0.01047	-0.00185	0.0358	0.07246	*	0.01986	*

According to the statistically significant F_{ST} values, only between 3.4% and 7.4% of the genetic variation in the Alföld cultures occur between populations (Table 32). The variation between the Central European hunter-gatherers and the Alföld cultures is tenfold higher in comparison. The Körös culture differs quite strongly from the eastern Tisza group, but about equally from the Tisza culture als a whole and the later Alföld LBK (5% and 4 %, respectively), while the differences to the early Alföld LBK are statistically insignificant. The earliest ALBK differs significantly from the Tisza culture, but not from the later ALBK, except for the Szakálhát subgroup, in particular the southern Szakálhát subset

When looking at the regional groups of the ALBK, there are significant and also quite large differences between the Körös culture and the (southern) Szakálhát and Tiszadob/Bükk groups. Both southern and northern Szakálhát groups show a comparatively large distance from the Esztár group, at 6.8% and 7.4%, respectively. The river group of the Tisza culture shows large differences from the early ALBK and the Esztár group.

When the linearised F_{ST} values of the regional subgroups of the Alföld Neolithic are plotted in a two-dimensional space using MDS (Figure 36), three distinct groupings become visible: The earliest Alföld LBK and the Esztár group lie fairly close to each other, as do eastern Tisza group and the Tiszadob/Bükk

group. The two groups Szakálhát group and the River group of the Tisza culture form the third group, while the Körös culture remains an outlier.

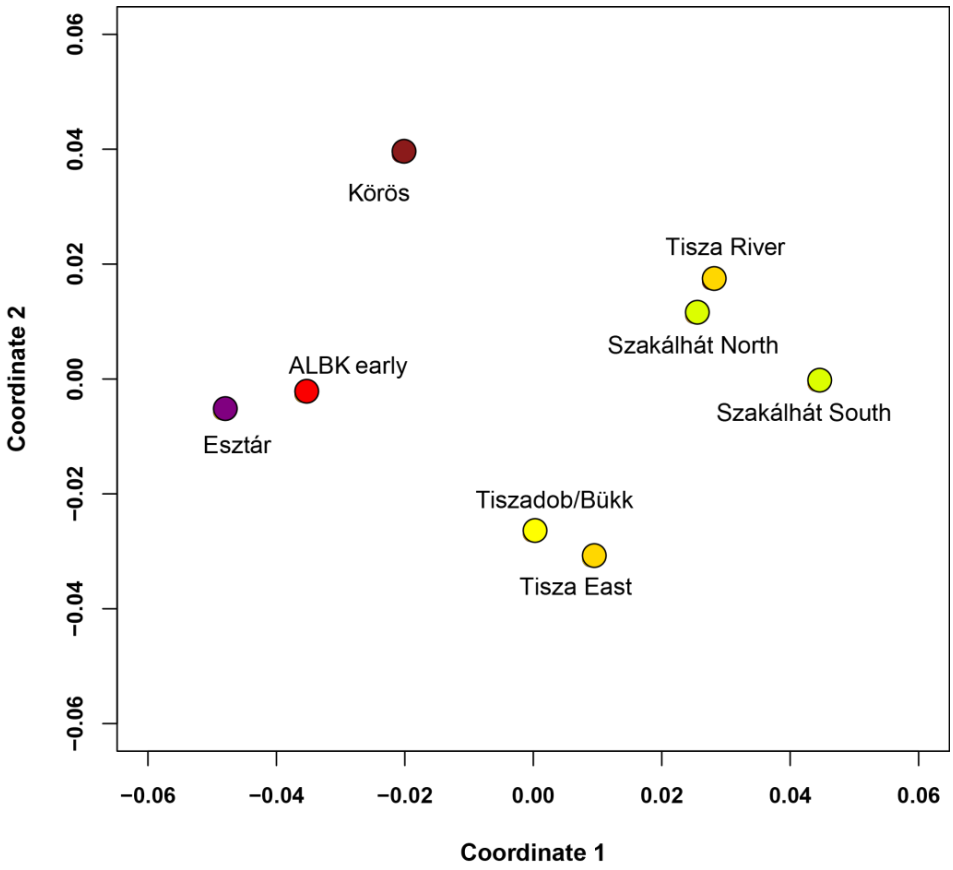

Figure 36: MDS of the Neolithic Alföld cultures divided by regional groups. The HGC dataset was not included in Figure 36 and Figure 37, since its high genetic distance to the Alföld groups distorted the plot too extensively for an informative display.

3.7.2 Carpathian Basin

Table 33: F_{ST}-values for the Neolithic cultures of the Carpathian Basin.

	Starčevo	TLBK	Vinča	Sopot	Lengyel
Körös	-0.00839	0.04634	0.01541	0.04494	0.01772
ALBK early	-0.00498	0.02129	-0.00897	-0.00138	-0.00971
ALBK later	0.00252	0.00698	0.01353	-0.00436	0.00918
Szakálhát	0.02440	0.01298	0.04174	0.01576	0.03865
North	-0.00349	-0.00626	0.02461	0.00248	0.01796
South	0.03148	0.01827	0.04022	0.01935	0.04389
Tiszadob/Bükk	0.01023	0.01789	0.02322	0.00344	0.01725
Esztár	0.00883	0.05014	0.00840	0.01772	0.00840
Tisza	0.00950	0.01841	0.02726	0.01189	0.02235
Tisza East	0.00914	0.00876	0.01189	-0.00490	0.00973
Tisza River	0.01339	0.03534	0.04042	0.03901	0.04213

The F_{ST}-values of the pairwise comparisons between Alföld and Transdanubian Neolithic groups remain within the same order of magnitude as in the Alföld-only analyses, ranging between 2.4% and 5% (Table 33). The comparison between the early Neolithic Körös and Starčevo cultures yields extremely low, insignificant F_{ST} –values. The *ALBK early* set also shows low, statistically insignificant genetic distances to all Transdanubian groups. The classical and later ALBK as a whole (*ALBK later*) shows the same pattern; only the genetic distance to the Lengyel culture achieves statistical significance, but the resulting F_{ST}-value is still very low. The regional subgroups of the later ALBK show slightly more differentiation. The genetic distances of the Szakálhát group (especially Szakálhát South) to the Vinča and Lengyel cultures lie in the upper range of all F_{ST} -values observed. The Esztár group exhibits a comparatively high distance from the TLBK, while the Tiszadob/Bükk group shows no pronounced differentiation from the Transdanubian cultures.

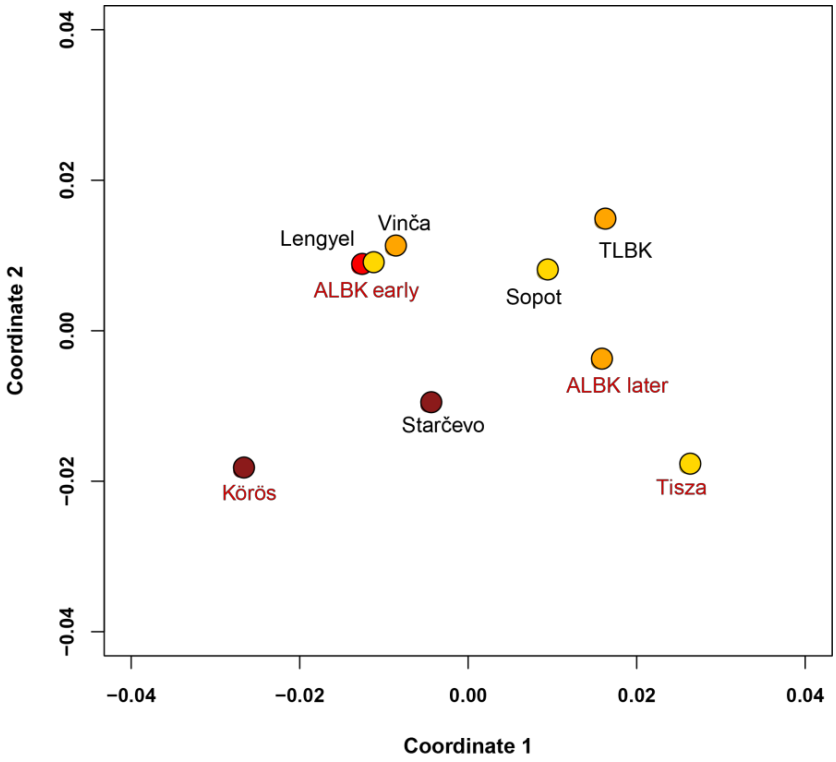

Figure 37: MDS of the Carpathian Basin Neolithic.

There is no clear separation between Transdanubian and Alföld Neolithic Cultures visible in the MDS plot (Figure 37). Unlike in the PCA (Figure 21), there is also no separation between early, middle and late Neolithic. The Körös culture is set slightly apart from the other groups in the lower left quadrant, while the Starčevo culture assumes an intermediate position between the Körös culture and the middle and late Neolithic groups. The *ALBK early*, Lengyel and Vinča cultures form a tight cluster near the centre of the plot, while the Sopot culture as well as the Transdanubian and the later ALBK are grouped around them. The Tisza culture is closest to the later ALBK along the first axis and to the Körös culture on the second axis.

Regional

When the later ALBK and Tisza culture are split into regional subgroups, the Esztár group falls close to the *ALBK early*, Vinča and Lengyel cultures (Figure 38). The Tiszadob/Bükk group and the Eastern Tisza group lie as closely together as they did in Figure 36, with no Transdanubian group in proximity. The river group of the Tisza culture occupies approximately the same position as the entire Tisza culture did in Figure 37, with the two Szakálhát groups lying between the Tisza river group and the TLBK. The positions of the Körös culture, *ALBK early* and the Transdanubian groups remain largely the same as in Fig. 36.

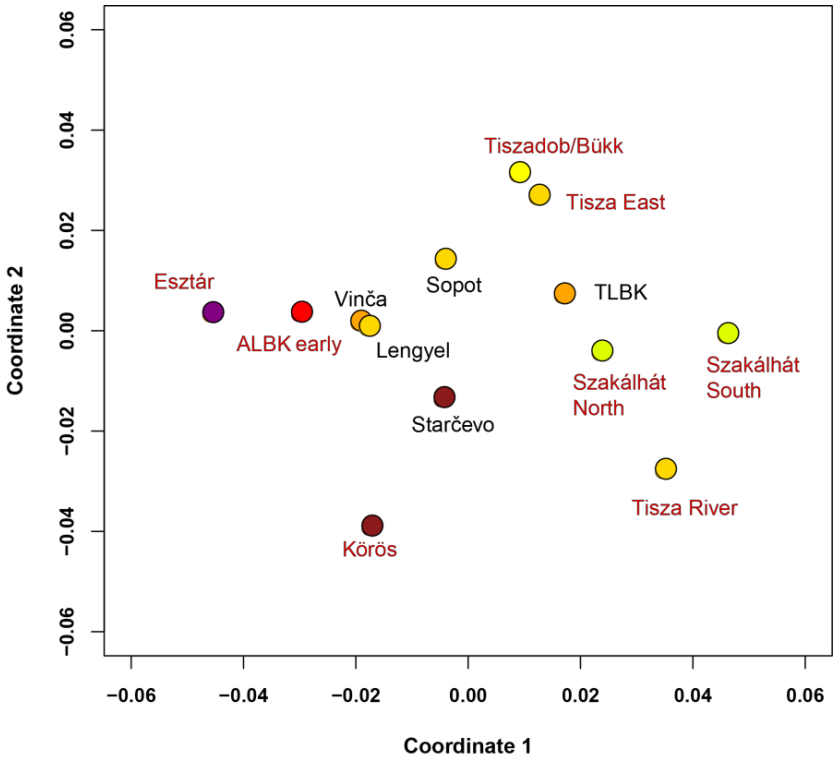

Figure 38: MDS of the Carpathian Basin Neolithic, with the middle and late Neolithic Alföld cultures divided into regional groups.

3.7.3 Europe

Table 34: F_{ST} values between Alföld Neolithic cultures and European cultures 6000-4500 BC. LBK= Central European LBK, RSC= Rössen culture, NUK= Neolithic Ukraine, CPE= early Neolithic central Portugal, CARcat= Cardial culture Catalonia, NSE= early Neolithic northern Spain, HGS= hunter-gatherers southwestern Europe, HGC= hunter-gatherers Central Europe, HGE= hunter-gatherers Eastern Europe. For the comprehensive table, see appendix G.

	LBK	RSC	NUK	CPE	CARcat	NSE	HGS	HGC	HGE
Körös	0.02087	0.07018	0.19474	0.15083	-0.03919	0.13913	0.16385	0.32351	0.13733
ALBK early	0.00623	-0.00583	0.09926	0.03102	0.00110	0.01306	0.06070	0.21272	0.07364
ALBK later	0.00933	0.0053	0.09632	0.02562	0.03242	0.03036	0.07113	0.18668	0.08949
Tisza	0.01645	0.04459	0.14402	0.07913	0.04836	0.07628	0.12574	0.26673	0.13360

The Alföld cultures show low, non-significant genetic distances to the Central European LBK and the Catalonian Cardial group. The early and late Neolithic Alföld shows slightly higher distances to the Central European Rössen culture. High and statistically significant genetic distances are observed between the Alföld groups and the hunter-gatherer metapopulations, the Ukrainian Neolithic and the Spanish and Portuguese early Neolithic (Table 34).

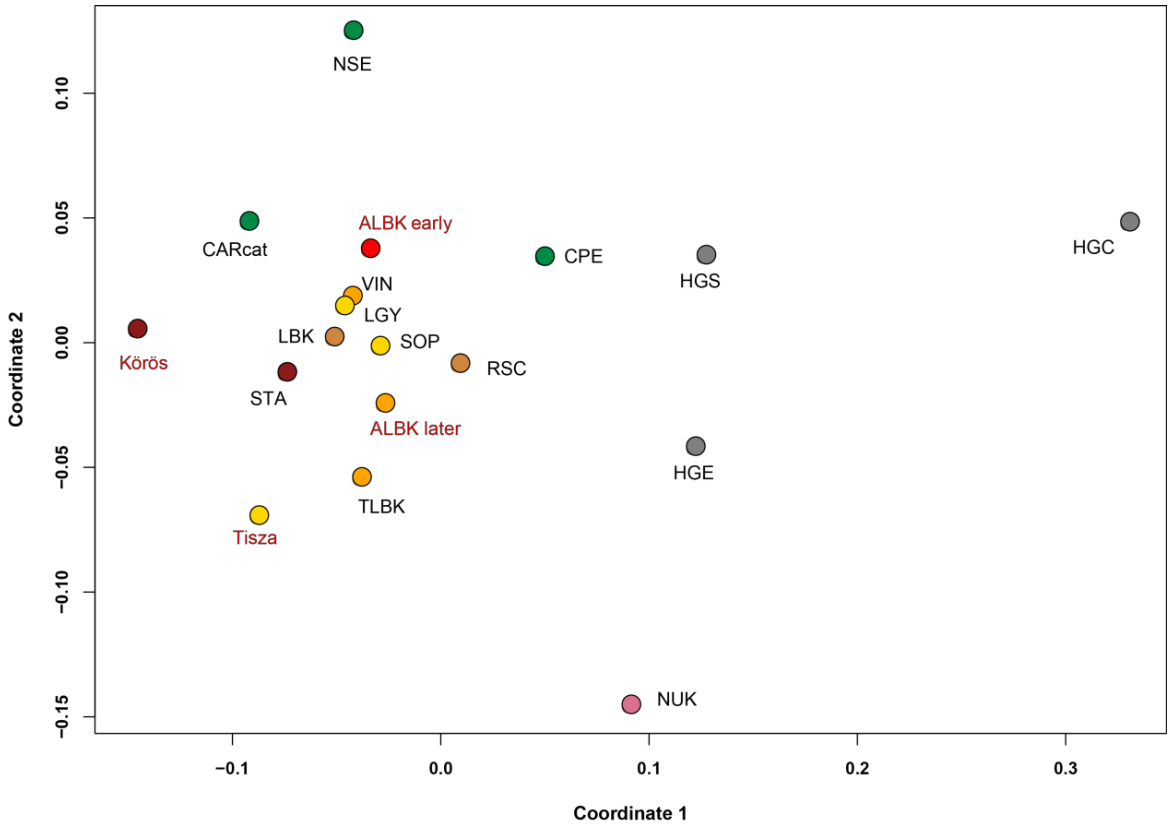

Figure 39: MDS of European Neolithic Cultures 6000-4500 BC and hunter-gatherer metapopulations. STA= Starčevo culture, TLBK= Transdanubian LBK, VIN= Vinča culture, SOP= Sopot culture, LGY= Lengyel culture, LBK= Central European LBK, RSC= Rössen culture, NUK= Neolithic Ukraine, CPE= early Neolithic central Portugal, CARcat= Cardial culture Catalonia, NSE= early Neolithic northern Spain, HGS= hunter-gatherers southwestern Europe, HGC= hunter-gatherers Central Europe, HGE= hunter-gatherers Eastern Europe.

In the MDS plot, the first coordinate separates the preneolithic cultures from the Neolithic ones (Figure 39). Along the second coordinate, the separation shows a loose geographical structure: the Neolithic cultures from the Iberian Peninsula congregate in the upper left quadrant. The intermingled Neolithic Cultures of Central Europe and the Carpathian Basin lie slightly below, whereas the Eastern European Neolithic Sample (NUK) occupies the lower two quadrants. The Körös and Tisza cultures are set slightly apart from the other Carpathian Basin groups, but are not notable outliers. Of all Carpathian Basin and Central European groups, the earliest ALBK falls closest to the southwestern European Neolithic groups, which may be due to the relatively high frequencies of haplotypes belonging to haplogroups U and H.

3.8 AMOVA

When performing an AMOVA on the Alföld Neolithic dataset with the regional/cultural sets sorted into three groups, the best constellations have the following in common (Table 35)

a) The Szatmár/early group of the Alföld LBK is grouped together with the Esztár group of the Alföld LBK

b) The River Group of the Tisza Culture and the Southern Szakálhát group of the Alföld LBK lie within the same group

c) The eastern Tisza group lies in the same group as the Tiszadob/Bükk (except for model no.5)

In four of the five best group arrangements, the early Neolithic *Körös* sample set is grouped together with the Szatmár/ early Alföld LBK and the Esztár group. The maximum variation between groups is achieved when in addition to this, the eastern group of the Tisza Region is grouped together with the Tiszadob/Bükk group and the northern and southern Szakálhát datasets are in the same group together with the river group of the Tisza Culture. Alternatively, the northern Szakálhát group can be included with the Tiszadob/Bükk and eastern Tisza grouping, or the *Körös-ALBK early*-Esztár group, which each result in slightly decreased F_{CT} values. The fourth-best arrangement is achieved when the Körös culture set is grouped together with the Szakálhát regional groups and the river group of the Tisza Culture. The fifth-best arrangement is a variation of arrangement no.1, but with switched positions of the northern Szakálhát group and the eastern group of the Tisza culture.

Table 35: The five best groupings for the Alföld populations when three groups are proposed.

	Among groups			Among populations within groups		
Model	**% of variation**	**F_{CT}**	**p-values**	**% of variation**	**F_{SC}**	**p-values**
1 (KÖR_ALBKe_ALBKearly) + (TiszaEast_ALBKtb) + (SzakS_TiszaRiver_SzakN)	4.34	0.04342	0.00307+-0.00059	-0.12	-0.00128	0.44495+-0.00407
2 (KÖR_ALBKe_ALBKearly) + (TiszaEast_SzakN_ALBKtb) + (SzakS_TiszaRiver)	4.02	0.04019	0.00703+-0.00076	0.17	0.00173	0.37842+-0.00471
3 (KÖR_ALBKe_ALBKearly_SzakN) + (TiszaEast_ALBKtb) + (SzakS_TiszaRiver)	3.51	0.03512	0.00554+-0.00075	0.56	0.00580	0.19842+-0.00409
4 (ALBKe_ALBKearly) + (TiszaEast_ALBKtb) + (KÖR_SzakS_TiszaRiver_SzakN)	3.48	0.03478	0.01188+-0.00117	0.61	0.00629	0.21337+-0.00428
5 (KÖR_ALBKe_ALBKearly) + (SzakN_ALBKtb) + (TiszaEast_SzakS_TiszaRiver)	3.31	0.03306	0.01109+-0.00103	0.72	0.00740	0.18050+-0.00378

When performing an AMOVA on the Alföld Neolithic with four groups (Table 36), the best combinations are similar to the ones already found in the three-group AMOVA:

a) The eastern group of the Tisza culture is always paired with the Tiszadob/Bükk group of the Alföld LBK (save for model no.4)

b) The early Alföld LBK is preferentially combined with the Esztár group of the Alföld LBK

The pairings of the Szakálhat subgroups, the Körös culture and the river group of the Tisza culture are fairly flexible. Three out of the five best models pair the southern Szakálhát group with the river group of the Tisza culture. The Körös culture is paired with the river group of the Tisza culture in two of the

five best models. The northern Szakálhát group meanwhile is paired with a different group in each model.

Table 36: The five best groupings for the Alföld populations in a four-group model.

		Among groups			Among populations within groups		
		% of variation	F_{CT}	p-values	% of variation	F_{SC}	p-values
1	(ALBKe_ALBKearly) + (TiszaEast_ALBKtb) + (SzakS_TiszaRiver) + (KÖR_SzakN)	4.11	0.04106	0.00960+-0.00103	-0.24	-0.00250	0.50950+-0.00506
2	(ALBKe_ALBKearly) + (TiszaEast_ALBKtb) + (KÖR_TiszaRiver) + (SzakS_SzakN)	3.77	0.03769	0.02040+-0.00141	0.03	0.00027	0.40386+-0.00557
3	(KÖR_ALBKearly) + (ALBKtb_TiszaEast) + (TiszaRiver_SzakS) + (ALBKe_SzakN)	2.89	0.02888	0.02624+-0.00151	0.80	0.00820	0.15535+-0.00397
4	(ALBKe_ALBKearly) + (SzakS_TiszaEast) + (KÖR_TiszaRiver) + (ALBKtb_SzakN)	2.77	0.02773	0.03663+-0.00189	0.88	0.00902	0.17822+-0.00394
5	(SzakN_ ALBKearly) + (ALBKtb_TiszaEast) + (TiszaRiver_SzakS) + (ALBKe_KÖR)	2.76	0.02756	0.04762+-0.00230	0.91	0.00931	0.14208+-0.00390

4 Discussion

4.1 Amplification success, contamination rates

4.1.1 Amplification success

In this study, reproducible HVS-I sequences could be obtained from 74.6% of all 320 investigated individuals. By analysing diagnostic coding-region SNPs in addition to the HVS-I, a reliable haplogroup assignment could be obtained from 76.6% of individuals.

A survey of the literature shows that the amplification success of aDNA samples from the European Neolithic and Chalcolithic varies widely between studies (Table 37) as well as between sites within the same study (not shown). At 74.6% sequence recovery for the HVS-I, the overall amplification success of the Alföld data lies on the high end of the range. However, between individual sites the success rates range between 41% and 100% (for sites ≥ 10 individuals).

Table 37: Amplification success rates for various aDNA studies of European ("peri")Neolithic sites and populations. The "age" column is meant as a rough guide, for exact dates see the original publications. The success rates are displayed as reported by the authors, with the exception of the studies by Hervella and Bollongino, where the preneolithic individuals were excluded for this table. The numbers in brackets in the "success rate" column give the number of successfully typed individuals out of the total of analysed individuals

Age	Cultural group(s)	Success rate of haplogroup determination and/or HVS-I sequences (%)	Reference
5500- 4700 cal BC	Neolithic Ukraine	38.8 (7/18)	(Nikitin et al. 2012)
8000 – 3350 cal BC	Mesolithic to Chalcolithic Portugal	31.5 (35/111)	(Chandler et al. 2005)

7500-7500 BP	Hunter-gatherers northeastern Europe	24.4 (11/45)	(Der Sarkissian et al. 2013)
5500-3700 cal BC	Neolithic Spain	42.8 (21/49)	(Gamba et al. 2012)
6185- 3400 BP	Neolithic to Chalcolithic Spain	90.0 (45/50)	(Hervella et al. 2012)
5300-5150 cal BC	LBK (Vedrovice, Czech Republic)	37.5 (6/16)	(Bramanti 2008)
9000-3000 cal BC	Neolithic Central Europe (Blätterhöhle)	86.2 (21/24)	(Bollongino et al. 2013)
5200- 4900 cal BC	LBK (Derenburg, Germany)	71 (22/31)	(Haak et al. 2010)

The amplification success in general depends on several factors: the DNA extraction and analysis techniques, the level of contamination in the samples and/or the laboratory and the preservation of endogenous DNA in the sample itself. In this study, all samples were processed in the same manner (the two different extraction methods notwithstanding) and contamination in the laboratory was continuously monitored. Thus, the main determinant of amplification success seemed to be endogenous DNA preservation, which is in turn determined by taphonomical processes that act on the remains both *in-situ* and after excavation.

Because the climatic conditions throughout the Alföld are fairly uniform, a geographic component of DNA preservation within the studied area is unlikely, and no such association was noted in this study.

The excavation date also appeared to have little influence on sample preservation. For instance, the sites of Mezőkeresztes-Cethalom (MECE) and Mezőkövesd-Mocsolyás (MEMO) were both excavated in the mid- nineties, but the amplification success at MEMO was twice as high (41% and 91.6%, respectively). As another example, the site of Vésztö-Mágor (VSM), which was excavated in the seventies, was one of the best -preserved sites in this study (82.6%) in spite of the long storage period of the remains. In this particular case, the storage conditions may have contributed to the good preservation, as the skeletal remains were kept in a basement and thus cool and dark.

The age of the samples may have played some role in DNA preservation: for instance, the “failed” individuals at the site of Berettyóújfalu Nagy-Bócs dülö (BENA) predominantly belonged to the Körös culture, while the younger Esztár individuals yielded more reproduced sequences. However, in general age was not strongly correlated with sample preservation. Two other factors probably contributed to the variation in DNA preservation on the Alföld: soil type and storage conditions. However, since the storage conditions since excavation and the particular environmental circumstances were not known for all sites, their influence was not studied in detail in this study.

DNA preservation also affects the size and condition of the fragments that can be amplified by the PCR: Extensive DNA damage will lead to sequences with a large number of ambiguous sites, and highly fragmented DNA will yield better results when amplified in short segments. Furthermore, the efficacy of the primer system also plays a role, as primers with poor affinities to the target sequence will yield lower results, exacerbating the scarcity of target DNA in a sample. When looking at the amplification

success of the primer systems, it is noticeable that the multiplex primer systems show higher success rates than the HVS-I primers. This is to be expected, since the amplicon length of these systems is much lower than that of the HVS-I primers. Accordingly, among the HVS-I primers one would expect the highest success rates in the short-fragment system, followed by the medium and long fragment primers. Indeed, the success rates of the "long" two-fragment system averaged about 50%, which is lower than the average success of the primers in the medium-length system at 70%. This seems somewhat surprising, because due to the small amplicon size, the short-fragment system would be expected to show the highest average amplification success of the three systems. However, except for fragments 1 and 2, the fragments of the short system did not exceed the success rates of the medium-length system primer pairs. Fragment 6 of the short- fragment system even showed the lowest amplification success of all used primer systems. While it is possible that the primer pairs for fragments 3 to 6 were generally less effective, the likely explanation lies in the fact that the short-fragment system was only used when the medium length fragments proved to be difficult to amplify. Thus the amplification success of the short –fragment system was skewed by the most poorly preserved samples in the dataset, while the success rates of the primer pairs in the medium-length system were "boosted" by the well preserved samples.

The most efficient primers overall were fragment II of the medium-length system (np 16117-16233) and the first two fragments of the short-fragment system (np 16018-16097, np 16072-16144). This observation has also been made in other studies using these systems (Roth 2014 unpublished; Brandt 2014 unpublished).

4.1.2 Contamination rates

Unfortunately, few aDNA studies offer detailed analyses of their contamination rates, and the different methodologies presented can make it difficult to assess what contamination rates are to be expected in human aDNA studies. Contamination is usually only reported in terms of individuals, and in cases of non-reproducible DNA profiles there is not always a distinction between contamination and amplification failure (Haak et al. 2010 do not; Chandler 2003 Tab. 4.2 offers some differentiation; Der Sarkissian et al. 2013; Gamba et al. 2012). Contaminated samples or amplification sets may also be discarded immediately and thus not factor into the further analyses (Hervella et al. 2012; Gamba et al. 2012; Bramanti et al. 2009). Haak *et al*. 2005 discussed the contamination rates of their clones, which ranged between 0% and 18.3%. Gamba *et al.* 2012 reported a contamination rate of 7% in their extraction blanks, using the Qiagen Multiplex PCR kit. Using short fragments targeting nucleotide positions typical for U5, Bramanti *et al.* observed contamination in 5% of selected PCR blanks (Bramanti et al. 2009), Bollongino *et al.* 2013 detected contamination in 0.04% of their PCR blanks and none in extraction or milling blanks; Lacan *et al.* observed no contamination at all (Bollongino et al. 2013; Lacan, Keyser, Ricaut, Brucato, Duranthon, et al. 2011).

The overall PCR contamination rate of 3.9% in controls and 4.4% in individuals in the Alföld study falls within the lower half of the range outlined by these studies, which speaks for the effectiveness of the contamination prevention measures. Furthermore, it has to be kept in mind that the previously described studies included considerably fewer individuals than the Alföld study. The high throughput of samples in this study may have increased the contamination risk of blanks and samples.

Only 3.5% of contaminant lineages found in individuals matched contaminated blanks from the same PCR. This speaks for sporadic rather than systemic contamination of chemicals, tubes or surroundings. The milling blanks were twice as prone to contamination during the PCR than PCR blanks and extraction blanks. A possible explanation for this is the "carrier effect": microbial DNA and organic molecules in an aqueous solution can act as binding surfaces for "stray" DNA molecules, making them accessible for the polymerase during the PCR. Without "carriers", the DNA molecules would bind to the plastic of the reaction tubes, preventing their amplification (Handt et al. 1994). Unlike extraction and PCR blanks, which only contain the respective extraction and reaction chemicals in an aqueous solution, the milling blanks are extracted from powdered hydroxapatite. It seems that the hydroxapatite can also act as a carrier, enabling contaminant DNA molecules to become suspended in the solution where they are eluted during the extraction, leading to higher rates of sporadic contamination.

In one instance (2.27% of the total of extractions), the contamination in a milling blank could be traced back to the DNA extract, but the contamination was not detected in the other samples and controls from the affected extraction, so the results were not discarded. However, contaminations stemming from the DNA extract were detected in 2.5% of individuals. Since the accompanying extraction and milling blanks of the affected extractions proved to be clean, these contaminations likely occurred prior to the aDNA analysis, or at the very least prior to milling.

Fragments II and IV of the medium-length system and fragments 3 and 6 of the short system showed slightly elevated contamination rates in the PCR controls as well as in the individuals (the correlation is less pronounced for fragment IV). This is in concordance with a contamination occurring during the PCR, possibly via the chemicals. In the medium-length system, the higher contamination rate of fragments II and IV may be due the high sensitivity/effectiveness of these particular primer pairs (see section amplification success). However, this did not hold true for the short-fragment system, where the two most efficient primer pairs showed no contamination at all, while fragments 3 and 6 showed only moderate to low amplification success, but elevated contamination rates. In these cases, the low efficiency of the primer pair may have resulted in the preferential amplification of modern contaminants.

Because of the short length of the amplified HVS-I fragments, it was not always possible to determine the haplogroup of every contaminating lineage. A conclusive match between a contaminating lineage and one of the researchers involved could not be made in any instance. In general, it can be noted that

both European and non-European haplogroups were among the identifiable contaminants, even though most researchers involved in this study- and all researchers working in the aDNA laboratory- belonged to European haplogroups. Furthermore, the ancient specimens studied in the Mainz laboratory facilities were all of European descent, which excludes the possibility of cross-contamination in those samples where Asian or Sub-Saharan contaminant lineages were found. This points to the reaction chemicals as the likely main contributing factor to the contamination of controls.

In the case of the L0f lineage, which appeared in multiple individuals, it is interesting to note that a) the contamination occurred exclusively in fragment II and b) it was not detected in the blanks. This points toward a contamination of the primer system, with the DNA in the samples acting as a "carrier" for the contaminating lineages (since the controls were clear). In that case, the contamination must have occurred in the primer stock solution, since several different aliquots were used on the affected samples.

4.2 Genetic continuity between Mesolithic and Neolithic populations on the Alföld

The hunter-gatherer populations of Central Europe have so far been found to exclusively exhibit subclades of U, in particular U4, U5a, U5b, U2 and U8 (Bramanti et al. 2009; Bollongino et al. 2013; Fu et al. 2013; Lazaridis et al. 2013). The frequencies of these subclades in Neolithic populations can therefore be used to estimate potential genetic introgression by hunter-gatherers. In the Alföld Cultures, this influence appeared to be generally quite low. The combined frequencies of U4, U5a/b and U8 were 0% in the Körös culture, 17% in the early Alföld LBK and 10-12% in the later Alföld LBK and Tisza Culture. U2 was totally absent in the Alföld data. It is interesting to note that these clades were present in almost every regional group of the ALBK and Tisza culture except for the northern Szakálhát group, where its absence may be due to the small size of the dataset (as may be the case with the Körös culture set).

There is a single site from the earliest ALBK/Szatmár period where an argument can be made for a more substantial hunter-gatherer introgression into the Neolithic maternal gene pool: the earliest ALBK/Szatmár site of Mezőkövesd-Mocsolyás (MEMO) in the northwestern Alföld. Here, 27% of individuals were found to belong to subclades of U (

Table 21).Fisher´s exact test showed that its haplogroup composition differred strongly from the other two early ALBK- sites as well as from the later ALBK and the Tisza culture. The location of the site- close to the mountains- puts it in the vicinity to hypothetical refuge areas of local hunter-gatherers. Its chronology assigns it to a period where significant cultural change occurred in the Alföld- possibly due to external influences. Taken at face value, a high percentage of U-clades may reflect these characteristics and mark Mezőkövesd as a place of admixture between Alföld farmers and hunter-gathering communities. The osteological analyses of the site showed the presence of a robust stature type that was been associated by the author with an "autochthonous "population (Zoffmann 2014; Zoffmann 2000). In this study, no link was found between haplogroup U or subclades thereof and "robust" stature in the analysed individuals (Table 38).

Table 38: Osteological classification and mitochondrial haplogroups from MEMO individuals in direct comparison.

Grave No.	Laboratory Name	Osteological classification according to (Zoffmann 2014)	mtDNA haplogroup
2/75	MEMO02	robust	K
8/192	MEMO07	robust	HV
11/195	MEMO10	gracile	n.d.
13/197	MEMO12	robust	U5a
18/287	MEMO15	gracile	R1
19/341	MEMO16	robust	H
20/344	MEMO17	gracile	U4a1
22/353	MEMO19	robust	K
23/365 (adult)	MEMO20	gracile	K

The archaeological analysis did not show notable cultural ties between Mezőkövesd and Mesolithic populations, but put it in a context between the early Neolithic Körös culture and the classical ALBK (Kalicz & Koós 2001) . Furthermore, the discovery of Körös sites in the northern Alföld (Domboróczki & Raczky 2010) had already shown that a Mesolithic contribution was not required for the formation of the earliest Alföld LBK.

Moreover, in spite of its high content of haplogroup U, Mezőkövesd still differed significantly from the Central European hunter-gatherer metapopulation, while the differences to the rest of the early ALBK and the later ALBK were not statistically significant.

Table 39: Fisher's exact test result of Mezőkövesd-Mocsolyás (MEMO) against the total of the Alföld Neolithic.

	HGC	Körös	ALBK early	ALBK later	Tisza
MEMO (n=22)	$2*10^{-4}$	0.1556	0.05659	0.05589	$3*10^{-4}$

Thus, even if the Mezőkövesd site bears signs of admixture between hunter-gatherers and early farmers, this seems to have been of little consequence to the further development of the ALBK.

Among the regional groups of the classical and later ALBK, the highest frequency of U-clades was present in the Tiszadob/Bükk group at 16%. This regional variant of the ALBK occupied the northern Alföld including parts of the Bükk and Mátra mountains (Csengeri 2010b), an area that has been suggested as a "stronghold" for hunter-gatherers (Domboróczki 2003). While the question of connections between hunter-gatherers and the Tiszadob group, has been discussed in archaeological research, definitve evidence for these connections between hunter-gatherers is lacking, while its ties to other regional groups of the ALBK is not doubted (Bánffy 2006 and citations therein). The genetic analyses show strong differences between the Central European Mesolithic metapopulation and the Tiszadob/Bükk group and place the latter firmly among the other regional groups of the late and classical ALBK. The genetic data thus de-emphasizes the influence of (putative) hunter-gatherer communities on the Tiszadob and Bükk groups.

Anthropological studies have proposed the presence of two morphologically distinct Neolithic populations in the Alföld: A study from 2000 found notable osteological differences between "gracile" Körös groups and robust or "protonordic" ALBK groups. The latter were presumed to be of hunter-gatherer descent (Zoffmann 2000). The population genetic analyses performed in this study have failed to show any meaningful differences between early and middle Neolithic populations on the Alföld, let alone differences that would suggest a strong involvement of hunter-gatherers in the middle Neolithic. A single potential link between mtDNA and osteological typology was observed at the Tisza culture site of Hódmezővásárhely-Gorzsa, where the skeleton of one young male was described as "protonordic", while the other skeletons (where typing was possible) were "gracile Mediterranean" and "cromagnoid" types (Farkas & Marcsik 1988). The individual in question (burial no. 18, laboratory name HMG02) was found to belong to haplogroup U5b, the only instance of this haplogroup in the entire Tisza dataset. In this case, both osteological and genetic data support hunter-gatherer ancestry for this particular individual. The appearance of a "morphologically Mesolithic" individual in the late Neolithic of the southern Alföld could be explained by immigration from a population with a stronger hunter-gatherer substrate. Unfortunately, no isotopic data is available for this individual, so that his provenance could not be established. The population genetic data obtained in this study yielded no possible source populations in the Alföld with a sufficiently strong Mesolithic component in the maternal gene pool (the site of Mezőkövesd notwithstanding). Furthermore, this "Mesolithic

component" would have had to persist for nearly 1500 years in the Alföld or its surroundings in order for it to (re)appear in the late Neolithic in the southern Alföld.
In general, osteological typology and the mitochondrial DNA cannot be expected to correspond with each other, even though both can be used to differentiate between populations. The mitochondrial haplogroup is maternally inherited and is not subject of selection, while genetic factors influencing skeletal morphology are expected to be autosomal markers and subject to recombination and sexual/ natural selection. Since anthropological data was not available for all studied individuals, the association between mitochondrial haplogroup and skeletal morphology could not be comprehensively assessed in this study, but may be an area for further research.

The interpretation of population discontinuity at the beginning of the Neolithic rests on the assumption that the Central-European hunter-gatherer metapopulation adequately represents the Mesolithic population of the Alföld. Unfortunately, there is currently no aDNA available from the preneolithic Alföld or the adjacent Iron Gates. However, the Central European hunter-gatherer-dataset covers a wide geographic range, including regions to the north, south and west of the Alföld. Within this dataset, there is no apparent geographic structuring or noticeable outliers, so it seems fair to presume that the preneolithic population of the Alföld would fit within the mitochondrial variability of the other Central European hunter-gatherers.
It is also possible that there was genetic admixture between the Mesolithic and Neolithic populations of the Alföld that was almost exclusively driven by males, in which case one would not see such a signal in the mtDNA of the farming populations. However, male migration rates are generally much lower than female migration rates in human populations (Seielstad et al. 1998), so that admixture between populations is primarily female-driven. Furthermore, the Neolithisation of Europe is closely associated with a strong male genetic component (Balaresque et al. 2010; Chikhi et al. 2002; Rosser et al. 2000). In the light of these findings, a population admixture between Neolithic and Mesolithic populations driven by Mesolithic, but not Neolithic males seems unlikely. However, until Y-chromosomal and/or autosomal data is available for the Alföld individuals, this issue cannot be conclusively addressed.

To summarise: both frequency- and sequence-based statistical analyses (PCA and cluster analysis, Fisher's exact test, F_{ST}-values) showed significant genetic distances between hunter-gatherers and all Alföld Neolithic groups and failed to confirm any links between hunter-gatherers and the Neolithic. Population continuity could be excluded down to the level of the regional groups, pointing to immigration as a major factor in the transition from Mesolithic to the Neolithic on the Alföld. The discontinuity in material culture between the Mesolithic and early Neolithic has already been noted elsewhere (Kertész 1996; Kertész 2002).

The existence of “pockets” of acculturating hunter-gatherers was not well supported by the data; even in the case of the Tiszadob/Bükk group and Mezőkövesd population discontinuity has to be assumed. The answer to question **a)** formulated in section 1.6 therefore is: The mitochondrial data shows genetic discontinuity between hunter-gatherers and the Neolithic populations of the Alföld.

4.3 Genetic continuity from early to late Neolithic on the Alföld

Both frequency- and sequence-based methods revealed strong similarities between early, middle and late Neolithic groups on the Alföld and the dominance of mitochondrial haplogroups J, T2, K and H throughout the Neolithic. At the sequence level, a substantial number of lineages persisted from the early until the late Neolithic (see ASHA). Especially frequent were basal lineages of haplogroup J, H (rCRS) and T2b. Haplogroup N1a, which is strongly associated with the Central European LBK (Haak, Forster, et al. 2005; Brandt et al. 2013), was present at stable frequencies from the earliest ALBK onwards. Interestingly, while haplogroup N1a was present in about 5% of individuals throughout the Neolithic, only few individuals share haplotypes. This high diversity was already noted in the Central European LBK (Haak, Forster, et al. 2005), and this study shows that the diversity of N1a may have been an “LBK- wide” phenomenon.

The frequency-based analyses also showed some development through time. Even in a simple diagram the increase in J and the concomitant decline of K and H from the early to the late Neolithic of the Alföld are quite noticeable (Figure 40). These differences may have contributed to the clear separation between early, middle and late Neolithic seen in the PCA. The results of Fisher’s exact test of the Körös culture showed the greatest similarity to the early ALBK, closely followed by the later ALBK (p-values =0.7516 and 0.7031, respectively) while the difference to the Tisza culture was more pronounced (p-value = 0.1287). Likewise, the early ALBK showed a higher similarity to the chronologically close *ALBK later* dataset than to the Tisza culture. However, the changes from early to late Neolithic appeared less severe than in the PCA. The test of population continuity further showed that the changes between early and late Neolithic could be adequately explained by genetic drift.

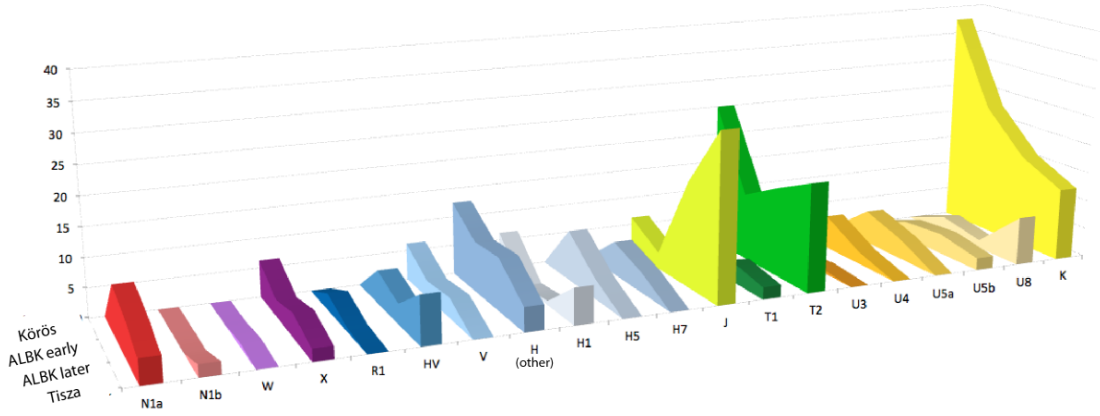

Figure 40: Temporal changes in haplogroup frequencies in the Alföld Neolithic. The values on the y-axis are given in %.

Unlike the frequency-based methods, the sequence-based analyses did not show a chronological development in the Alföld cultures- on the contrary, the F_{ST} values showed only small differences between the early, middle and late Neolithic of the Alföld. The ASHA showed that at any given point, between 50% (*ALBK early*) of individuals and up to 80 % (Tisza culture) of individuals carried lineages that originated in earlier phases of the Carpathian Basin Neolithic. The proportion of individuals carrying haplogroups that could be traced back to earlier periods was even higher. The percentage of individuals carrying unique lineages remained stable through time, giving no indication of a major influx of novel haplotypes in any period.

In conclusion, the early, middle and late Neolithic populations of the Alföld were genetically highly similar to each other, thus a population continuity within the Neolithic as proposed in question **b)** can be presumed. Many of the defining haplogroups/ lineages of the Alföld Neolithic were already present during the early Neolithic (see ASHA) and persisted through time. While the genetic composition of the Alföld Neolithic population underwent some changes over time, observed changes were not very strong and could be adequately explained by genetic drift over time. There were no detectable outside influences.

4.4 Regionalisation in the Alföld cultures

Multiple analyses were performed to investigate whether the regional stylistic groups of the later ALBK- Szakálhát, Tiszadob/Bükk and Esztár groups- were genetically distinct from each other. It was also investigated whether culturally uniform groups with a large distribution area, i.e. the Szakálhát group of the ALBK and the Tisza culture, showed geographically structured differentiation within their respective populations.

Regional groups of the middle and late Neolithic

The statistical results from both frequency-based and sequence-based analyses showed that in general, the regional groups of the middle and late Neolithic were highly similar to each other. Question **c)** of section 1.6 thereofore has to be answered in the negative: there is very little visible regional differentiation in the maternal gene pool of the ALBK, certainly less than the often distinct cultural characteristics of the regional groups might suggest. A likely explanation for this lies in the territory itself: the Alföld is a comparatively small region and is not divided by prominent geological barriers. It is traversed by several rivers running in a north-south (Tisza) and east-west (Maros, Körös) direction. These waterways provide an excellent means of transportation, and it has been hypothesized that already the Körös farmers used these "aquatic highways" for cultural exchange and trade (Whittle 2004). The potential influence of waterways on the process of Neolithisation has also been noted elsewhere (Davison et al. 2006). A network of communities connected by waterways would have facilitated genetic exchange across the Alföld, thus "homogenising" the genetic composition of the population and mitigating the effects of drift in small populations. Archaeological research has yielded ample evidence of territorial overlap and trade connections between the regional groups of the ALBK, which lends support to the hypothesis of the Alföld as an area that was both culturally and genetically interconnected.

Additionally, it has to be noted that the early and middle Neolithic of the Alföld directly (and according to the maternal genetic evidence, exclusively) derived from the Starčevo-Körös-Criş complex. There may have simply not been enough time for significant genetic differentiation to occur within among groups that ultimately derived from a single source population.

Nevertheless, it was possible to identify some patterns among the Alföld groups:

Regionalisation within of the Szakálhát group and the Tisza culture

Originally the Tisza settlements were divided into three "clusters" situated in the central Alföld, southern Alföld and southeastern Alföld. The sites of the Tisza culture in the southern and central Alföld lay in direct proximity to the Tisza and turned out to be very similar to each other genetically. This led to them being eventually combined into the "river" group. The sites representing the southeastern (later referred to as "eastern") group, Vésztő-Mágor and Békés-Povadzug, showed a quite differend haplogroup composition from the river group. Effects were most pronounced in the PCA and cluster analysis, but also present in the AMOVA, where the river and eastern Tisza dataset were assigned to separate groups in the best models. Thus referring back to question **d)**: the mitochondrial data show some substructure within the Tisza culture, although the possible mechanisms driving it are not entirely clear. The genetic homogeneity of the Tisza culture communities along the banks of the Tisza is readily explained by the fast and direct connection between them via the river itself. The Tisza-communities in the Middle Tisza region may have been direct "offshoots"

from those further downriver and thus share the same gene pool. However, the genetic differences between the "river" Tisza sites and the eastern Tisza sites cannot be fully explained by geographic distance or accessibility: the eastern sites lie close to several other Tisza sites of the river group, such as Hódmezővásárhely-Gorza, and they were by no means cut off from the "aquatic highway system", since they lie close to the Körös river, which runs into the Tisza. However, the eastern Tisza sites, in particular Vésztö-Mágor, may have been influenced by a group not included in this study: both sites lay on the border to the Herpály territory (Kalicz & Raczky 1987, p.14). It is therefore possible that the eastern Tisza sites reflect a genetic influence from the Herpály culture, which stretched from the Berettyó and Körös valleys into modern day Romania. Unfortunately, since there are currently no aDNA data from the Herpály culture, this question could not be further investigated in this study. Alternatively, the eastern Tisza group may have received some additional genetic input from Transdanubia- as the ASHA showed, one third of the individuals from this group initially found to carry "unique" lineages did in fact belong to haplotypes that were present in the Transdanubian Neolithic.
A more comprehensive dataset encompassing samples from the entire distribution area of the Tisza culture could help to further address the question, as there were quite large distances between the Tisza sites sampled in this study, and Tisza sites from the Upper Tisza Valley were entirely missing. While this aided the separation into geographical groups, it may have also had the effect of sampling only the endpoints of a spectrum, thus giving the appearance of genetically differentiated subpopulations where there really was a continuous population throughout the Tisza territory.
The genetic distances and Fisher´s exact test on the northern and southern Szakálhát groups was not conclusive evidence for a separation between the two, but they were frequently placed in different groups in the cluster analysis and the AMOVA. However, one of the best models in the latter paired the two regions of the Szakálhát group together. The MDS showed them to be similar on the sequence level. Therefore it presently seems likely that the northern and southern Szakálhát groups are both part of the same genetically homogeneous population. A larger sample size of northern sites of the Szakálhát group may be necessary to explore this issue further.

Earliest ALBK/Szatmár and the Esztár group

Fisher's exact test showed the earliest Alföld LBK/Szatmár group and the Esztár group (p-value 0.8993) to be extremely similar in their haplogroup composition. This was mirrored by an extremely low (but not statistically significant) F_{ST} value. The effect was less pronounced in the PCA and cluster analysis, but clearly visible in the sequence-based analyses. In the AMOVA, models where early ALBK and Esztár were grouped together consistently performed better than models where they were separated. Notably, both groups share a lineage of haplogroup R1 that was not observed elsewhere in the Carpathian Basin or even in the pan-European comparison data. While the earliest Alföld LBK preceded the development of the Esztár group, both groups occupied adjacent areas in the northern Alföld. It

appears as if the genetic legacy of the earliest Alföld LBK was preserved in the Esztár group to a larger degree than in the other ALBK groups. One possible reason is a decreased genetic exchange between the Esztár group and the other areas of the Alföld. The Esztár sites which were sampled for this study lie at some distance (ca. 25-50km) from the Berettyó and Tisza (Figure 3, Figure 8). While not insurmountable, this distance to these major waterways may have inhibited travel over longer distances.

The Szakálhát group and the Tisza culture

The Szakálhát group of the ALBK and the Tisza culture were shown to be genetically highly similar to each other- when taking the regional subgroups of both into account, the similarity was strongest for the southern Szakálhát group and the river group of the Tisza culture. In Fisher's exact test, the pairing between the southern Szakálhát group and the Tisza river group yielded the highest p-value of all pairings involving the southern Szakálhát group and vice versa. The PCA and cluster analysis confirmed the strong ties between the two, as did the F_{ST} values, although they did not reach statistical significance. In the MDS, both northern and southern Szakálhát groups were placed in close proximity to the Tisza river group. In the AMOVA, the best models nearly invariably put the southern Szakálhát and river Tisza groups into the same group.

Although C-14 dates are not available for all sites, it is generally accepted that the Szakálhát group was seamlessly succeeded by the Tisza culture in the southern and central Alföld (see also introduction of Kalicz & Raczky 1987). There is a large territorial overlap between the two groups in the southern and central Alföld (Figure 41), and a number of Szakálhát sites remained in use during the Tisza culture. The high similarity between the southern Szakálhát sites and the Tisza sites from the same region points to strong local continuity in the population.

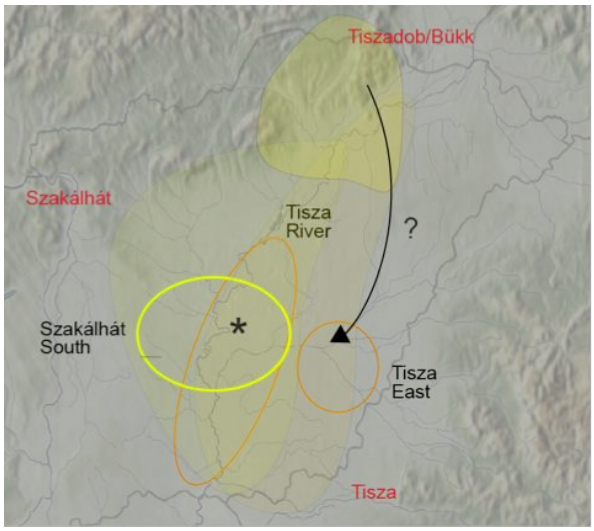

Figure 41: Relationships between regional groups of the ALBK and the Tisza culture. The asterisk marks the overlap between the territory of the southern Szakálhát group and that of the river group of the Tisza region. The arrow indicates the possible influence of the Tiszadob/Bükk group on the eastern Tisza group.

The Tiszadob/Bükk group and the eastern Tisza sites

Based on F_{ST}-values, an unexpected affinity was found between two regional groups, which are not only separated by chronology, but also geography: the eastern Tisza group in the southeastern Alföld and the Tiszadob/Bükk group in the far north.

Both groups had some unusual characteristics: Besides the elevated proportion of U-clades, it they also exhibited an unusually high frequency of haplogroup X, which could not be caused bydue to maternal kinship alone, since only few of the observed haplotypes were identical. Probably partly due to this, the Tiszadob/Bükk group also contained a higher percentage of unique lineages than the other Alföld groups: 29 % of its individuals carry lineages which were unique in the Alföld. This percentage declined by one third when Transdanubia was included in the analysis, but still 20% of individuals carried lineages that were unique to the entire Carpathian Basin. It is not entirely clear why the Tiszadob/Bükk dataset exhibited such a high proportion of lineages that were not found elsewhere in the Carpathian Basin. A hunter-gatherer legacy is unlikely, given the population discontinuity to the Mesolithic metapopulation and the fact the unique lineages did not belong to U or subclades thereof, but rather to lineages such as N1a and T1. Barring as-yet undetected (genetic) influences from neighbouring areas with no available aDNA data, e.g. Romania, it appears that “Tiszadob/Bükk” lineages were limited in their dispersal across the Alföld, but there may have been a somewhat more lively genetic exchange with Transdanubia. Cultural practices may have played a role in this, because the lively trade contacts between the Tiszadob and Bükk groups and neighbouring cultures, .e.g the Szakálhát and Esztár groups, indicates that genetic exchange was not a technical impossibility within the Alföld. The link to Transdanubia is quite interesting and would be a matter of further investigation by archaeologists.

Only about 35% of the individuals in the eastern Tisza group shared lineages with the other Neolithic groups of the Alföld. Interestingly, the percentage of lineages shared with the Transdanubian cultures was higher, reaching up to 56%. Concurrently, the high percentage of unique lineages (24%) originally observed in the eastern Tisza group dropped considerably when also taking the Transdanubian lineages into account. This indicates contact of the eastern Tisza group with Transdanubia.

It appears unlikely that the Tiszadob/Bükk group had a direct influence on the late Neolithic Tisza culture considering the considerable geographic distance. On the other hand, the Tiszadob and Bükk groups were highly involved in the regional trade, providing the rest of the Alföld (and beyond) with lithic materials and high-quality pottery (Kalicz & Makkay 1977, p.102). Bükk material was discovered in the lowest layers of a number of Tisza tells, indicating that the early Tisza phase overlapped with the Bükk group (Kalicz & Raczky 1987, pp.21–22). The eastern Tisza group may have retained genetic traces of previous contacts between the two regions. Another possible link between the Tiszadob/Bükk group and the eastern Tisza sites could be the Herpály culture, whose northern extent was close to or may have even overlapped with the Tiszadob/Bükk group in the North and bordered on the Tisza territory in the Körös region of the eastern Alföld (Kalicz & Raczky 1987, pp.8–9 map).

It also has to be noted that the association between the two groups was notable only in the F_{ST} values/ MDS and the AMOVA, where the best-fitting models grouped the two together. In Fisher's exact test, the Tiszadob/Bükk group was the most similar to the Körös culture, the earliest ALBK and the northern Szakálhát group, with the eastern Tisza group coming in fourth place. The eastern Tisza group in turn appeared to be more similar to the northern Szakálhát group than the Tiszadob/Bükk group. In the other frequency-based methods (PCA and cluster analysis), the results were similar: the Tiszadob/Bükk and eastern Tisza groups showed similarities, but their pairing did not stand out as particularly close. Of the 11 eastern Tisza individuals carrying haplotypes that could be traced back to the later ALBK, two (18%) showed lineages that were specific to the Tiszadob/Bükk group, but this was not particularly remarkable either- two individuals also showed Esztár-specific lineages.

Without more data this question cannot be satisfactorily solved, and at present another explanation has to be considered: The apparent affinity between the Tiszadob/Bükk and eastern Tisza group in the MDS plot may reflect that they both occupy outlier positions with respect to the other Alföld group rather than a "true" similarity

A "Southern Alföld group"?

In the ASHA involving only the Alföld cultures, it appeared that the Szakálhát groups and the river group of the Tisza region showed a higher early Neolithic influence than the other groups. This suggested a geographical variation in the degree of Körös ancestry, where groups from the lower and middle Tisza region retained a higher early Neolithic genetic influence than groups of the northern and eastern

Alföld. This pattern could be explained with the presumed movement of the first farmers on the Alföld-: coming from the south and staying close to the main waterways, particularly the Tisza- and indicate increased population continuity for this "core area". The AMOVA offered only moderate support for this thesis: one model grouping the Körös culture, the Szakálhát groups and the Tisza River group together was among the five best models. However, the inclusion of the Starčevo culture in the ASHA revealed that the early Neolithic influence was similarly high in all regional groups except for the earliest Alföld LBK. While there is a strong connection between the southern Szakálhát group and the river group of the Tizsa culture (see previous section), both frequency- and sequence-based methods failed to clearly and consistently link these two to the northern Szakálhát group and the Körös culture.

Regionalisation during the early Neolithic?

Archaeological research has shown that the Körös culture first entered the Alföld from the south and spread northward along the Tisza and other river systems, with settlements becoming smaller and more transitory in the process (Mester & Rácz 2010; Domboróczki et al. 2010; Whittle 2004; Bánffy 2012; Domboróczki & Raczky 2010). Findings of Körös remains in the upper Tisza region have raised the possibility of a second branch of the Körös culture entering the northeastern Alföld from Romania (Domboróczki & Raczky 2010; Domboróczki 2010). It would have been interesting to study whether there were genetic differences between the two branches and subsequently between Körös settlements from the southern and northern Alföld. However, the question of a regionalisation of the Körös culture was not addressed in this thesis because of the small size of the Körös dataset and its lack of sites from the northern Alföld. As far as the geographical structuring of the Körös population in the lower and middle Tisza region is concerned, the following can be stated: few of the haplogroups found in the Körös dataset were unique to a single site. Most were present at multiple sites, hinting at a rather uniform haplogroup distribution. However, additional data would be required to further investigate this question

4.5 The Neolithic Cultures of the Alföld compared to their contemporaries

4.5.1 Transdanubia

The roots of the Neolithic of the Carpathian Basin go back to the Starčevo-Körös-Criş complex and its core area in the northern Balkans. Farmers of the Starčevo culture settled Transdanubia, while the Alföld was settled by the Körös culture. Their communities developed in parallel, giving rise to a number of distinct cultural groupings. However, there were trade connections between the two regions, in particular during the middle and late Neolithic.

In general, both frequency- and sequence-based analyses showed the Transdanubian and Alföld cultures to be highly similar to each other throughout the Neolithic. Fisher's exact test and the F_{ST}

values of pairwise comparisons between Transdanubian and Alföld cultures lay within the same low range as comparisons involving only the Alföld cultures. The MDS showed no clear separation between Alföld and Transdanubian cultures either.

It is interesting to note that the frequencies of U-clades in the middle and late Alföld Neolithic were higher than in the early Neolithic of Central Europe, i.e. the LBK (Brandt *et al.* 2013) and in the early and middle Neolithic of Transdanubia (Szécsényi-Nagy et al. 2014). While population continuity between hunter-gatherers and farmers in the Alföld is not supported by the data and the overall hunter-gatherer-influence on the Alföld Neolithic was shown to be insignificant, it is possible that the Alföld cultures had more genetic exchange with local hunter-gatherers than the Transdanubian or Central European LBK farmers. Sites of the northern Alföld such as Mezökövesd and their unusual haplogroup composition may be traces of the "interaction zones" postulated by archaeological research (Bánffy & Sümegi 2012).

Starčevo

The ASHA revealed that a large proportion of individuals throughout the Alföld carried haplotypes that were already present in the early Neolithic Starčevo culture. The Körös culture in particular was genetically highly similar to the Starčevo culture, as both frequency- and sequence based methods consistently showed. A common origin of the Starčevo and Körös cultures therefore seems not only highly likely from an archaeological point of view, but is also well-supported by the genetic evidence. Furthermore, the similarities between the Transdanbian and Alföld cultures over the entire Neolithic period likely stem from this shared genetic substrate.

Vinča

The Vinča culture originated in Serbia, where it represents the middle to late Neolithic. Vinča settlements appeared in Transdanubia during the middle Neolithic, but no sites have been found on the Alföld. In the PCA and cluster analysis, the Vinča culture was close to the Starčevo -Körös cluster, but that affinity was not reflected in the sequence-based methods. A possible explanation for the frequency-based similarities between the Vinča culture and the early Neolithic cultures may be that the Vinča culture had a similar haplogroup composition to both, but contained different haplotypes. Since the territory of the Vinča culture overlapped with the source region of the Starčevo and Körös cultures, they may have shared the same genetic origin/ variability, explaining their similarity. The differences on the sequence level may be explained by the Körös and Starčevo culture containing only a subset of the total variation present in the Balkans.

It is known that the Szakálhát group of the Alföld LBK and the Tisza culture had trade contacts to Vinča sites south of the Maros (Kalicz & Raczky 1987). However, the affinities of these two groups to the

Vinča culture were not particularly strong in the analyses- in fact, the genetic distance between the southern Szakálhát group and the Vinča culture were comparatively large at 0.04.
However, the analysed Vinča sites were settlements from middle Neolithic Transdanubia. Without samples from the core area of the Vinča culture it cannot be ascertained whether the Transdanubian sites accurately represent the actual genetic variability of the Vinča culture. The closeness between the Carpathian Basin early Neolithic and the Vinča culture could simply be the result of genetic admixture occurring at the Transdanubian sites.

Lengyel

Archaeological research has shown strong ties between the late Neolithic Lengyel culture from Transdanubia and the Tisza culture (Sebők 2012; Kalicz & Raczky 1987, pp.21–22). Lengyel and Tisza cultures showed a strong affinity towards each other in the PCA (together with the Sopot culture), but the sequence-based analyses (MDS, ASHA and AMOVA) did not confirm a particularly close connection between the two cultural entitities. This does not disprove the cultural contacts as observed by archaeologists, but once more underscores the strong inherent similarity of the Carpathian Basin Neolithic cultures among themselves. This homogeneity makes it very difficult to determine whether there was any increased genetic admixture between the Lengyel and Tisza cultures occurring alongside the trade connections. An increased resolution of haplotypes, for instance by HVS-II typing or entire mitochondrial genomes, would help address this problem in the future.

In summary, the mitochondrial data from the Alföld Neolithic showed strong parallels to the Transdanubian Neolithic. A common origin of these two cultural spheres is not just possible, but strongly supported by the data, thus answering question **e)** in the affirmative. Unfortunately, because of the general similarity of the Neolithic cultures in the Carpathian Basin it may be difficult to detect finer patterns in the dataset. Analysis methods which yield higher genetic resolution, such as Next Generation Sequencing, will therefore be required to conclusively address the relationships between the Alföld and Transdanubia.

Influences from Romania?

The Esztár group in the eastern Alföld had a pottery style that was also common in the Szamos region of neighbouring Romania (Bánffy 2006). Unfortunately, Romanian aDNA data from the Neolithic is still lacking, so that the genetic relationships and possible influences between the Esztár group and contemporaneous Romanian groups could not be investigated in this study. On the other hand, Romania was settled by the Criş- culture, which was culturally closely related to the Körös and Starčevo cultures. It does therefore not seem far-fetched to assume that the mitochondrial gene pool of the

Romanian Neolithic population was very similar to the rest of the Carpathian Basin. Genetic introgression and admixture may therefore not be easily recognizable, if at all.

4.5.2 Europe

The defining culture of the early Neolithic in Central Europe was the LBK, which originated in Transdanubia. Culturally, the Alföld LBK is closest to the Transdanubian and Central European LBK, but until now it was not known whether this was also true for its genetic composition. Therefore, the Alföld LBK was compared with European cultures from the same period (6000- 4500 BC), including populations from eastern, southwestern and Central Europe.

The analyses showed the Alföld LBK can be regarded as a part of a "LBK continuum" that includes the Transdanubian and Central European LBK as well as its immediate successors in Central Europe, thus answering question **f)**. Haplogroup N1a, one of the characterizing haplogroup of the Central European LBK, is also present throughout the Alföld Neolithic. Incidentally, N1a shows high haplotype variability in the Carpathian Basin: the SHA revealed few matching N1a lineages between the Alföld, Transdanubia and Central Europe. Interestingly, a particular subclade of T2, T2b23, is found in the Alföld and Transdanubian Neolithic (Szécsényi-Nagy 2014 unpublished), but not in the LBK of Central Europe and thus possibly is an example of genetic variability that was "lost on the way". The slightly larger differences between the Körös culture, Tisza culture and the Central European Rössen culture may reflect the fact that they precede or follow the actual LBK period in both regions, strengthening the argument that the main link between the Carpathian Basin and Central Europe was established during the LBK period.

In contrast, there were no affinities between the Neolithic Alföld and neighbouring Ukraine. The latter was much more similar to the hunter-gatherer metapopulations than to any other European group. The Ukrainian Neolithic sample set was classified as "Neolithic" based on the use of pottery, but it represents a very early stage of Neolithisation in the Ukraine. The Dniepr-Donetsk cultural complex, which the individuals in the Ukrainian dataset belonged to, retained a largely Mesolithic lifestyle and had cultural ties to the hunter-gatherers of the region (Lillie 1998). Osteological analyses have linked the Dniepr-Donetsk culture to the Mesolithic population of Lepenski Vir (Zoffmann 2000). It therefore is not unexpected that the Ukrainian Neolithic sample set associated more closely with the preneolithic European hunter-gatherer populations than with the Neolithic populations of the Iberian Peninsula, Central Europe or the Carpathian Basin. However, the Ukrainian population in the analyses was very small and may not be representative of the Neolithic population of that region. Without additional data, a genetic link between the Alföld and Eastern Europe -while seeming unlikely- cannot be conclusively disproven.

Except for the Catalonian Cardial, the early Neolithic groups of the Iberian Peninsula were clearly distinct from the Alföld cultures. The Iberian Peninsula was settled by farming communities expanding

along the Mediterranean coasts, and thus on a different route than the Alföld. Multiple models of Neolithisation have been proposed for the Iberian Peninsula, and it has been supposed that local hunter-gatherers played a more active role in propagating the new subsistence strategy in southwestern Europe than in Central Europe. What can be seen from the frequency- and sequence-based analyses is that the Iberian Neolithic cultures genetic background than the Alföld Neolithic. The only exception is the Catalonian Cardial sample set, which shows high affinities to the Central European Neolithic (Rössen culture) in the PCA, and to the earliest ALBK in the MDS. Both the Rössen and the earliest ALBK dataset have high frequencies of H and K, which may explain this similarity. Since H was not split into subgroups for the MDS, the affinities between the earliest ALBK and the Catalonian Cardial may have been overstated in the MDS (see next section).

In summary and to answer questions **f)** and **g)**: the Alföld Neolithic and the Central European early and middle Neolithic were closely related genetically, and both were distinct from the Neolithic populations of the Iberian Peninsula and (probably) Eastern Europe.

The curious case of haplogroup H

H is the dominant haplogroup in present-day European populations, but aDNA research has shown that this was not always the case: In preneolithic Europe, it was detected only in few instances on the Iberian and Italian peninsulae, while its frequencies in Neolithic to Bronze Age Europe were higher, but nowhere near the modern-day levels of roughly 40%. The designation “H” covers a vast number of subclades with different frequencies and distribution areas. The most common subclade, H1, has been linked to the postglacial expansion of AMH from the Franco-Cantabrian refugium about 18 000 years ago (Achilli et al. 2004; Soares et al. 2010). A similar history has been reconstructed for H3. Subclade H5, on the other hand, is the most common common in the western Caucasus and the Balkans, as is H7 (Roostalu et al. 2007), which does not conclusively prove, but indicates an Eastern European origin for these clades (Brotherton et al. 2013).

Part of this thesis was to assess the H-variability in the Alföld Neolithic and compare it to data from the rest of Europe. By using the HPlex-17, which resolves the most frequent European subclades of H, it was possible to more finely resolve haplogroup H in the Alföld than with the HVS-I and GeneCoRe22 alone. The prehistoric comparison data set was assembled based on studies where H was resolved to a similar level. These studies are still in the minority among aDNA-publications, and thus the “H-dataset” differed from the dataset for the bulk of the population genetic analyses by covering the European Neolithic to the early Bronze Age for a sufficiently large dataset.

An interesting observation in the ancient data is the ubiquitous presence of haplogroup H1: It was found in large frequencies in Neolithic to Bronze-Age populations of the Iberian peninsula (C. Roth, personal communication), has been observed in the Central European LBK (Brotherton et al. 2013) and could also be confirmed in the Alföld Neolithic. Here, its presence is detectable already in the early

Neolithic Körös culture and persists into the late Neolithic. This widespanning distribution of H1 combined with its early appearance indicates that H1 may have been part of the Mesolithic substratum in all of Europe. It has already been detected in Mesolithic populations of the Iberian Peninsula (Chandler 2003), but not yet in Central and Eastern Europe.

Subhaplogroups H5 and H7 are absent on the Iberian Peninsula, but they have been detected in Central Europe/Germany. The Alföld Neolithic also contains stable proportions of H5 and H7, in higher frequencies than the studied Central European groups. Given that both clades are still more frequent in the Balkans and the Caucasus than in western Europe and that the coalescence ages of H5 and H7 have been estimated at 13 000 and 15 000 years, two scenarios are possible: both H5 and H7 may have already been present in the Mesolithic population of the Carpathian Basin; Admixture with the local Mesolithic population or neighbouring groups carrying H5 and H7 would have then led to their incorporation into the Alföld (and probably Transdanubian) maternal gene pool. However, no actual instances of H5 and H7 have been observed in Central or Eastern European Mesolithic individuals yet. The two clades may also have arrived in the Alföld with the first farmers- while the Körös dataset exhibited no individuals belonging to either H5 or H7, the earliest ALBK group did.

Another interesting link between the Alföld and its neighbouring regions to the east is provided by haplogroup R1, which was detected in two individuals from the ALBK: R1 is also quite rare in modern populations. Its origins are not entirely clear: on the one hand, it has been associated with the Neolithic immigration from the Near East, while on the other hand, its distribution and variability suggest an origin in the northern Caucasus (Torroni et al. 2006; Malyarchuk et al. 2008).

Haplogroup H3, which is frequent in the prehistoric Iberian samples, is completely absent in the Alföld Neolithic, which would be concordant with the proposed western European origin of this particular sub-haplogroup.

It is interesting how well the modern distributions and presumed origins of H1, H3, H5 and H7 match the data from the ancient populations. H1 is nowadays the most common subclade of H, but retains a frequency peak on the Iberian Peninsula (Achilli et al. 2004)- which corresponds well to the ubiquity of H1 in the ancient datasets and its high frequencies in the Iberian prehistory populations. H3 is still more common in Western Europe according to modern population data (Loogväli et al. 2004), and it was rare or absent in ancient Central Europe and the Alföld. The subhaplogroups H5 and H7 were only detected in ancient Central Europe and the Alföld, and their modern frequency peaks lie in the Balkans and the Caucasus (Roostalu et al. 2007). The basic distribution patterns of H1, H3, H5 and H7 thus appear to have not changed remarkably since the Neolithic, and the Alföld fits within the observed patterns.

The PCA showed a clear separation between the prehistoric cultures of the Iberian Peninsula and those of the Alföld. The early and middle Neolithic of Hungary clustered closely together, with the Unetice

culture as their nearest neighbor. The Unetice culture originates in Eastern Europe, which would support a geographical component in the variability of haplogroup H. The early Neolithic of Central Europe was also fairly close to the Alföld Neolithic, which may reflect its origins in the Carpathian Basin. The middle and late Neolithic of Central Europe occupied an intermediate position between the Alföld cultures and the Iberian Peninsula, which may reflect their position "halfway" between those two areas and a growing influence of southwestern Europe on Central Europe as the Neolithic wore on. The affinity of the late Neolithic Alföld group to the Iberian prehistoric groups is somewhat surprising, but is probably due to the sample size of just five individuals, of which 60% carry haplogroup H1. Additionally, since these three individuals also come from the same site, maternal kinship could not be excluded. The early and middle Neolithic datasets from the Alföld are larger and presumably offer a more accurate representation of ancient H-variability on the Alföld. The majority of individuals belonging to haplogroup H in the Alföld dataset could not be resolved with the HPLEX17. Since this set is geared towards modern-day populations, its comparatively weak discriminatory power on prehistoric data indicates the modern variability of H has been influenced and shaped by various events since Neolithic times. This is also supported by findings made in an earlier study involving whole mitochondrial genomes from Neolithic and Bronze Age Central Europe. Here, the majority of H-individuals belonged to haplogroups that are rare in modern populations (Brotherton et al. 2013).

In summary and in answer to question **h)**: while a large portion of H within the Alföld Neolithic could not be resolved in this study, the subclades that could be detected place the Alföld population closer to eastern and Central European Neolithic and Bronze Age groups than to groups from the Iberian Peninsula. The distribution of H1, H3, H5 and H7 in the entire dataset is largely compatible with the presumed population history of each clade. However, the full history of haplogroup H will only be adequately addressed with high-resolution analysis methods.

4.6 Summary

Population genetic analyses of aDNA data from 243 Neolithic individuals from the Alföld show that the beginning of the Neolithic on the Alföld was characterised by a large-scale introduction of new mitochondrial lineages. In some sites on the Northern Alföld, a certain degree of hunter-gatherer admixture may be presumed, but overall local hunter-gatherer communities contributed very little to the maternal gene pool of the Alföld Neolithic population. In this, the process of Neolithisation of the Alföld mirrors the Neolithisation of Transdanubia and Central Europe (Szécsényi-Nagy et al. 2014; Brandt et al. 2013).

There is clear population continuity from the early to the late Neolithic on the Alföld, and a low degree of differentiation between regional groups, which is likely caused by the persistent influence of a common source population and the high degree of territorial overlap and trade contacts between different groups. Geographical proximity corresponds with increased similaritiy in some, but not all cases. The data support a regional subdivision of the Tisza culture into an eastern and a "Tisza-adjacent" group, while the case is less clear in the Szakálhát group.

The Alföld cultures are genetically highly similar to their Transdanubian contemporaries. This genetic affinity between Transdanubia and the Alföld during the Neolithic is already evident in the early Neolithic (probably associated with the Starčevo-Körös-Criş complex), persisted into the late Neolithic and may have masked gene flow between Transdanubian and Alföld groups.

In the larger European context, the Alföld Neolithic shows the highest genetic similarities to those groups to which it is also culturally closest: the Transdanubian Neolithic, the Central European LBK and its successor, the Rössen culture in modern-day Germany.

In contrast to this, the Alföld Neolithic is different from the early Neolithic of the Iberian Peninsula, with the exception of the Catalonian Cardial culture. The differences between these two regions were also visible in the phylogeography of H: the Iberian Peninsula was dominated by H1 and H3, while the Alföld showed lower frequencies of H1, but exhibited H5 and H7. Interestingly, this pattern is reflected in modern European populations, where H5 and H7 are more common in Eastern Europe, whereas H3 is more frequent in western Europe.

The genetic distances between Alföld and the Iberian Peninsula may reflect the different routes of Neolithisation, i.e. the continental route vs. the Mediterranean route. The Carpathian Basin marks an important waypoint on the continental route. Although the Alföld Neolithic remained confined to its region of origin, it can claim "kinship" with the Transdanubian Neolithic- and the Central European cultures that descended from it – by their shared roots.

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Appendices

A: Equipment and chemicals

Uses	Chemicals	Producer
cleaning	HPLC water	Fisher Scientific GmbH, Schwerte, Germany
	powder detergent Alconox	Alconox Inc, New York, USA
	bleach DanKlorix (2.8% sodium hypochlorite)	Palmolive-Colgate GmbH, Hamburg, Germany
	DNA-Exitus	Applichem GmbH, Darmstadt, Germany
	oligonucleotides (lyophilised)	BioSpring GmbH, Frankfurt, Germany
Pre-PCR		
Sandblasting	corundum EW60/250my and 30B/50my	Harnisch+ Rieth GmbH und Co.KG, Winterbach, Germany
Milling	hydroxyapatite	Sigma-Aldrich Chemie GmbH, Steinheim, Germany
	sterilised silica sand (silica, SiO_2)	Carl Roth GmbH, Karlsruhe, Germany
Extraction	EDTA molecular biology grade 0.5M pH 8.0	Ambion GmbH, Darmstadt, Germany
	N-lauroylsarcosine sodium salt	Merck KGaA, Darmstadt, Germany
	proteinase K, recombinant, PCR grade, solution	Roche Diagnostics, Mannheim, Germany
	phenol/chloroform/isoamylalcohol 25:24:1 pH 7,5-8,0 Roti	Carl Roth GmbH, Karlsruhe, Germany
	trichloromethane/chloroform ROTISOLV	Carl Roth GmbH, Karlsruhe, Germany
	QG-buffer	Qiagen GmbH, Hilden, Germany
	Triton X-100	Sigma-Aldrich Chemie GmbH, Steinheim, Germany
	sodium chloride (NaCl) solution 5M	Sigma-Aldrich Chemie GmbH, Steinheim, Germany
	acetic acid 2M	Sigma-Aldrich Chemie GmbH, Steinheim, Germany
	ethanol 99%	Sigma-Aldrich Chemie GmbH, Steinheim, Germany
	Tris-EDTA (TE) buffer	Sigma-Aldrich Chemie GmbH, Steinheim, Germany
	silicon dioxide (SiO_2)	Sigma-Aldrich Chemie GmbH, Steinheim, Germany
	sodium acetate solution 5M	Sigma-Aldrich Chemie GmbH, Steinheim, Germany
PCR	bovine serum albumin (BSA)	Roche Diagnostics, Mannheim, Germany
	dNTP mix PCR grade 10mM	Qiagen GmbH, Hilden, Germany
	$MgCl_2$ Solution	Applied Biosystems GmbH, Darmstadt, Germany
	DNA Polymerase AmpliTaq Gold and 10x PCR buffer	Applied Biosystems GmbH, Darmstadt, Germany

Uses	Chemicals	Producer
Post-PCR		
Agarose gel electrophoresis	agarose UltraPure	Invitrogen GmbH, Darmstadt, Germany
	EDTA disodium salt (Na_2 EDTA)	Carl Roth GmbH, Karlsruhe, Germany
	boric acid	Merck KGaA, Darmstadt, Germany
	bromophenol blue	Carl Roth GmbH, Karlsruhe, Germany
	ethidium bromide solution 1%	Carl Roth GmbH, Karlsruhe, Germany
	DNA size standard Gene-Ruler 50bp DNA Ladder	MBI fermentas GmbH, St. Leon-Rot, Germany
	sucrose	Sigma-Aldrich Chemie GmbH, Steinheim, Germany
	Tris buffer	Carl Roth GmbH, Karlsruhe, Germany
LB growth medium and plates	agar-agar	Carl Roth GmbH, Karlsruhe, Germany
	ampicillin sodium salt	Carl Roth GmbH, Karlsruhe, Germany
	sodium chloride (NaCl)	Carl Roth GmbH, Karlsruhe, Germany
	yeast extract	Carl Roth GmbH, Karlsruhe, Germany
	IPTG	Carl Roth GmbH, Karlsruhe, Germany
	X-gal	Carl Roth GmbH, Karlsruhe, Germany
	tryptone	Carl Roth GmbH, Karlsruhe, Germany
Vector preparation	Sma I	MBI fermentas GmbH, St. Leon-Rot, Germany
	TTP-Mix	peQLab Biotechnologie GmbH, Erlangen, Germany
Ligation	T4-Ligase and 10x buffer	MBI fermentas GmbH, St. Leon-Rot, Germany
	pUC18 vector	in-house
Colony PCR	dNTP mix 10mM	MBI fermentas GmbH, St. Leon-Rot, Germany
	$MgCl_2$ Solution 25mM	Thermo Fisher Scientific Inc. Waltham, USA
	Thermo-Start Taq DNA polymerase and 10x buffer	Thermo Fisher Scientific Inc. Waltham, USA
Enzymatic purification	exonuklease I and 10x buffer	MBI fermentas GmbH, St. Leon-Rot
	Shrimp Alkaline Phosphatase (SAP) and 10x buffer	MBI fermentas GmbH, St. Leon-Rot
	thermosensitive Alkaline Phosphatase FastAP and 10x buffer	MBI fermentas GmbH, St. Leon-Rot
Cycle-Sequencing	cycle sequencing kit Big Dye Terminator v 1.1 (contains Ready Reaction Mix and 5x sequencing buffer)	Applied Biosystems GmbH, Darmstadt, Deutschland
	oligonucleotides	BioSpring GmbH, Frankfurt, Germany

Uses	Chemicals	Producer
SBE	ABI PRISM SNaPshot Multiplex Kit (Ready Reaction Mix)	Applied Biosystems GmbH, Darmstadt, Germany
	oligonucleotides	BioSpring GmbH, Frankfurt, Germany
Capillary gel electrophoresis	EDTA buffer 10x	Applied Biosystems GmbH, Darmstadt, Germany
	Performance Optimized Polymer (POP)6	Applied Biosystems GmbH, Darmstadt, Germany
	Hi-Di formamide	Applied Biosystems GmbH, Darmstadt, Germany
	GeneScan 120 LIZ Size Standard	Applied Biosystems GmbH, Darmstadt, Germany
Kits	Invisorb Spin Swab Kit DNA for DNA extraction from swab materials	Invitek GmbH, Berlin-Buch, Germany
Media and buffers		
LB medium	1% tryptone, 0.5% yeast extract, 0.5% NaCl	
LB plates for blue/white selection	1% tryptone, 0.5% yeast extract, 0.5% (85.56 mM) NaCl, 1.5% agar-agar, 0.01% ampicillin, 0.0476% ITPG, 0.1% X-gal	
1x TBE buffer	89mM Tris, 90mM boric acid, 1.25 mM EDTA	

Machines and Disposables	Producer
Pre-PCR	
handheld electric saw, Dremel Multitool	Dremel Europe B.V.,Breda, Netherlands
magnetic stirrer, Variomag Mobil Direct	Thermo Fisher Scientific GmbH, Schwerte, Germany
magnetic stirrer IKA-Combimag RCT	IKA-Werke GmbH & Co. KG, Staufen, Germany
submergible UV-lamp, customised	UV-Consulting Peschl e.K., Mainz, Germany
UVC-immersion unit, sterilAqua AQT2020	sterilAir GmbH, Kürten, Germany
mixer mill, model MM200	Retsch GmbH, Haan, Germany
circonium oxide milling cups for MM200	Retsch GmbH, Haan, Germany
reverse osmosis water purification unit	IEM-Industrial Equipment and Machinery GmbH, Mainz, Germany
pH-Meter, FiveEasy LE409	Mettler Toledo GmbH, Gießen, Germany
electric handheld saw, KaVO EWL	KaVO Elektrotechnisches Werk, Neukirchen, Germany
Mini centrifuge Rotilabo®	Carl Roth GmbH, Karlsruhe, Germany
table centrifuge, Micro-centrifuge 120	Hettich GmbH & Co.KG, Tuttlingen, Germany
table centrifuge, Universal 320	Hettich GmbH & Co.KG, Tuttlingen, Germany
compressor JUN-AIR, type OF1202-40B	JUN-AIR GmbH, Ahrensburg Germany
extraction unit D-LE 28	Harnisch+ Rieth GmbH und Co.KG, Winterbach, Germany
sandblaster P-G 400 (customised)	Harnisch+ Rieth GmbH und Co.KG, Winterbach, Germany
sandblaster P-G 400- K (customised)	Harnisch+ Rieth GmbH und Co.KG, Winterbach, Germany
Pipettes 5ml, 1000µl, 200µl, 20µl, 10µl Discovery Comfort	Abimed GmbH, Langenfeld, Germany
scale PCB 1000-2	Kern & Sohn GmbH, Balingen, Germany
glass beakers and measuring cylinders	Carl Roth GmbH, Karlsruhe, Germany; Schott AG, Mainz, Germany
Dispenser Dispensette® organic 0,5-5ml	Brand GmbH & Co. KG, Wertheim, Germany
vortexer M52 Minishaker	IKA-Werke GmbH & CO. KG, Staufen, Deutschland
hybridisation oven	Appligene, Illkirch, France
rotator SB2	stuart/ Bibby Scientific Ltd., Staffordshire, UK
Post PCR	
ABI PRISM™ 3130 Genetic Analyzer	Applied Biosystems GmbH, Darmstadt, Germany
digital gel documentation system	INTAS Science Imaging Instruments GmbH, Göttingen, Germany
electrophoresis chambers midi	Carl Roth GmbH, Karlsruhe, Germany
power supply Consort EV243	Carl Roth GmbH, Karlsruhe, Germany
centrifuge 5415R, 5415C und 5402	Eppendorf AG, Hamburg, Germany
thermocycler Eppendorf Mastercycler Gradient 5331	Eppendorf AG, Hamburg, Germany
thermocycler Eppendorf Mastercycler nexus	Eppendorf AG, Hamburg, Germany
thermocycler Eppendorf Mastercycler 5333	Eppendorf AG, Hamburg, Germany
Eppendorf® Thermomixer comfort 5355	Eppendorf AG, Hamburg, Germany
electroporator EQUIBIO Easyject Prisma	peQLab Biotechnologie GmbH, Erlangen, Germany
magnetic stirrer Combimag RCT	IKA-Werke GmbH & CO. KG, Staufen, Germany
reverse osmosis water purification unit	IEM-Industrial Equipment and Machinery GmbH, Mainz, Germany
Pipettes Discovery Comfort 5ml, 1000µl, 200µl, 20µl, 10µl	ABIMed GmbH, Langenfeld, Germany

Machines and Disposables	Producer
vacuum filtration system MultiScreen-HTS (incl. 96- well and 384-well filtration plates)	Millipore GmbH, Schwalbach, Germany
Pipettes 5ml, 1000µl, 200µl, 20µl, 10µl Discovery Comfort	Abimed GmbH, Langenfeld, Germany
incubator B 5042	Heraeus Holding GmbH, Hanau, Germany
vortexer "lab dancer"	IKA-Werke GmbH & CO. KG, Staufen, Germany
Disposables pre- and post PCR	
Safe-Lock PCR tubes 0.5ml	Eppendorf AG, Hamburg, Germany
0,5 ml PCR-tubes	Sarstedt AG & Co., Nürnbrecht, Germany
Safe-Lock PCR-tubes 1.5ml, 2ml	Sarstedt AG & Co., Nürnbrecht, Germany
low profile PCR 8-tube strips 0.1ml	Biozym Scientific GmbH, Hessisch Oldendorf, Germany
PCR 8-tube strips Rotilabo 0.2ml	Carl Roth GmbH, Karlsruhe, Germany
filtration tubes, Amicon Ultra-15 (50 kDa)	Millipore GmbH, Schwalbach, Germany
falcon tubes 15ml, 50ml	Sarstedt AG & Co., Nürnbrecht, Germany
Pipette tips Art Barrier Tips 10µl, 20µl, 100µl, 200µl, 1000µl	Thermo Fisher Scientific GmbH, Schwerte, Germany
Pipette tips EcoLine 200µl, 1000µl	MS-L GmbH, Wiesloch, Germany
Pipette tips OMNITIP 10µl	Abimed GmbH, Langenfeld, Germany
Pipette tips epT.I.P.S. Dualfilter 5000µl	eppendorf AG, Hamburg, Germany
electroporation cuvettes 2mm	peQLab Biotechnologie GmbH, Erlangen, Germany
polythene oversleeves DA01	HPC Healthline Ltd., Morden, UK
TyvekR Overshoes, model UH-TY-50	DuPont de Nemours GmbH, Neu-Isenburg, Germany
Coveralls CHF5 Classic	DuPont de Nemours GmbH, Neu-Isenburg, Germany
surgical face masks	Hansa Medical/ Industrial, Kirchhoff Group, Hamburg, Germany
head covers	Hansa Medical/ Industrial, Kirchhoff Group, Hamburg, Germany
laboratory sealing film Parafilm M(R)	Pechiney Plastic Packaging, Inc., Chicago, USA
latex gloves Medical 24 (non-sterile)	Hansa Medical/ Industrial, Kirchhoff Group, Hamburg, Germany
nitril gloves Medical 24 (non-sterile)	Hansa Medical/ Industrial, Kirchhoff Group, Hamburg, Germany
filter plates MultiScreen384-SEQ	Millipore GmbH, Schwalbach, Germany
filter plates MultiScreen 96 wells	Millipore GmbH, Schwalbach, Germany
petri dishes 92x16mm	Sarstedt AG & Co., Nürnbrecht, Germany
cutting discs Horico H350 220	Hopf, Ringleb & Co. GmbH & CIE, Berlin, Germany
Plastic face shield Sekuroka®	Carl Roth GmbH, Karlsruhe, Germany
cotton swabs for buccal cell samples	Heinz Herenz Medizinbedarf GmbH, Hamburg, Germany
sealable plastic bags Rotilabo, different sizes	Carl Roth GmbH, Karlsruhe, Germany
Sequencing plates MicroAmp™ Optical 96-Well Reaction Plate und 96-Well Plate Septa,	Applied Biosystems GmbH, Darmstadt, Germany
weighing paper MN226	Macherey & Nagel via Carl Roth GmbH, Karlsruhe, Germany
lint-free cosmetic wipes, kitchen rolls (non-sterile)	various brands

B: Complete list of samples taken for aDNA analysis

R/L H= right/ left humerus

R/L F= right/left femur

R/L T= right/left tibia

PP= Pars petrosa

Samples for which no reproducible HVS-I or SNP data could be obtained are marked grey.

* *the cal BC dates for HAJE are based on unpublished C14-dates from 7 graves (A.Anders, personal communication)*

Site	Dating		Burial Information					References	Individuals		Samples						Extractions														
	Cultural group	C14	Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
Abony, Serkeszék-dűlő 60. lh.	Tiszapolgár		008.	1				Kovacs (2011)	**ABO01**	**18**	M2 (75.)	0.66	M1 (36.)	1.24	right PP.				0.2						0.2							
	Tiszapolgár		008.	2					**ABO02**		M2 (65.)	0.7	M2 (55.)	0.67	M2 (85.)				0.24						0.21							
	Szakálhát		46						**ABO03**		LH	1.54	RF	1.8			VM14	120	0.23				VN14	120	0.23						
	Szakálhát		47						**ABO04**		RH	1.69	LF	1.69			VO3	130	0.2	WP14	200	0.23	VP3	100	0.25						
	Szakálhát		48						**ABO05**		M1 (46.)	1.21	M2 (47.)	1.12	M3 (48.)		VO4	120	0.22				VP4	130	0.2						
	Szakálhát		55						**ABO06**		M2 (37.)	1.49	M1 (26)	2.01	M2 (27.)		VO5	130	0.23				VP5	120	0.2						
	Szakálhát		65						**ABO07**		LF	1.32	RH	1.49			VO6	100	0.21				VP6	120	0.21						
	Szakálhát		75						**ABO08**		M2 (65.)	0.72	M2 (85.)	0.72	right PP.		VY1	140	0.25				VZ1	160	0.23						
	unknown		77						**ABO09**		M1 (27.)	1.28	M2 (26.)	1.65	M3 (28.)	0.82	VY2	160	0.25				VZ2	220	0.21				WO10	200	0.26
	Szakálhát		81						**ABO10**		M1 (26.)	1.37	M2 (47.)	1.26	M38		VY3	120	0.21				VZ3	100	0.23						
	Szakálhát		95						**ABO11**		M1 (46.)	1.78	M2 (47.)	1.83	M38		VY4	120	0.22				VZ4	160	0.2						
	Szakálhát		97						**ABO12**		RF	0.69	M2 (27.)	1.34	C (23.?)		WA18	130	0.23				WB18	120	0.26						
	Szakálhát		111						**ABO13**		M1 (45.)	1.42	M2 (27.)	1,44	M3 (28.)		WC1	120	0.23				WD1	100	0.24						
	Szakálhát		116						**ABO14**		LH	1.8	RH	1.9			WC2	160	0.25				WD2	120	0.28						
	Szakálhát		121						**ABO15**		left PP.	1.12	M2 (85.)	0.7	M2 (75.)		WC3	140	0.23				WD3	120	0.25						
	Szakálhát		122						**ABO16**		M1 (46.)	1.39	M2 (47.)	1.45	M3 (48.)		WE6	200	0.26				WF6	200	0.3						

Site	Dating			Burial Information					References	Individuals		Samples						Extractions															
	Cultural group	C14		Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
	Szakálhát			135						ABO17		M2 (37.)	1.38	M1 (36.)	1.4	M16/M17		WE7	200	0.25				WF7	200	0.24						
	Szakálhát			149						ABO19		RF	0.78	LH	1.3			WE8	200	0.24				WF8	200	0.23						
Adács, Mancsos-rét	Szakálhát			58					Domboróczki (2006), no individual description of the graves available yet	ADMA01	4	M16/26	1.92	M17/27	1.91	M18/28		VU3	160	0.23				VV3	160	0.24						
	Szakálhát			71						ADMA02		LF	3.18	RF	2			VU4	200	0.24				VV4	160	0.25						
	Szakálhát			89						ADMA03		M1 maxilla	1.77	I21	0.79			VU5	120	0.23				VV5	200	0.21						
	Szakálhát			101						ADMA04		M26	2	M37/47	1.8	C13	1.11	VU6	100	0.24				VV6	120	0.21				OWG1	200	0.28
Békés-Povádzug	Tisza				1.			2249.	Farkas, (1975), p. 61;Gulyás & Turcsányi (2009); Trogmayer (1962); Turcsányi (2007); Zalai-Gaál (1958)	BÉP01	8	M46.	1.79	M48.	1.37	long bone		VE1	-	0.2	VG1	140	0.22	VF1	160	0.24						
	Tisza				42.					BÉP02		M36	1.02	M37	0.85	M18.		VE2	-	0.23	VG2	120	0.2	VF2	120	0.21						
	Tisza				43.					BÉP03		M38.	1	M36.	1.62	long bone		VE3	-	0.23	VG3	120	0.2	VF3	120	0.22						
	Tisza				44.			2292		BÉP04		M48.	1.32	M46.	0.43	long bone		VE4	120	0.23				VF4	140	0.21						
	Tisza				46.			2294		BÉP05		M26.	1.55	M18	0.96	long bone		VE5	140	0.21				VF5	120	0.24						
	Tisza				47.			2295.		BÉP06		RF	1.34	LF	1.52			VE6	140	0.2				VF6	120	0.25						
	Tisza				68.			2316.		BÉP07		RF	1.92	LF	1.98	incisor		VE7	120	0.22				VF7	160	0.22						
	Tisza				69.			2317.		BÉP08		M36.	1.22	M75.	0.96			VE8	140	0.21				VF8	160	0.24						
Berettyóújfalu, Nagy-Bócs dűlő	Körös	CEZA-14834	5622-5560 (1 sigma)	368	27				Dani et al. (2006), Z. K. Zoffmann (2007), p. 46, individual descriptions of the graves not published yet	BENA01	11	M46	1.61	M47	1.42			VJ8	140	0.23				VL7	100	0.24						
	Esztar	CEZA-14136	5480-5384 (1 sigma)	369	27					BENA02		M48	1.19	LF	1.76	M48 M1(?) mandibula		VJ9	160	0.22				VL8	120	0.21						
	Kőrös	CEZA-14137	5517-5479 (1 sigma)	380	27					BENA03		m65	0.76	m85	0.67	m84		VJ10	120	0.2				VL9	100	0.23						
	Hungarian Conquest Period	CEZA-14138	830-950 (1 sigma)	419	175					BENA04		M16	2.15	M37	2.05	PM25		VJ11	120	0.25				VL10	120	0.24						
	Esztar			420	176					BENA05		M36/46	1.1	long bone	2.03	long bone	3.69	VM1	100	0.21				VN1	160	0.23				WO11	200	0.26
	Esztar			427	173					BENA06		M26	1.24	M37	1.08	M46		VM2	120	0.2				VN2	140	0.21						
	Esztar			476	179					BENA07		M16	1.11	I21	0.92	long bone		VM3	120	0.22				VN3	160	0.22						

Site	Dating		Burial Information					References	Individuals		Samples						Extractions													
	Cultural group	C14	Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
	Esztar		540	179					BENA08		M38/48	0.98	molar maxilla	0.79	I22		VM4	100	0.22				VN4	120	0.2						
	Kőrös		2142	940					BENA09		left pars petrosa	1.16	right pars petrosa	1.34			VM5	140	0.2				VN5	160	0.2						
	Kőrös		2146	941					BENA10		PM loose	0.36	piece of molar	0.51	jaw bone		VO1	120	0.2				VP1	120	0.22	WI18	200	0.29			
	Kőrös		2304	998					BENA11		piece of femur	2.07	piece of femur	2.08			VO2	120	0.21	VS18	160	0.29	VP2	90	0.23	VX16	180	0.25			
Cegléd, Váróczi-Hodula-dűlő, 4/1 lh	Szakálhát		215.					Kovacs (2011)	CEG01	15														140							
	Szakálhát		439.						CEG02		left PP	3.05	LF	1.27	M36		VU8	160	0.24				VV8		0.23						
	Szakálhát		451.						CEG03		right PP	2.06	m64	0.44	m65		VU9	240	0.23				VV9	120	0.2						
	Szakálhát		540						CEG04		M47	1.41	M38	0.9	M46		VU10	130	0.22				VV10	160	0.23						
	Szakálhát		544						CEG05		RF	1.97	M26	1.36	right PP.		VW8	140	0.27				VX6	120	0.24						
	Szakálhát		545.						CEG06		M46	1.47	M47	1.3	M16		VW9	120	0.25				VX7	200	0.25						
	Szakálhát		546.						CEG07		M16	1.68	M17	1.36	M27		VY15	120	0.23				VZ15	200	0.24						
	Szakálhát		560.						CEG08		M48	1.17	M37	1.16	M36		VY16	120	0.24				VZ16	200	0.26						
	Szakálhát		610.						CEG09		m74	0.58	m75	1.13	m85		VY17	120	0.24				VZ17	180	0.25						
	Szakálhát		662						CEG10		RF	2.34	LF	1.66			VY18	160	0.25				VZ18	140	0.21						
	Szakálhát		680.						CEG11		M46	1.28	M47	1.5	M48		WA1	120	0.25				WB1	160	0.28						
	Szakálhát		685.						CEG12		LF	2,29	RT	1.91			WA2	120	0.28				WB2	160	0.26						
	Szakálhát		686.						CEG13		RF	3,35	RH	1,89			WA3	200	0.27				WB3	120	0.28						
	Szakálhát		726.						CEG14		M46	1.5	m85	0.65	m84		WA4	160	0.26				WB4	120	0.22						
	Szakálhát		728.						CEG15		RF	1,68	m75	0.73	C13		WA5	160	0.26				WB5	120	0.23						
											LF	1,15	M16	1.25	PM1 (14.)	0.77	WA6	160	0.22				WB6	130	0.23				WP11	200	0.23
Cegléd Ipari-Park	Szakálhát		1	-				Tari (2001)	CGIP01	9	LT	1.87	LF	2.34			VI3	160	0.22				VK2	120	0.22						
	Szakálhát		4	125					CGIP02		M37	1.16	M26	1.66	M48		VI4	160	0.21				VK3	100	0.21						
	Szakálhát		5	-					CGIP03		M36/46	1.06	M37/47	0.94			VI5	100	0.21				VK4	100	0.2						
	Szakálhát		6	-					CGIP04		M1 (?)	0.66	left PPr.	1.92	2 pieces of bone	2.35	VI6	120	0.22				VK5	120	0.24				OWG3	200	0.23
	Szakálhát		7	147					CGIP05		LF	1.3	RH	1.39	I 11	0.45	VI7	120	0.22	VS16	200	0.27	VK6	80	0.22	VT16	130	0.27	OWG4	200	0.25

Site	Dating			Burial Information					References	Individuals		Samples						Extractions														
	Cultural group	C14		Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
	Szakálhát			8	-					CGIP06		M16/26	1.38	M36	1.5	M46		VJ4	120	0.22				VL3	100	0.22						
	Szakálhát			9	146					CGIP07		deciduous molar	0.19	piece of long bone	0.5			VJ5	80	0.19				VL4	140	0.23						
	Szakálhát			10	-					CGIP08		RF	1.91	LF	1.54			VJ6	120	0.21				VL5	120	0.2						
	Szakálhát			-	228					CGIP09		M16 (?)	1.26	M17	N.N.	left PPr.		VJ7	100	0.2				VL6	140	0.2						
Csanytelek-Újhalastó	Szakálhát				115.				Hegedus (1985,), Zoffmann (2001)	CSAN01	1	LF	1.16	RH	1.24			VQ4	160	0.24				VR4	200	0.2						
Debrecen, Tócópart Erdőalja	Esztár				101	278				TOPE01	13	M46	1.41	M47	1.07	PM		VS1	160	0.25				VT1	130	0.25						
	Esztár				221	576				TOPE02		M47	1.75	RH	2.78	femur (?)		VS2	280	0.24				VT2	200	0.25						
	Esztár				222	577				TOPE03		femur	2.77	femur	3.21			VS3	160	0.22				VT3	100	0.23						
	Esztár				223	578				TOPE04		M26	1.41	M27	1.57	PM		VS4	160	0.23				VT4	160	0.24						
	Esztár				312	757				TOPE05		humerus	0.97	femur (?)	1.49			VS5	200	0.2				VT5	130	0.25	WL15	160	0.33			
	Esztár				353	828			Hajdú, Nagy Emese (2009,2010) no individual descriptions of the graves available yet	TOPE06		M28	0.7	M36	0.97	M37		WA7	120	0.24				WB7	200	0.22						
	Esztár				930	989				TOPE07		M36	1.25	M48 (?)	0.97	M37		WA8	200	0.25				WB8	200	0.22						
	Esztár				889	1515				TOPE08		M46	1.54	M47	1.42	PM45		WA9	160	0.25				WB9	200	0.2						
	Esztár				921	1557				TOPE09		M46	1.61	M47	1.61	M37		WA10	160	0.26				WB10	160	0.23						
	Esztár				994	1625				TOPE10		RH	2.05	LH	2.15			WA11	200	0.24				WB11	220	0.26	WK16	200	0.31			
	Esztár				1412	1761				TOPE11		M46	1.29	M3 (?)	0.91	M47		WC8	200	0.21				WD8	160	0.22						
	Esztár				1420	1769				TOPE12		RF	1.63	LF	1.86			WC9	160	0.28				WD9	160	0.28						
	Esztár				1421	1770				TOPE13		M48	1.46	LF	1.53	right PP.		WC10	160	0.27				WD10	120	0.28						
Deszk -1. olajkút	Szakálhát	OxA-9376	5320 BC (95.4%) 5030 BC (2 sigma) 6010 BC (95.4%) 5780 BC (2 sigma)		5.			5253.	Trogmayer (1969), Lipták (1976)	DES05	2	femur	1.26	RF	1.41			VC8	160	0.19				VD8	160	0.24						
	Körös	OXA-9396			6.			5254.		DES06		M46	0.56	M38	0.76	femur	1.42	OWG2	200	0.24				VC9	120	0.22				VD9	140	0.22
Deszk-Ordos	Tisza				1.				Horváth (1977); Farkas,Marcsik (1988)	DEOR01	1	M28	0.9	M27	1.5			VS15	140	0.23				VT15	120	0.23						
Ebes, Sajtgyár 19.lh	Esztár				41		62		J. Dani (Déri Múzeum,	EBSA01	4	RF	2.3	LH	1.41			VU18	240	0.23				VW1	140	0.20						

Site	Dating			Burial Information					References	Individuals		Samples						Extractions																
	Cultural group	C14		Grave No.	Obj.	SN R	ST R	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1			
	Esztár				56		99		Debrecen)., personal communication	EBSA02		M26	1.63	M27	1.72	M28		VW2	160	0.21				VX1	200	0.22										
	Esztár				75		147			EBSA03		piece of tibia	1.97	piece of femur	1.92			VW3	120	0.24				VX2	120	0.22										
	Esztár				95		194			EBSA04		RF	1.23	LF	2.03			VW4	200	0.2				VX3	200	0.24										
Ebes, Zsong-Völgy út	Esztár				1311		2676			EBVÖ01	5	tibia	2.41	M47	1.19	femur	1.61	VU11	160	0.24										VV11	160	0.24			
	Esztár				1313		2678			EBVÖ02		LF	1.62	RF	2.67			VQ12	160	0.22				VR12	140	0.24										
	Esztár				1370		2891		Dani (2004)	EBVÖ03		M36	0.8	M37/47	0.82			VQ13	160	0.22				VR13	400+	0.22										
	Esztár				1408		2985			EBVÖ04		M38	1	LF	1.87			VQ14	160	0.21				VR14	400+	0.25										
	Esztár				1412		2989			EBVÖ05		M26	1.07	M27	1.31			VQ15	160	0.21				VR15	220	0.2										
Füzesabony-Gubakút	early ALBK/ Szatmár (II)	VERA-4237	5350 - 5210	1					Domboróczki (2009)	FUGU01	12	canine	0.83	PM	0.75	femur		VU14	160	0.2				VV13	140	0.21										
	early ALBK/ Szatmár (II)	deb-11092	5300 - 5080 (1 sigma)	2	119					FUGU02		humerus	0.88	M36/46	1.36	LF		VU15	160	0.21				VV14	160	0.23										
	early ALBK/ Szatmár (II)	VERA-4238	5350-5200	3						FUGU03		M46	1.27	M47	1.28	femur		VU16	200	0.2				VV15	170	0.22										
	early ALBK/ Szatmár (II)	VERA-4236	5380 - 5210	4	122					FUGU04		M16	1.52	M36	1.63	femur		VU17	100	0.21				VV16	120	0.2										
	early ALBK/ Szatmár (II)	VERA-4239	5470 - 5210	5						FUGU05		M17	1.67	M18	1.13	LF		VW5	140	0.22				VX4	160	0.25										
	early ALBK/ Szatmár (II)	VERA-4240	5350 - 5210	6						FUGU06		humerus	1.17	long bone	1.22			VW6	160	0.25				VX5	100	0.24										
	early ALBK/ Szatmár (II)	VERA-4241	5320 - 5070	7						FUGU07		M36	1.3	M46	1.28	piece of long bone	2.37	WA12	180	0.21				WB12	160	0.23				WO13	200	0.24			
	early ALBK/ Szatmár (II)			8						FUGU08		m54/64	0.22	m75	0.21	m85		WA13	160	0.22				WB13	200	0.21										
	early ALBK/ Szatmár (II)	deb-13042	5493-5385 (1sigma)	9						FUGU09		M36	1.23	M46	1.09	femur li		WA14	200	0.23				WB14	120	0.21										
	early ALBK/ Szatmár (II)	VERA-4242	5370 - 5200	10						FUGU10		M38	1.39	M48	1.32	femur li		WA15	120	0.23				WB15	200	0.24										
	early ALBK/ Szatmár (II)			12						FUGU11		M26	1.67	M36/46	1.54	piece of long bone		WA16	200	0.24				WB16	160	0.21										
	early ALBK/ Szatmár (II)			13						FUGU12		m54/64	0.29	m75/85	0.3	i51/61		WA17	120	0.29				WB17	140	0.3										
Garadna, Elkerülő 2.lh	Bükk			20					Csengeri (2010); Kővári, Szathmáry (2004)	GAEL01	13	M26	1.7	M48	1.25	M27		VW12	240	0.21				VX10	160	0.25										
	Bükk			38						GAEL02		RF	2.9	LF	1.8	Left PP		VW13	120	0.28				VX11	140	0.21										
	Bükk			57						GAEL03		M36	0.94	M48	0.97	M47		VW14	120	0.23				VX12	160	0.21										
	Bükk			62						GAEL04		M36	1.47	M37	1.38	M46	1.35	VW15	160	0.23				VX13	120	0.22				WO14	200	0.21			
	Bükk			83						GAEL05		RF	1.25	LF	2.51			VW16	140	0.21				VX14	160	0.24										

Site	Dating		Burial Information					References	Individuals		Samples						Extractions														
	Cultural group	C14	Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
	Bükk		86 + 52						GAEL06		left PPr.	2.24	right PP.	2.17			WG8	200	0.25				WH8	200	0.24						
	Bükk		109						GAEL07		M26	1.48	M27	1.41	PM15		WG9	200	0.24				WH9	200	0.22						
	Bükk		119						GAEL08		m55	0.81	m65	0.82	m75		WG10	200	0.2				WH10	200	0.21						
	Bükk		120						GAEL09		M48	0.93	M46	1.01	M47		WG11	200	0.22				WH11	200	0.23						
	Bükk		138						GAEL10		m65	0.65	m75	0.62	m64		WG12	200	0.25				WH12	200	0.24						
	Bükk		168						GAEL11		M28/27	0,95	M3 Mand	0.63	canine maxilla		WK10	200	0.28				WL10	160	0.31						
	Bükk		187						GAEL12		M16	1.59	M46	1.61	M47		WK11	200	0.28				WL11	160	0.3						
	Bükk		191						GAEL13		M36	1.41	M46	1.51			WK12	200	0.27				WL12	160	0.3						
Hajdúnánás, Eszlári ut, M3-45	late ALBK (phase III-IV)	5300-4995 cal BC*		50	93			Ráczky, Anders (2012), individual graves not published yet	HAJE01	20	M28	0.8	M26	1.12	M27		VO7							120	0.23						
																		100	0.2				VP7								
	late ALBK (phase III-IV)			52	95				HAJE02		M36	0.92	M17	0.97	M18		VO8	90	0.21				VP8	160	0.24						
	late ALBK (phase III-IV)			57	102				HAJE03		right p. petr.	2.32	M85	0.42	M55(?) deciduous molar maxilla		VO9	120	0.23				VP9	120	0.2						
	late ALBK (phase III-IV)			58	103				HAJE04		M27	1.47	M47	1.47			VO10	120	0.21				VP10	160	0.2						
	late ALBK (phase III-IV)			65	112				HAJE05		RF	1.92	LF	1.7			VO11	120	0.22	WJ18	200	0.33	VP11	120	0.25						
	late ALBK (phase III-IV)			74	128				HAJE06		M36	1.22	M3 maxilla	0.8			WM6	160	0.21				WN6	200	0.26						
	late ALBK (phase III-IV)			80	147				HAJE07		M47	1.3	M48	1.35	M46		WM7	160	0.2				WN7	200	0.22						
	late ALBK (phase III-IV)			106	195				HAJE08		LF	2.69	RF	2.64			WM8	160	0.26				WN8	200	0.27						
	late ALBK (phase III-IV)			107	196				HAJE09		M17	1.11	M38	0.79			WM9	160	0.21				WN9	200	0.21						
	late ALBK (phase III-IV)			108	197				HAJE10		M36/M46	1.74	M37/M47	1.7			WM10	160	0.24				WN10	200	0.25						
	late ALBK (phase III-IV)			111	201				HAJE11		P.petrosa links	3.42	M84	0.42	M85		WM11	160	0.25				WN11	200	0.2						
	late ALBK (phase III-IV)			113	203				HAJE12		M47	1.03	M36	1.25	M3 maxilla	0.86	WM12	160	0.23				WN12	200	0.23						0.21
	late ALBK (phase III-IV)			117	207				HAJE13		M1 mandibula	1.14	M55/M65	0.47			WM13	160	0.2				WN13	200	0.21						
	late ALBK (phase III-IV)			118	208				HAJE14		M36	0.97	molar maxilla	1.1	maxillary canine		WO1	200	0.25				WP1	200	0.2						

Site	Dating		Burial Information				References	Individuals		Samples						Extractions															
	Cultural group	C14	Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
	late ALBK (phase III-IV)			121	211				**HAJE15**		M26	1.37	left PPr.	2.64			WO2	200	0.23				WP2	200	0.25						
	late ALBK (phase III-IV)			124	214				**HAJE16**		LF	2.48	RF	2.06			WO3	200	0.22				WP3	200	0.28						
	late ALBK (phase III-IV)			127	218				**HAJE17**		humerus	1,09	ulna	1,58			WO4	200	0,29				WP4	200	0,24						
	late ALBK (phase III-IV)			128	219				**HAJE18**		humerus	2,56	femur	2,09	long bone		WO5	200	0,29				WP5	200	0,23						
	late ALBK (phase III-IV)			129	220				**HAJE19**		M46	1,25	M47	1,26	M48	1.03	WO6	200	0,25				WP6	200	0,27						0.25
	late ALBK (phase III-IV)			133	225				**HAJE20**		M36	1,51	M37	1,28	PM35		WO7	200	0,28				WP7	200	0,23						
Hejőkürt, Lidl logisztikai központ	Tiszadob		6					Kővári, Szathmáry (2006), no archaeological publication yet	**HELI01**	**15**	tibia	2.47	femur	2.56			WE1	200	0.29				WF1	200	0.26						
	Tiszadob		8						**HELI02**		M36	1.54	M28	1.22	M47		WE2	200	0.24				WF2	200	0.26						
	Tiszadob		10				2005.6.6		**HELI03**		M1 (?) maxilla	1.91	M3 (?) mandibula	1.44	femur		WE3	200	0.28				WF3	200	0.29						
	Tiszadob		35						**HELI04**		PM	0.84	femur	1.3	left PPr.		WE4	200	0.25				WF4	200	0.26						
	Tiszadob		84						**HELI05**		M16	1.27	M46	1.21	I21		WE5	200	0.28				WF5	200	0.24						
	Tiszadob		133				2005.6.18		**HELI06**		M16	1.43	M37	1.3	femur re		WI5	200	0.27				WJ5	200	0.23						
	Tiszadob		134				2005.6.19		**HELI07**		M26	1.03	M38	1.01	femur re		WI6	200	0.28				WJ6	200	0.22						
	Tiszadob		138				**2005.6.2**		**HELI08**		RF	2.39	LF	2.45			WI7	200	0.3				WJ7	200	0.27						
	Tiszadob		149						**HELI09**		RT	1.32	LF	2.18			WM1	160	0.22				WN1	200	0.28						
	Tiszadob		150						**HELI10**		m54	0.49	m55	0.86			WK13	200	0.23				WL13	160	0.27						
	Tiszadob		153						**HELI11**		M16/26	2.36	M37/47	2.53	M17(?)		WK14	200	0.3				WL14	160	0.33						
	Tiszadob		155						**HELI12**		M26	1.5	M28	0.98	M27		WM2	160	0.26				WN2	200	0.22						
	Tiszadob		163						**HELI13**		M36	1.23	M38	1.12	M37		WM3	160	0.22				WN3	200	0.25						
	Tiszadob		192				2005.632		**HELI14**		M46	1.85	m84	0.89	LF		WM4	160	0.22				WN4	200	0.23						
	Tiszadob		193						**HELI15**		M16	2.27	M26	2.22	m74		WM5	160	0.2				WN5	200	0.22						
Hódmezővásárhely-Kökénydomb	Tisza			1.				Farkas, Szalai (1992), Horváth (1992)	**KÖKE01**	**3**	m65	1.29	M26	1.27			VS14	140	0.24				VT14	220	0.22						
	Tisza			3.					**KÖKE02**		M48	1	M46	1.41			VU1	140	0.22				VV1	120	0.23						
HMV Kökénydomb, Vörös tanya	Tisza			159.				Farkas (1975); Banner,Foltiny (1945)	**KÖKE03**		M46	1.4	M38	1.1			VU2	100	0.24				VV2	200	0.21						

Site	Dating			Burial Information					References	Individuals		Samples						Extractions														
	Cultural group	C14		Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
Hódmezővásárhely-Gorzsa	Tisza				12				Horváth (1982, 1987); see Farkas,Marcsik (1988) for osteological analysis of burials 5 through to 19	**HMG01**	**10**	RF	1.84	RT	1.14	-	-	VE9	100	0.2				VF9	200	0.21						
	Tisza				18					**HMG02**		RF	1.4	LF	1.71	-	-	VE10	160	0.22				VF10	160	0.2						
	Tisza				19					**HMG03**		RF	1.53	LF	2.12	-	-	VE11	100	0.2				VF11	160	0.24						
	Tisza				27					**HMG04**		RF	1.87	LF	1.75	-	-	VE12	100	0.2				VF12	200	0.21						
	Tisza				29					**HMG05**		RF	1.79	LF	1.82	-	-	VE13	160	0.2				VF13	180	0.2						
	Tisza				60					**HMG06**		RF	2.12	LH	2.26	-	-	VE14	100	0.2				VF14	160	0.25						
	Tisza				61					**HMG07**		RF	1.64	LF	1.6	-	-	VE15	140	0.24				VF15	140	0.22						
	Tisza				68					**HMG08**		LF	1.71	RH	2.08	-	-	VE16	140	0.22				VF16	160	0.21						
	Tisza				5					**HMG09**		LF	1.79	RF	2.25	-	-	VG4	-	0.24	VJ1	140	0.24	VH1	140	0.21						
	Tisza				10					**HMG10**		RF	2.13	LF	1.57	-	-	VG5	200	0.22				VH2	160	0.2						
Hódmezővásárhely-Kotacpart	Körös			3/8	112				Banner (1935), Trogmayer (1969), Farkas (1975)	**HOKO01**	**2**	M18	0.81	M16	1.56			VQ1	200	0.25				VR1	160	0.24						
	Körös			25/1	131					**HOKO02**		M26	1.53	M28	0.87	femur		VQ2	200	0.21				VR2	140	0.21						
Kompolt, Kigyós-ér	classical to late ALBK			5/2					Domboróczki (2003) no individual descriptions of graves published yet	**KOKI01**	**5**	M16	1.63	PM14	0.79	PM25		VY5	140	0.23				VZ5	100	0.22						
	classical to late ALBK			17/7						**KOKI02**		PM15	0.71	LF	1.85	tibia		VY6	120	0.21				VZ6	160	0.21						
	classical to late ALBK			24/8						**KOKI03**		RH	2.28	LH	2.21	femur	1.93	VY7	140	0.25				VZ7	200	0.24						0.25
	classical to late ALBK			25/9						**KOKI04**		femur	2.2	tibia	2.03	left (?) humerus		VY8	140	0.24				VZ8	200	0.24						
	classical to late ALBK			26/10						**KOKI05**		LF	2.32	RF	2.69	long bone		VY9	140	0.24				VZ9	160	0.24						
Maroslele-Pana	Körös	OxA-9399	5920 BC (87.4%) 5720 BC		1.			3861.	Farkas (1975), Trogmayer (1964, 1969)	**MAP01**	**4**	LF	2.59	long bone	1.45	-	-	VC4	120	0.25				VD4	160	0.25						
	Körös				2.			3862.		**MAP02**		LF	1.61	long bone	0.71	-	-	VC5	160	0.21				VD5	120	0.23						
	Körös	OxA-9400	5730 BC (82.2%) 5600 BC		3.			3863.		**MAP03**		LH	1.01	piece of tibia	1.25	-	-	VC6	160	0.24				VD6	100	0.25						

Site	Dating			Burial Information					References	Individuals		Samples						Extractions															
	Cultural group	C14		Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
	Körös	OxA-9401	5750 BC (92.0%) 5610 BC		5.			3865.		MAP05		RF	1.43	long bone	2.21	-	-	VC7	160	0.25				VD7	120	0.23							
Mezőkeresztes-Cethalom	Late classical ALBK (phase II-III)			1						MECE01	12	C13	0.97	M28	1.12	RF		VS6	160	0.22				VT6	160	0.2							
	Late classical ALBK (phase II-III)			2						MECE02		M16	1.11	M17	0.94	PM34		VS7	160	0.21				VT7	160	0.22							
	Late classical ALBK (phase II-III)			6						MECE04		C13	0.8	LF	3.31			VS8	160	0.21				VT8	140	0.24							
	Late classical ALBK (phase II-III)			7						MECE05		femur	0.83	tibia	1.14			VS9	180	0.24				VT9	160	0.22							
	Late classical ALBK (phase II-III)			8						MECE06		LF	0.74	RF	1.3			VS10	120	0.22				VT10	160	0.21							
	Late classical ALBK (phase II-III)			11					Wolid, Simonyi (1995), descriptions of individual graves not published yet	MECE08		M36	1	LF	1.91	RF		WG5	200	0.25				WH5	200	0.27							
	Late classical ALBK (phase II-III)			15						MECE09		M36	1.16	M37	1.17	M47		WG6	200	0.26				WH6	200	0.22							
	Late classical ALBK (phase II-III)			18				2006.74.13		MECE10		M17	1.5	maxillary (?) PM	0.84	I11		WG7	200	0.26				WH7	200	0.21							
	Late classical ALBK (phase II-III)			18				2006.74.1		MECE11		m65	0.62	m85	0.61			WI1	200	0.23				WJ1	200	0.25							
	Late classical ALBK (phase II-III)			20						MECE12		m74	0.39	m64	0.39	RF		WI2	200	0.2				WJ2	200	0.23							
	Late classical ALBK (phase II-III)			21				2006.74.6		MECE13		humerus	1.01	left PPr.	1.74			WI3	200	0.21				WJ3	200	0.24							
	Late classical ALBK (phase II-III)			23						MECE14		M28	1.26	M47	1.11	M27		WI4	200	0.23				WJ4	200	0.24							
Mezőkövesd-Mocsolyás	Szatmár			1	32				Kalicz, Koós (2001), Zoffmann (2014)	MEMO01	24	M26	1.45	M36	1.43	M28		WG13	200	0.24				WH13	200	0.23							
	Szatmár			2	103 (lower body), 75a (upper body)					MEMO02		M38	1.08	PM	0.7	right PP.		WG14	200	0.24				WH14	200	0.28							
	Szatmár			3	106					MEMO03		right PP.	3.13	left PPr.	2.03			WG15	200	0.38				WH15	200	0.38							
	Szatmár			6	170					MEMO04		M37	1.81	M47	1.68	bone		WG16	200	0.26				WH16	200	0.31							
	Szatmár			6a	2006.69.6					MEMO05		M46	1.85	M47	1.88			WG17	200	0.31				WH17	200	0.25							
	Szatmár			7	190					MEMO06		right PP.	2.12	left PPr.	0.78			WI8	200	0.25				WJ8	200	0.21							
	Szatmár			8	192					MEMO07		M26	1.79	M27	1.59	M38		WI9	200	0.21				WJ9	200	0.23							
	Szatmár			9	193					MEMO08		deciduous molar	0.3	deciduous molar	0.3	right (?) p.petr.		WI10	200	0.21				WJ10	200	0.2							

Site	Dating		Burial Information					References	Individuals		Samples						Extractions														
	Cultural group	C14	Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
	Szatmár		10	194					MEMO09		C	0.43	C	0.38	femur		WI11	200	0.22				WJ11	200	0.2						
	Szatmár		11	195					MEMO10		M16	1.67	M46	1.41	M47		WI12	200	0.23				WJ12	200	0.24						
	Szatmár		12	196					MEMO11		M27	1.24	femur	1.23	I31/41		WI13	200	0.21				WJ13	200	0.23						
	Szatmár		13	197					MEMO12		M26	1.69	M16	1.82	mandibular PM		WI14	200	0.21				WJ14	200	0.26						
	Szatmár		14	198					MEMO13		m65	1.05	left (?) p.petr.	0.91	m75		WI15	200	0.2				WJ15	200	0.21						
	Szatmár		17	216					MEMO14		LT	1.37	RT	2			WI16	200	0.24				WJ16	200	0.23						
	Szatmár		18	287					MEMO15		M47	1.21	LF	1.19	LH		WI17	200	0.21				WJ17	200	0.2						
	Szatmár		19	341					MEMO16		PM24	0.74	C23	1.05	mandibular PM		DA13	200	0.22				DB13	200	0.23						
	Szatmár		20	344					MEMO17		RF	1.35	LF	1.28	bone		DA14	200	0.23				DB14	200	0.23						
	Szatmár		21	352					MEMO18		LF	1.74	RF	1.96			DA15	200	0.27				DB15	200	0.23	WP13	200	0.26			
	Szatmár		22	353					MEMO19		LT	1.43	RT	1.44	bone		DA16	200	0.24				DB16	200	0.25						
	Szatmár		23	365					MEMO20		M36	1.34	PM14	0.58	bone		DA17	200	0.24				DB17	200	0.22						
	Szatmár		23	365					MEMO21		m54	0.46	m55	0.91	M1 maxilla		DA18	200	0.21				DB18	200	0.23						
	Szatmár		24	383					MEMO22		M36/46	1.17	M18/28	1.15			WK7	200	0.25				WL7	160	0.23						
	Szatmár		24	383					MEMO23		m84	0.3	m85	0.57			WK8	200	0.2				WL8	160	0.2						
	Szatmár		25	448					MEMO24		M16	2.19	M27	1.81	M38		WK9	200	0.24				WL9	160	0.24						
Mezőszemere, Kismari-fenék	ALBK		12					Domboróczki (1997, 2003)	MEKI01	2	M36 (?)	0.35	M46 (?)	0.51	I11		VW7	160	0.2				VV12	120	0.2						
	ALBK		46						MEKI02		m55/65	0.47	m54/64	0.23	canine	0.12	VU12	160	0.21				VU13	160	0.23				WP12	200	0.12
Mezőzombor, Községi temető	Tiszadob		4					P. Csengeri (Herman Ottó Múzeum, Miskolc), personal communication	MEKÖ01	7	M46	1.33	M18	1.24	M47		VQ5	200	0.2				VR5	160	0.22						
	Tiszadob		5						MEKÖ02		RF	1.81	LF	1.78			VQ6	160	0.24				VR6	140	0.24						
	Tiszadob		10 (2000)						MEKÖ03		M37/47	1.21	M38/48	0.65			VQ7	160	0.2				VR7	160	0.2						
	Bükk		21/A					Csengeri (2001)	MEKÖ04		M16	1.19	M28	0.92	M17	1.13	VQ8	160	0.23				VR8	160	0.21				WO12	200	0.23
	Tiszadob		48					Csengeri (2004)	MEKÖ05		M36	1.35	M38	1.12	M37		VQ9	160	0.22				VR9	150	0.25						
	Tiszadob		49						MEKÖ06		m51	0.26	m62	0.17	m82		VQ10	160	0.26				VR10	100	0.17						

Site	Dating		Burial Information					References	Individuals		Samples						Extractions														
	Cultural group	C14	Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
	Tiszadob		62						MEKÖ07		M16/26	1.74	M17/27	1.45	right p-petr.		VQ11	160	0.23				VR11	120	0.21						
Polgár, Piócási-dűlő	earliest ALBK/ Szatmár		37	31				Dani,Nagy Emese (2007) no individual descriptions of the graves available yet	POPI02	5	mandibular molar	1.57	piece of humerus	2.46			WC12	160	0.26				WD12	160	0.24						
	earliest ALBK/ Szatmár		38	32					POPI03		incisor	0.77	canine	0.46	LH		WC13	240	0.22				WD13	140	0.23						
	earliest ALBK/ Szatmár		76	61					POPI04		RF	2.52	LF	2.67			WC14	160	0.24				WD14	220	0.29						
	earliest ALBK/ Szatmár		173	108					POPI05		M36	1.89	M38	1.51	M27		WC15	160	0.28				WD15	160	0.25						
	earliest ALBK/ Szatmár		177	111					POPI06		M46	1.5	M47	1.63	M28		WC16	160	0.25				WD16	200	0.25						
Pusztataskony-Ledence, 1.lh.	Tisza			17		17		Sebők (2010); grave 65 only: Raczky, Anders (2010); cultural information on single graves personal communication from K. Sebők and A. Anders (Eötvös Loránd University, Institute of Archaeological Sciences, Budapest)	PULE1.1	26	M36	1.08	M28	0.92	M48		VM6	160	0.22				VN6	160	0.22						
	Szakálhát			26		26			PULE1.2		M46	1.05	m74	0.61	left PPr.		VM7	100	0.23				VN7	120	0.21						
	Tisza			36		36			PULE1.3		m75	0.68	m74	0.37	M65		VM8	100	0.22				VN8	120	0.22						
	Szakálhát			40		40			PULE1.4		m65	0.75	m64	0.48	right PP.		VM9	100	0.21				VN9	120	0.21						
	Szakálhát			41		41			PULE1.5		mandibular M1	1.21	mandibular M2	1.21			VM10	160	0.25				VN10	100	0.2						
	Tisza			48		56			PULE1.6		RH	2.23	LH	1.38	radius (?)		VM11	120	0.2				VN11	120	0.25						
	Tisza			65		85			PULE1.7		PM	0.49	PM	0.6			VM12	100	0.24				VN12	120	0.21						
	Tiszapolgár (probably)			67		87			PULE1.8		M46	1.61	M38	1.62			VM13	160	0.23				VN13	100	0.24						
	Tiszapolgar			130		150			PULE1.9		M48	1.28	M46	1.11			WE9	200	0.24				WF9	200	0.25						
	Tiszapolgár (probably)			135		155			PULE1.10		M17	1.45	M36	1.46			WE10	200	0.27				WF10	200	0.25						
	Tiszapolgar			191		235			PULE1.11		mandibular incisor	0.38	femur (?)	1.69	femur (?)		WE11	200	0.38				WF11	200	0.25						
	Tiszapolgar			191		238			PULE1.12		RF	1.65	deciduous molar	0.37	tibia (?)		WE12	200	0.26				WF12	200	0.37						
	Tiszapolgar			192		236			PULE1.13		M37	1.16	M48	0.77			WE13	200	0.24				WF13	200	0.28						
	Tisza			231		283			PULE1.14		m74	0.39	m75	0.48	deciduous maxillary molar		VS11	120	0.2				VT11	120	0.25						
	Szakálhát			237		293			PULE1.15		M18	1.16	M17	1.23	M16		WE14	200	0.27				WF14	200	0.25						
	Tisza			243		304			PULE1.16		LF	1.5	RF	1.72	tibia		VS12	140	0.25				VT12	160	0.22						
	Tisza			251		312			PULE1.17		M84	0.54	M85	0.71			VS13	120	0.2				VT13	170	0.2						

Site	Dating		Burial Information					References	Individuals		Samples						Extractions																
	Cultural group	C14	Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
	Szakálhát			269		335			PULE1.18		M46	0.98	M47	1.14	M48		WE15	200	0.26				WF15	200	0.25								
	Tiszapolgar			290		364			PULE1.19		LF	2.64	RF	1.55			WE16	200	0.28				WF16	200	0.29								
	Szakálhát			291		365			PULE1.20		M27 (?)	1.75	mandibular M1(?)	1.64	M26 (?)		WG4	200	0.27				WH4	200	0.25								
	Szakálhát			292		366			PULE1.21		M36	1.79	M37	1.65			WK1	200	0.22				WL1	160	0.21								
	Tiszapolgar			319		396			PULE1.22		M37	1.41	M36	1.37			WK2	200	0.22				WL2	160	0.25								
	Szakálhát			328		407			PULE1.23		M17	1.61	M46	1.5			WK3	200	0.21				WL3	160	0.2								
	Tisza			365		460			PULE1.24		M16	1.09	M37	1.08	M18		WK4	200	0.23				WL4	160	0.2								
	Tisza			399		513			PULE1.25		M36	1.73	M27	1.45	M38		WK5	200	0.2				WL5	160	0.22								
	Tisza			419		537			PULE1.26		M28	1	M36	1.12			WK6	200	0.25				WL6	160	0.23								
Pusztataskony Ledence 2.lh.						217				3															0.21							
	Tisza			89					PULE2.1		M46	1.56	M47	1.36	M48		VY10	160	0.23				VZ10										
	Szakálhát			162		203			PULE2.2		M46	1.09	M28	0.89	PM45		VW10	220	0.22				VX8	200	0.25								
	Tisza			170		219			PULE2.3		M16	1.66	M27	1.33	M48		VW11	160	0.25				VX9	160	0.22								
Sajószentpéter, vasúti őrház	Bükk		189	78				unpublished, personal communication by P. Csengeri ((Herman Ottó Múzeum, Miskolc)	SAVÖ01	1	M36	2.09	M37	1.03	M47	2.21	VU7	120					VV7	220	0.2				WP10	200	0.23
Szegvár-Tűzköves	Tisza			1.				Korek (1987)	SZEG01	1	M38	1.42	M36	1.19			VQ3	160	0.24				VR3	180	0.2								
Tiszabura Bónishát	late ALBK (phase III-IV)			86		161		unpublished, personal communication by A. Anders (Eötvös Loránd University, Institute of Archaeological Sciences, Budapest)	TIBO 1	5	right PP.	2.08	M74(?)	0.2			VI8	120	0.24				VK7	90	0.2								
	late ALBK (phase III-IV)			118		186			TIBO 2		M16	0.96	M37	1.09	M3 maxilla (M18?)		VI9	120	0.2				VK8	120	0.86								
	late ALBK (phase III-IV)			273		394			TIBO 3		M36	1.13	M1 maxilla	1.04			VI10	140	0.23				VK9	140	0.23								
	late ALBK (phase III-IV)			273		424			TIBO 4		M37	1.7	M36	2.13			VI11	120	0.21	VS17	160	0.28	VK10	100	0.22	VX15	160	0.25					
	late ALBK (phase III-IV)			273		428			TIBO 5		RF	1.09	LF	1.18	M1 (?) mandibula		VI12	120	0.24				VK11	120	0.21								
Tiszadob-Okenéz	Tiszadob		251-01	2011.6.12				Scholtz (2007) no individual grave descriptions published yet	TISO01	17	C13/23	0.86	C33/43	0.69			VO12	120	0.21				VP12	110	0.2								
	Tiszadob		315	2011.6.20					TISO02		RF	2.25	RT	2.84			VO13	120	0.25				VP13	160	0.21								

Site	Dating		Burial Information					References	Individuals		Samples						Extractions														
	Cultural group	C14	Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
	Tiszadob		328	2011.6.21					**TISO03**		M16	1.14	M17	1.21	M18		VO14	90	0.21				VP14	120	0.22							
	Tiszadob		422-424	2011.6.22 a,b					**TISO04**		PM34	0.46	M36	1.14	C43		VO15	100	0.21				VP15	160	0.22							
	Tiszadob		423-03	2011.6.6					**TISO05**		M26/27	1.04	M27/28	0.97			VO16	100	0.2				VP16	90	0.22							
	Tiszadob		424	2011.6.5, 2011.6.19					**TISO06**		M37	1.56	M16	1.84	M36		DA1	200	0.2				DB1	200	0.24							
	Tiszadob		428	2011.6.1					**TISO07**		M46	1.42	M47	1.33	C43		DA2	200	0.25				DB2	200	0.25							
	Tiszadob		440-01	2011.6.10					**TISO08**		RF	1.67	LF	2.04			DA3	200	0.22				DB3	200	0.25							
	Tiszadob		455						**TISO09**		LF	1.42	tibia	1.64			DA4	200	0.23				DB4	200	0.23							
	Tiszadob		464						**TISO10**		M36	1.25	M26	1.31	PM14		DA5	200	0.24				DB5	200	0.24							
	Tiszadob		472						**TISO11**		M18	1.46	M46	1.63	M38		DA6	200	0.23				DB6	200	0.21							
	Tiszadob		474	2011.6.4					**TISO12**		LF	2.14	RF	1.18			DA7	200	0.25				DB7	200	0.23							
	Tiszadob		478-01	2011.6.8					**TISO13**		M46	1.63	M26	1.39	M47		DA8	200	0.23				DB8	200	0.25							
	Tiszadob		493-01	2011.6.11					**TISO14**		M36	1.54	left PPr.	1.59	m85		DA9	200	0.24				DB9	200	0.26							
	Tiszadob		496	2011.6.2, 2011.6.7					**TISO15**		m85	0.78	m65	0.82	m64		DA10	200	0.26				DB10	200	0.21							
	Tiszadob		519	2011.6.3					**TISO16**		RF	1.6	RT	1.68			DA11	200	0.28				DB11	200	0.25							
	Tiszadob		604	2011.6.11					**TISO17**		M47	1.79	M36	2.04	M48		DA12	200	0.25				DB12	200	0.23							
Tiszaföldvár-Téglagyár	Szakálhát			41			-	Mende (2000), Oravecz (2000)	**TITÉ01**	**6**	RF	2.67	LF	2.54			VG13	140	0.22				VH10	160	0.22							
	Szakálhát			42			-		**TITÉ02**		M85	0.64	RF	2.01	M16		VG14	200	0.23				VH11	120	0.2							
	Szakálhát			98			-		**TITÉ03**		M27	1.09	PM14	0.47	PM		VG15	120	0.22				VH12	140	0.2							
	Szakálhát			101			-		**TITÉ04**		LF	2.26	RF	2.02			VI1	160	0.22				VH13	120	0.2							
	unknown		pit 11/b	-	3				**TITÉ05**		RF		LF																		
	Szakálhát			-			1985/13a		**TITÉ06**		right PP.	2.79	left PPr.	2.66			VI2	140	0.2				VK1	120	0.21							
Tiszalök-Hajnalos	Tiszadob			45				Kurucz (1989)	**TIHA01**	**1**	RF	1.29	LF	1.37			WC11	160	0.22				WD11	200	0.27							
Tiszaszőlős, Domaháza-puszta, Réti-dűlő	Szakálhát	deb-10901 5010 - 4840 cal BC		1				Domboróczki (2010)	**TIDO01**	**5**	M47	1.5	M46	1.42	PM34		VI13	100	0.23				VK12	100	0.22							

Site	Dating			Burial Information					References	Individuals		Samples						Extractions															
	Cultural group	C14		Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
			(1 sigma)																													
	Körös	deb-11804	5710-5615 cal BC (1 sigma)		2					TIDO02		M26	1.06	PM44	0.71	LF		VI14	120	0.22				VK13	120	0.22						
	Körös				5					TIDO03		M16	1.15	M17	0.86			VI15	100	0.22				VK14	120	0.24						
	Szakálhát	deb-11084	5060-4840 cal BC (1 sigma)		6					TIDO04		M47	0.95	M48	0.8	bone		VI16	120	0.22				VK15	100	0.2						
	classical ALBK	VERA-4243	5300-5210 cal BC (1 sigma)		7					TIDO05		M36	1.11	M37	1.12	M38		VJ12	100	0.23				VK16	100	0.23						
Törökszentmiklós-Tiszapüspöki, Karancs háromág, 3. lh.	Körös			83			137		Sümegi (2004), Zoffmann (2005)	TÖSM01	7	RF	2.53	LF	1.85			VG6	160	0.21				VH3	140	0.22						
	Körös			162			312			TÖSM02		left PPr.	2.29	RF	2.06			VG7	120	0.22				VH4	140	0.2	WL16	160	0.34			
	Körös			165			315			TÖSM03		RF	2.22	LF	1.55			VG8	100	0.21				VH5	160	0.22						
	Körös			166			316			TÖSM04		m75	0.66	right PP.	1.73	m85		VG9	200	0.2				VH6	140	0.25						
	Körös			167			317			TÖSM05		right PP.	2.22	LH	1.94			VG10	120	0.24				VH7	120	0.21						
	Körös			168			318			TÖSM06		LF	2.8	RF	2.1			VG11	100	0.24				VH8	120	0.2						
	Körös			169			319			TÖSM07		RF	2.66	LH	2.26			VG12	120	0.21				VH9	160	0.2						
Vésztő-Mágor	Tisza			30.				8411.	Hegedüs,Makkay (1987) no individual grave descriptions published yet	VSM01	23	LF	0.83	RF	0.71			VG16	100	0.24	VL1	100	0.2	VH14	120	0.2						
	Tisza			31.				8412.		VSM02		M36.	1.93	M75.	0.76			VA1	200	0.28				VB1	170	0.21				-		
	Tisza			32.				8413.		VSM03		M17.	1.31	M18.	0.9			VA2	240	0.22				VB2	150	0.25				-		
	Tisza			33.				8414.		VSM04		RF	0.71	RH	1.84			VA3	160	0.25				VB3	170	0.25				-		
	Tisza			34.				8415.		VSM05		LF	1.21	LH	0.33			VA4	200	0.21	VL2	120	0.24	VB4	120	0.33				-		
	Tisza			36.				8417.		VSM06		RF	1.39	LH	1.91			VA5	150	0.25	VJ2	140	0.22	VB5	140	0.23				-		

Site	Dating		Burial Information					References	Individuals		Samples					Extractions															
	Cultural group	C14	Grave No.	Obj.	SNR	STR	Inv. No.		Lab Name	n	A	gram	B	gram	C	gram	Ex A1	µl EX A1	g EX A1	EX A2	µl EX A2	g EX A2	EX B1	µl EX B1	g EX B1	EX B2	µl EX B2	g EX B2	EX C1	µl EX C1	g EX C1
	Tisza		39.				8420.		VSM07		LF	0.4	RT	0.54			VA6	200	0.25	VJ3	100	0.15	VB6	150	0.21				-		
	Tisza		42.				8423.		VSM08		LH	1.57	RH	1.40			VC1	160	0.22				VD1	100	0.23						
	Tisza		43.				8574.		VSM09		LH	1.13	RH	1.28			VC2	120	0.25				VD2	160	0.23						
	Tisza		44.				8575.		VSM10		M16.	1.42	M18.	0.79			VC3	120	0.22				VD3	100	0.2						
	Tisza		1.				7963		VSM11		M26	1.68	M38	1.33			VY11	120	0.25				VZ11	120	0.2						
	Tisza		2.				7964		VSM12		M16.	1.35	PM15 loose	0.95			VY12	120	0.25				VZ12	160	0.21						
	Tisza		3.				7965		VSM13		M26/M16 loose	1.81	M28/M18 loose	1.31			VY13	120	0.25				VZ13	160	0.24						
	Tisza		4.				7966		VSM14		M48	0.9	PM15	0.62			VY14	160	0.25				VZ14	160	0.2						
	Tisza		6.				7968		VSM15		M26	1.31	M48	1.27			WC4	120	0.24				WD4	100	0.24						
	Tisza		7.				7969		VSM16		M38	1.09	M16	1.61			WC5	120	0.21				WD5	140	0.23						
	Tisza		8.				7970		VSM17		left PPr.	2.97	right PP.	3.05			WC6	200	0.23				WD6	160	0.29						
	Tisza		11.				7972.		VSM18		LT	1.13	RT	1.25			WC7	120	0.22				WD7	120	0.25						
	Tisza		12.				7973.		VSM19		left (?) femur	0.96	long bone leg	1.23			WE17	200	0.28				WF17	200	0.26						
	Tisza		36b						VSM20		RF	1.96	left (?) tibia	2.91			WE18	200	0.25				WF18	200	0.28						
	Tisza		13				7974		VSM21		M36	1.78	M28	1.56			WG1	200	0.26				WH1	200	0.25						
	Tisza		16				8398		VSM22		PM	0.68	right PP.	2.79			WG2	200	0.27				WH2	200	0.3						
	Tisza		14				7975		VSM23		LF	1.15	RF	1.67			WG3	200	0.25				WH3	200	0.25						

Reproduced HVS-II sequences: (Range np 0034-0397)

Lab Name	HVS-II
TÖSM01	263G 315.1C
TÖSM03	73G 263G 315.1C
TÖSM04	73G 263G 315.1C
TÖSM05	73G 114T 263G 315.1C
TÖSM06	73G 263G 315.1C
BEP08	73G 185A 228A 263G 295T 315.1C

C: Consensus SNP profiles

	derived
	ambiguous
	ambiguous,derived allele is majority consensus
UPPERCASE	observed in A and B
lowercase	only in either A or B
-	allelic dropout
A/g	A present in A and B, g only in one sample
A/G	G and A *both* present in A and B, i.e. two double peaks
a/g	one sample shows A, the other G
a/g*	double peak in one sample, dropout in the other

GenoCoRe22

		R9_13928	L3'4_3594	K_10550	A_4248	U_11467	W_8994	C_13263	T_13368	R0/preHV_11719	V,M3_4580	B_8280	X_6371	N1_10238	I_10034	H_7028	D_5178	HV_14766	R_12705	N_10873	J_12612	L2'6_2758	M_10400
		G/T	G	C	C	G	A	C	A	C	T	G	A	C	C	G	T	G	G	A	G	G	A
Individual	HG	C	A	T	T	A	G	T	G	T	C	A	G	T	T	A	G	A	A	G	A	A	G
ABO03	h	c	-	t	-	-	a/g	t	g	c/t	c	-	g	-	t	g	g	g	g	a	a	g	a
ABO05	J	C	G	T	T	A/g	G	T	G	T	C	A	G	T	T	A	G	A	G	A	G	G	G
ABO06	J	C	G	T	t	A	G	T	G	T	C	A	G	T	T	A	G	A	G	A	G	G	G
ABO08	J	C	G	T	T	A	G	T	G	T	C	A/g	G	T	T	A/g	G	A	G	A	G	G	G
ABO10	J	C	g	T	T	A	G	T	G	T	C	A/g	G	T	T	A/g	G	A	G	A	G	G	G
ABO11	T	C	-	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
ABO12	U	C	-	T	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
ABO13	J	C	G	T	T	A/G	G	T	G	T	C	A/g	G	T	T	A/G	G	A	G	A	G	G	G
ABO15	J	C	G	T	T	A/G	G/a	T	G	T	C	A/g	G	T	T	a/g	G	A	G	A	G	G	G
ABO16	J	C	g	T	T	A/g	G	T	G	T	C	A/g	G	T	T	A	G	A	G	A	G	G	G
ABO17	T	C	-	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A/g	G	G
ABO19	U	C	g	T	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
ADMA01	HV	C	g	T	T	A	G	T	G	C	C	A	G	T	T	A	G	G	G	A	A	G	G
ADMA02	J	c/g*	G	t	T	A	G	T	G	T	C	A/g	G	T	T	A/g	G	a	G	A	G	G	G
ADMA03	H	C	g	T	T	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A	G	G
ADMA04	H	C	-	t	t	A	G	t/c	G	C	C	A	G	T	T	G	G	a/G	G	A	A	G	G
BENA01	H	C/g	G	T	t	A	G	T	G	C	C	A/g	G	T	T	G	G	G	G	A	A	G	G
BENA02	H	C	G	T	T	A	G	T/c	G	t/C	C	A	G	T	T	G	G	G/A	G	A	A/g	G	G
BENA03	K	C	G	C	T	G	G	T	G	T	C	A/g	G	T	T	A	G	A/g	G	A	A	G	G
BENA06	HV	C	G	T	T	A	G	T	G	C	C	A	G	T	T	A	G	G	G	A	A	G	G
BENA08	K	C/g	G	C	T	G	G	T	G	T	C	A	G	T	T	A/g	G	A	G	g/A	A	G	G
BEP01	HV	C	G	T	T	A	G	T	G	C	C	A	G	T	T	A	G	G	G	A	A	G	G
BEP03	N1	C	G	T	T	A/g	G	T	G	T	C	A	G	C	T	A	G	A	A	A	A	G	G
BEP04	T	C	G	T	T	A	G	T	A	T	C	A	G	T	T	A/g	G	A	G	A	A	G	G
BEP05	N1	C	G	T	T	A	G	T	G	T	C	A	G	C	T	A	G	A	A	A	A	G	G
BEP06	K	C	G	C	T	G	G	T	G	T	C	A	G	T	T	A/g	G	A	G	A	A	G	G
BEP07	J	C	G	T	T	A	G	T	G	T	C	A	G	T	T	a/g	G	A	G	A	G	G	G
BEP08	J	C	G	T	T	A	G	T	G	T	C	A	G	T	T	A/g	G	A	G	A	G	G	G

Individual	HG	R9_13928	L3'4_3594	K_10550	A_4248	U_11467	W_8994	C_13263	T_13368	R0/preHV_11719	V,M3_4580	B_8280	X_6371	N1_10238	I_10034	H_7028	D_5178	HV_14766	R_12705	N_10873	J_12612	L2'6_2758	M_10400
		G/T	G	C	C	G	A	C	A	C	T	G	A	C	C	G	T	G	G	A	G	G	A
		C	A	T	T	A	G	T	G	T	C	A	G	T	T	A	G	A	A	G	A	A	G
CEG01	U	C	G	T	T	G	G	T	G	T	C	A	G	T	T	A	G	-	G	A	A	G	G
CEG02	W	C	g	T	T	A	A	T	G	T	C	a	G	T	T	A	G	a	A	A	A	G	G
CEG03	H	C	g	T	T	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A	G	G
CEG04	T	C	-	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	a	G	G
CEG05	T	C	-	T	T	A	G	T	A	T	C	A	G	T	T	A	G	-	G	A	A	G	G
CEG06	H	C	-	T	T	A	G	t/c	G	C	C	A	G	T	T	G	G	a/G	G	A	A	G	G
CEG07	J	C	G	T	T	A	G	T	G	T	C	A/G	G	T	T	A/g	G	A	G	A	G	G	G
CEG08	J	C	g	T	T	A	G	t/c	G	T	C	a/g	g	t	t	a	G	a	g	A	G	G	G
CEG10	J	C	G	T	T	A	G	t/c	G	T	C	A/G	G	T	T	A/g	G	A	G	A	G	G	G
CEG11	T	C	-	T	T	A	G	t/c	g/A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
CEG12	n.d.	c	-	t	t	a	-	c	g/a	t	-	-	g	t	t	a	g	a	g	a	a	-	g
CEG13	T	C	-	T	T	A	G	t/c	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
CEG14	J	C	g	T	t	a	G	t/c	G	T	C	A/g	G	t	t	a	G	A	G	A	G	g	G
CEG15	K	C	-	c	t	G	G	t/c	G	T	c	A	G	t	t	A	g	A	G	A	A	g	g
CGIP01	K	C	G	t/C	T	G	G	T	G	T	C	A	G	T	T	A/g	G	A/g	G	A	A	G	G
CGIP02	T	C	g	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
CGIP03	K	C	G	C	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
CGIP06	K	C	g	C	T	G	G	T	G	T	C	A	G	T	T	A	G	A/g	G	A	A	G	G
CGIP09	N1	C	G	T	T	A	G	T	G	T	C	A	G	C	T	A	G	A	A	A	A	G	G
DEOR01	HV	C	G	T	T	A	G	T	G	C	C	A	G	T	T	A	G	G	G	A	A	G	G
DES05	H	C	G	T	T	A	G	T	G	t/C	C	A	G	T	T	G	G	G	G	A	A	G	G
DES06	V	C	G	T	T	A	G	T	G	C	T	A	G	T	T	A/g	G	G	G	A	A	G	G
EBSA01	K	-	-	C	-	G	G	T	g	T	C	A	G	t	t	A	G	a	G	A	a	g	G
EBSA02	K	C	G	C	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
EBSA03	J	c	g	t	t	a/g*	g	T	g	T	C	a/g*	G	T	T	A/g	G	a	G	A	G	G	G
EBSA04	K	C	g	C	T	G	G	T	g	T	C	A	G	T	T	A	G	A	G	A	A	G	G
EBVÖ02	K	C	G	C	T	G	G	T	G	T	C	A	G	T	T	A	G	g	G	A	A	G	G
EBVÖ05	V	C	G	T	T	A	G	T	G	C	T	A	G	T	T	A	G	G	G	A	A	G	G
FUGU03	N1	C	g	T	T	A	G	T	G	T	C	A/g	G	C	T	A	G	A	A	A	A	G	G
FUGU04	T	C	g	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
FUGU05	H	c	-	T	t	a	G	T	G	C	C	g/a*	G	t	T	G	g	G	G	A	a	g	G
FUGU08	N1	C	-	T	T	A	G	t/c	G	T	C	A	G	C	T	A	G	A	A	A	A	G	G
FUGU09	T	C	-	T	t	a	G	T	a	T	c	a	G	t	t	a	g	a	g	a	a	g	g
FUGU10	H	c	g	t	t	a	G	t/c	G	c	C	a/G	G	t	t	G	g	a/g	G	A	a	g	G
FUGU11	K	C	G	C	T	G	G	T/c	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
FUGU12	T	C	-	T	T	A	G	t/c	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
GAEL01	U	C	g	T	t	G	G	T	G	T	C	a	G	T	T	A	g	-	G	A	A	G	G
GAEL02	T	c	-	-	-	-	G	t	A	t	c	a	G	t	t	a	g	-	G	A	a/g*	g	G
GAEL04	T	C	g	T	T	A	G	T	A	T	C	A	G	t	T	A	G	A	G	A	A	G	G
GAEL06	H	C	g	T	T	A	G	T	G	C	C	A/g	G	t	T	G	G	G	G	A	A/G	G	G
GAEL07	U	C/g	g	T	T	G	G	T	G	T	C	A/g	G	T	T	A	G	a	G	A	A	G	G
GAEL08	J	C	g	T	T	A	G	T	G	T	C	A	G	T	T	A	G	A	G	A	G	G	G
GAEL10	X	C	g	T	T	A	G	T	G	T	C	A	A/g	T	T	A/G	G	A	A/g	A	A/g	G	G
GAEL12	J	C	g	T	T	A	G	T	G	T	C	A	G	T	T	A/g	G	A	G	A	G	G	G

Individual	HG	R9_13928	L3'4_3594	K_10550	A_4248	U_11467	W_8994	C_13263	T_13368	R0/preHV_11719	V,M3_4580	B_8280	X_6371	N1_10238	I_10034	H_7028	D_5178	HV_14766	R_12705	N_10873	J_12612	L2'6_2758	M_10400
		G/T	G	C	C	G	A	C	A	C	T	G	A	C	C	G	T	G	G	A	G	G	A
		C	A	T	T	A	G	T	G	T	C	A	G	T	T	A	G	A	A	G	A	A	G
GAEL13	J	C	g	T	T	A	G	t	G	T	c	A	G	T	T	A/g	G	A	G	A	G	G	G
HAJE01	T	C	G	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
HAJE02	K	C	G	C	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
HAJE03	K	C	G	C	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
HAJE04	J	C	G	T	T	A	G	T	G	T	C	A	G	T	T	A	G	A	G	A	G	G	G
HAJE06	HV	C	g	T	T	A	G	T	G	C	C	A	G	t	T	A	G	G	g	A	A	g	G
HAJE07	K	C	-	C	T	G	G	t	G	T	c	A	G	t	t	A	G	A	G	A	A	G	G
HAJE08	N1	C	g	T	t	A	G	T	G	T	C	A	G	c	T	A	g	a	a	A	A	g	G
HAJE09	T	C	-	T	T	A	G	T	A	T	C	A	G	T	T	A/g	G	A	G	A	A	G	G
HAJE10	J	c	g	t	t	a	g	-	g	t	-	-	-	t	t	a	g	a	g	a	g	g	-
HAJE11	U	C	-	T	T	G	G	T	G	T	C	A	G	t	T	A	G	-	G	A	A	G	G
HAJE12	N1	C	-	T	T	A	G	t	G	T	c	a	g	c	T	A	G	a	a	A	A	G	G
HAJE15	K	C	g	C	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
HAJE18	K	C	-	c	-	G	G	T	G	T	-	A	G	-	-	a	g	A	G	A	-	g	-
HAJE20	T	C	g	T	T	A	G	T	A	T	C	A	G	t	T	A	G	a	G	A	A	G	G
HELI01	U	C	-	t	t	g	G	T	G	T	c	A	G	t	t	a	-	a	G	A	a	g	g
HELI02	U	C	-	T	T	G	G	T	G	T	C	a	G	T	t	A	g	A	G	A	A	G	G
HELI03	X	C	g	T	T	A	G	T	G	T	C	A	g/A	T	T	A/g	G	A	A	A	-	G	G
HELI05	T	C	-	T	T	A	G	T	g/A	T	C	A	G	T	T	A	G	A	a/G	A	A	G	G
HELI07	K	C	-	C	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
HELI08	T	C	-	T	T	A	G	t	A	T	C	A	G	t	T	A	G	a	G	A	A/g	a/G	G
HELI09	U	C	-	T	t	G	G	T	G	T	c	A	G	t	t	A	g	a	G	A	A	g	G
HELI10	X	C	-	T	T	A/g	G	T	G	T	c	a	g/A	T	T	A	G	A	A	A	A	G	G
HELI11	N1	C	-	t	T	A	G	t	G	T	C	A	G	C	T	A	G	A	A	A	A	G	G
HELI12	J	C	g	t	t	A/g	G	t	G	t	c	A	g	t	t	A	g	A	G	A	G	g	g
HELI13	X	C	-	t	t	A/g	G	t	G	T	c	A	A	t	t	A	g	a	a	A	a	g	G
HELI14	n1	C	-	T	T	A/g	G	T	G	T	C	A	G	c	T	A	G	A	a	A	A	g	G
HELI15	T	C	-	t	t	a	G	T	A	T	c	A	G	t	t	A	g	A	g	A	a	g	G
HMG01	T	C	g	T	T	A	G	T	A	T	C	A	G	T	T	A/g	G	A	G	A	A	G	G
HMG02	U	C	g	T	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
HMG03	K	C	G	C	T	G	G	T	G	T	C	A	G	T	T	A/g	G	A	G	A	A	G	G
HMG05	J	C	G	T	T	A	G	T	G	T	C	A/G	G	T	T	A/G	G	A	G	A	G	G	G
HMG06	T	C	G	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
HMG07	T/H	C	G	T	T	A	G	T	A	T	C	A/g	G	T	T	A/G	G	a/g	G	A	A	G	G
HMG10	J	C	g	T	T	A	G	T	G	T	C	-	G	T	T	A/G	G	A	G	A	G	G	G
HOKO01	H	C	G	T	T	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A	G	G
HOKO02	T	C	G	T	T	A	G	T	A	T	C	A	G/a	T	T	A	G	a/g*	G	A	A	G	G
KÖKE01	J	C	G	T	T	A	G	T	G	T	C	A	G	T	T	A/g	G	a	G	A	G	G	G
KÖKE02	J	C/g	G	T	T	A	G	T	G	T	C	A/g	G	T	T	A/G	G	a/g	G	A	G	G	G
KÖKE03	K	C	g	C	T	G	G	T/c	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
KOKI01	U	C	G	T	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
KOKI02	J	C	g	T	T	A	G	T	G	T	C	A/g	G	T	T	A	G	A	G	A	G	G	G
KOKI05	K	C	-	C	T	G	G	t/c	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
MAP01	T	C	g	T	T	A	G	T	A	T	C	A	G	t	T	A/g	G	A	G	A	A	G	G

Individual	HG	R9_13928	L3'4_3594	K_10550	A_4248	U_11467	W_8994	C_13263	T_13368	R0/preHV_11719	V,M3_4580	B_8280	X_6371	N1_10238	I_10034	H_7028	D_5178	HV_14766	R_12705	N_10873	J_12612	L2'6_2758	M_10400
		G/T	G	C	C	G	A	C	A	C	T	G	A	C	C	G	T	G	G	A	G	G	A
		C	A	T	T	A	G	T	G	T	C	A	G	T	T	A	G	A	A	G	A	A	G
MAP02	T	C	g	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
MAP03	T	C	G	T	T	A	G	T	A	T	C	A	G	T	T	A/g	G	A	G	A	A	G	G
MECE01	H	C	g	T	T	A	G	T	G	C	C	A/G	G	T	T	G	G	G	G	A	A	G	G
MECE08	H	C	g	T	T	A	G	T	G	C	c	A/g	G	T	T	G	G	G	G	A	a	g	G
MECE10	H	C	a/g*	T	T	A	G	T	G	C	C	A	G	T	T	G	G	-	G	A	A/G	G	G
MECE11	J	C	g	T	T	A	G	T	G	T	C	A	G	T	T	A	G	A	G	A	a/G	G	G
MECE12	N1	C	-	T	T	A	G	T	G	T	C	A	G	C	T	A	G	A	A	A	A	G	G
MECE14	J	C	G	T	T	A	G	t	G	T	C	A	G	t	T	A/g	G	A	G	A	G	G	G
MEKÖ01	H	C	G	T	T	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A	G	G
MEKÖ02	U	C	G	T	T	G	G	T	G	T	C	A	G	T	T	A/g	G	-	G	A	A	G	G
MEKÖ03	T	C	G	T	T	A	G	T	A	T	C	A	G	T	T	A/g	G	G	G	A	A	G	G
MEKÖ04	N1	C	g	T	T	A	G	T	G	T	C	A	G	C	T	A	g	-	A	A	A	G	G
MEKÖ07	N1	C	G	T	T	A	G	T	G	T	C	A/g	G	C	T	G/A	G	-	A	A	A	G	G
MEMO01	HV	C	G	T	T	A	G	t	G	C	C	A	G	T	T	A	G	G	G	A	A/G	G	G
MEMO02	K	C/g	-	C	T	G	G	t	G	T	C	A/g	G	T	T	A	G	a	G	A	A/G	G	G
MEMO03	K	C	-	T	T	G	G	T	G	T	C	A	G	T	T	A	G	a	G	A	A/g	G	G
MEMO04	h	c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g
MEMO05	J	C	-	T	T	A	G	T	G	T	C	A/g	G	T	T	A	G	A	G	g/A	G	G	
MEMO06	V	C	-	T	T	A	G	T	G	C	T	A	G	T	T	A	G	G	G	A	A/g	G	G
MEMO07	HV	C	-	T	T	A	G	T	G	C	C	A	G	T/c	T	A	G	G	G	A	A	G	G
MEMO08	H	C	g	T	T	A	G	t	G	C	c	A	G	T	T	G	G	G	G	A	A/g	G	G
MEMO09	H	C	-	T	T	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A/g	G	G
MEMO12	U	C	g	T	T	G	G	t	G	T	c	A	G	-	T	A	g	a	G	A	A	G	G
MEMO13	H	C	g	T	T	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A/g	G	G
MEMO14	U	C	g	T	T	G	G	t	G	T	C	A	G	T	T	A	G	a	G	A	A	g	G
MEMO15	R	C	g	T	t	a	G	T	G	T	c	A	G	t	t	A	G	A	G	A	a	G	g
MEMO16	H	C	-	t	T	A	G	t	G	C	c	A	G/a	t	T	G	G	a/G	G	A	A	G	G
MEMO17	U	C	-	T	T	G	G	T	G	T	C	A	G	t	T	A	G	-	G	A	A	G	G
MEMO18	k	C	g	c	t	G	G	t	G	T	c	A	G	t	t	A	G	a	G	A	A	g	G
MEMO19	K	c	-	C	T	G	G	t	G	T	C	A	G	t	T	A	G	A	G	A	A	g	G
MEMO20	K	-	-	C	T	G	G		G	T	c	a	g	T	T	A	G	a	G	A	A	G	g
MEMO21	H	C	-	T	T	A	G	T	G	C	C	A/g	G	T	T	G	G	G	G	A	A	G	G
MEMO22	X	C	g	T	T	A	G	T	G	T	C	A	g/A	T	T	A	G	A	A	A	A	a/G	G
MEMO23	U	C	G	T	T	G	G	t	G	T	c	a	g	T	T	A	G	A	G	A	A	a/G	-
MEMO24	U	C	g	T	T	G	G	t	G	T	C	A	G	T	T	A	G	A/g	G	A	A	G	G
POPI02	K	C	-	C	T	G	G	T	G	T	C	a	G	T	t	a	G	a	G	A	A	G	G
POPI03	N1	C	-	T	T	A/g	G	T	G	T	C	A/g	G	C	T	A	G	A	A	A	A	G	G
POPI04	T	C	-	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	a/g*	G	G
POPI05	K	C/g	g	C	T	G	G	T	G	T	C	a/G	G	t	t	a	G	a	G	A	A/g	G	G
POPI06	K	c	-	C	T	G	G	T	G	T	c	a	G	t	T	A	g	a	G	A	A	g	g
PULE1.1	J	C	G	T	T	A	G	T	G	T	C	A	G	T	T	A	G	A	G	A	G	G	G
PULE1.2	H	C	G	T		A	G	T	G	C	C	A/g	G	T	T	G	G	G	G	A	A	G	G
PULE1.3	J	C	G	T	T	A/g	G	T	G	T	C	A/g	G	t	T	a/g*	G	A	G	A	G	G	G
PULE1.4	T	C	G	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G

Individual	HG	R9_13928	L3'4_3594	K_10550	A_4248	U_11467	W_8994	C_13263	T_13368	R0/preHV_11719	V,M3_4580	B_8280	X_6371	N1_10238	I_10034	H_7028	D_5178	HV_14766	R_12705	N_10873	J_12612	L2'6_2758	M_10400
		G/T	G	C	C	G	A	C	A	C	T	G	A	C	C	G	T	G	G	A	G	G	A
		C	A	T	T	A	G	T	G	T	C	A	G	T	T	A	G	A	A	G	A	A	G
PULE1.7																							
PULE1.8	HV	C	G	T	t	A	G	T	G	C	C	A/G	G	T	T	A	G	G	G	A	A	G	G
PULE1.9	H	C/g	g	T	T	A	G	T	G	C	C	a/g	G	T	t	G	G	G	G	A	A/g	G	G
PULE1.10	T	C	g	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A/g	G	G
PULE1.11	T	c	-	t	-	-	G	T	g/ A	t	C	a	G	-	-	A	G	A	a/g*	A	g	a/g*	G
PULE1.12	T	C	g	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
PULE1.13	T	C	-	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
PULE1.14	T	C/g	G	T	T	A	G	T	A	T	C	A	G	T	T	A	G	g	G	A	A	G	G
PULE1.15	V	C	-	T	T	A	G	T	G	C	T	A	G	T	t	a	G	G	G	A	A	G	G
PULE1.16	J	C	G	T	T	A/g	G	T/c	G	T	C	A/g	G	T	T	A/G	G	-	G	A	G	G	G
PULE1.17	U	C	G	T	T	G	G	T	G	T	C	A	G	T	T	A	G	a	G	A	A	G	G
PULE1.18	T	C	-	T	T	A/g	G	T	g/ A	T	C	A	G	T	T	A	g	A	a/G	A	A	G	G
PULE1.19	T	C	-	T	T	A	G	T	g/A	T	C	A	G	T	T	A	G	A	a/G	A	A	G	G
PULE1.20	T	C/g	G	T	T	A	G	T	A	T	C	A/g	G	T	T	A	G	A	G	A	A/G	G	G
PULE1.21	T	C	G	T	T	A	G	T	A	T	C	A	g	T	T	A	G	A	G	A	A	G	G
PULE1.22	T	C	G	T	T	A	G	T	A	T	C	a	g	t	T	A/g	G	A	G	A	A	G	G
PULE1.23	H	C	g	T	T	A	G	t	G	C	C	A	G	T	T	G	G	G	G	A	A	G	G
PULE1.24	K	C	g	C	T	G	G	t	G	T	C	a	g	T	T	A	G	A	G	A	A	G	G
PULE1.25	K	C	g	C	T	G	G	T	G	T	c	A	g	t	T	A	G	A	G	A	A	G	G
PULE1.26	T	C	-	T	T	A	G	t	A	T	c	A	G	T	T	A	G	A	G	A	A	G	G
PULE2.1	T	C	-	T	T	A	G	T/c	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
PULE2.2	V	C	g	T	T	A	G	T	G	C	T	A	G	T	T	A	G	G	G	A	A	G	G
PULE2.3	HV	C	G	T	T	A	G	T	g	C	C	A	G	T	T	A	G	G	G	A	A	G	G
TIBO01	H	C	g	T	T	A	G	T	G	C	C	A	G	T	T	a/G	G	G	G	A	A	G	G
TIBO02	H	C	G	T	t	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A	G	G
TIBO03	U	C	G	T	T	G	G	T	G	T	C	A	G/a	T	T	A	G	A/g	G	A	A	G	G
TIBO04	K	C	G	C	T	G	G	T	G	T	C	A/g	G	T	T	A/G	G	A	G	A	A	G	G
TIBO05	T	C	G	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A/g	G	A	A	G	G
TIDO01	T	C	g	T	t	A	G	T	A	T	C	A	G/a	t	T	a	G	a/g	g	A	a	G	G
TIDO02	K	C	G	C	T	G	G	T	G	T	C	A/g	G	T	T	A/g	G	A	a/G	A	A	G	G
TIDO03	J	C	G	T	T	A	G	T	G	T	C	A	G	T	T	A/g	G	A/g	G	A	G	G	G
TIDO04	K	C	G	C	T	G	G	T	G	T	C	A	G	T	T	A/g	G	A/g	G	A	A	G	G
TIDO05	H	C	G	T	t	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A	G	G
TISO01	H	C	A/g	T	T	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A	G	G
TISO02	U	C	A/g	T	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
TISO03	U	C	G	T	T	G	G	T	G	T	C	A/g	G/a	T	T	A/g	G	A	G	A	A	G	G
TISO04	X	C	G	T	T	A	G	T	G	T	C	A	G/A	T	T	A	G	A	A	A	A	G	G
TISO05	X	C	G	T	T	A	G	T	G	T	C	A	G/A	T	T	A	G	A	A	A	A	G	G
TITE01	K	C	G	C	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
TITE02	J	C	G	T	T	A	G	T	G	T	C	A	G	T	T	A	G	a	G	A	G	G	G
TITE03	N1	C	G	T	T	A	G	T	G	T	C	A	G	C	T	A	G	A	A	A	A	G	G
TITE04	H	C	G	T	T	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A	G	G
TITE06	J	C	G	T	T	A	G	T	G	T	C	A/G	G	T	T	A	G	a	G	A	G	G	G
TOPE01	T	C	G	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A/g	G	A	A	G	G

Individual	HG	R9_13928	L3'4_3594	K_10550	A_4248	U_11467	W_8994	C_13263	T_13368	R0/preHV_11719	V,M3_4580	B_8280	X_6371	N1_10238	I_10034	H_7028	D_5178	HV_14766	R_12705	N_10873	J_12612	L2'6_2758	M_10400
		G/T	G	C	C	G	A	C	A	C	T	G	A	C	C	G	T	G	G	A	G	G	A
		C	A	T	T	A	G	T	G	T	C	A	G	T	T	A	G	A	A	G	A	A	G
TOPE02	HV	C	G	T	T	A	G	T/c	G	C	C	A	G	T	T	A/g	G	G	G	A	A	G	G
TOPE03	J	C	g	T	t	a	G	t	G	T	C	A/g	G	T	T	A/g	G	-	G	A	G	G	G
TOPE04	R	C	G	T	T	A	G	T	G	T	C	A	G	T	T	A	G	-	G	A	A	G	G
TOPE06	V	c/g	g	t	T	a	G	T/c	G	c	T	a/g	g	t	t	a		g	g	A	a	G	G
TOPE07	H	c	-	t	T	a	G	T	G	c	C	a/g	G	T	T	G	g	G	G	A	a	g	G
TOPE08	U	C	G	T	T	G	G	T	G	T	C	A/g	G	T	T	A	G	A	G	g/A	A	G	G
TOPE09	H	c	-	T	T		G	T	G	c	C	a/g	G	t	T	G	G	G	G	g/A	a	G	G
TOPE11	H	C/g	-	T	T	A	G	T	G	C	C	A/g	G	T	T	G	G	G	G	A	A/g	G	G
TOPE12	U	C	-	T	T	a/G	G	T	G	T	C	A	G/a	T/c	T	A	g	A	a/G	A	A	G	G
TOPE13	K	C/g		C	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	a/g*	G	G
TÖSM01	H	C	G	T	T	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A	G	G
TÖSM03	K	C	g	C	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	a	G	G
TÖSM04	K	C	G	C	T	G	G	T	G	T	C	A	G	T	T	A	G	A	G	A	A	G	G
TÖSM05	K	C	G	C	T	G	G	T	G	T	C	A	G/a	T	T	A	G	A/g	G	A	A	G	G
TÖSM06	K	C	G	C	T	G	G	T	G	T	C	A	G	T	T	A/g	G	A	G	A	A	G	G
TÖSM07*	k	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
VSM01	J	C	G	T	T	A/g	G	T	G	T	C	A	G	T	T	A/g	G	A	G	A	G	G	G
VSM02	J	C	G	T	T	A	G	T	G	T	C	A	G	T	T	A/G	G	A	G	A	G	G	G
VSM03	H	C	G	T	T	A	G	T	G	C	C	A	G	T	T	G	G	G	G	A	A	G	G
VSM04	J	C	G	T	T	A	G	T	G	T	C	A/g	G	T	T	A/G	G	A	G	A	G	G	G
VSM06	N1	C	G	T	T	A	G	T	G	T	C	A	G	C	T	A/g	G	A/g	A	A	A	G	G
VSM07	X	C	G	T	T	A	G	T	G	T	C	A	G/A	T	T	A	G	A/g	A	A	A	G	G
VSM08	HV	C	G	T	T	A	G	T	G	C	C	A	G	T	T	A	G	G	G	A	A	G	G
VSM09	T	C	G	T	T	A	G	T	A	T	C	A	G	T	T	A/g	G	A	G	A	A	G	G
VSM10	T	C	G	T	T	A	G	T	A	T	C	A	G	T	T	A	G	A	G	A	A	G	G
VSM11	H	C	g	T	T	A	G	t/c	G	C	C	A	G	T	T	G	G	a/G	G	A	A	G	G
VSM13	H	C	-	T	T	A	G	t/c	G	C	C	A	G	T	T	G	G	A	G	A	A	G	G
VSM14	J	C	g	T	T	A	G	T	G	T	C	A/g	G	T	T	A/g	G	A	G	A	G	G	G
VSM15	H	C	-	T	T	A	G	T	G	C	C	a/g	G	T	t	a/G	G	G	G	A	A	G	G
VSM16	T	C/t	-	T	T	A/g	G	T	a/G	T	C	A/g	G	T	T	A	G	A	G	A	a/g*	G	G
VSM17	U	C	g	T	T	G	G	T	G	T	C	A	G	T	T	A	g	A	G	A	A	G	G
VSM18	U	C	-	T	T	G	G	T	G	T	C	A	G	T	T	A	g	A	G	A	a	G	G
VSM19	U	C	-	T	T	G	G	T	G	T	c	a/g	G	t	t	a	g	-	G	A	A	G	G
VSM21	H	C	g	T	T	A	G	T	G	C	C	A/g	G	T	T	G	G	G	G	A	A/G	G	G
VSM22	K	C/g	-	C	T	G	G	T	G	T	C	A/g	G	T	T	A	G	-	G	A	A/G	G	G

HPLEX17

Individual	HG	H10	H7_4793	H1_3010	H18_14364	H4_3992	H11_8448	H16_10394	H15_6253	H9_13020/H12	H14_7645	H19_14869	H13_14872	H25_9620	H23_10211	H3_6776	H2_1438	H12_3636	H30_8200
		T	C	T	T	T	C	T	G	G	G	A	A	A	A	G	T	A	C
		A	T	C	C	C	T	C	A	A	A	G	G	G	G	A	C	G	T
ABO03	H(1)	-	-	T	C	c	t	c	A	-	A	G	G	G	g	A	c	g	n.d.
ABO09		a	T	C	C	-	-	C	A	a	a	g	G	g	g	A	c	g	
ADMA03		a	T	C	C	c	T	-	A	A	A	G	G	G	G	A	C	G	
ADMA04	H7	a	C	C	C	C	T	-	A	A	A	G	G	G	G	A	C	G	
BENA01	H1	A	T	T	C	c	T	-	A	A	A	G	G	G	G	A	C	G	T
BENA02		a	T	C	-	-	T	c	A	a	a	G	G	G	G	A	C	g	
CEG03		a	T	C	C	C	T	-	A	A	a	G	G	G	G	A	C	G	
DES05		a	T	C	C	C	t	C	A	-	A	G	G	G	G	A	C	G	
FUGU05		a	T	C	C	-	T	-	A	A	A	G	G	G	G	a	C	g	
FUGU10		a	T	C	C	c	T	c	A	A	A	G	G	G	G	a	C	G	
GAEL05		A	T	C	C	-	T	-	A	A	A	G	G	G	G	A	C	G	
GAEL06		a	T	C	C	-	T	-	A	A	A	G	G	G	G	A	C	G	
HOKO01		a	t	C	C	c	T	c	A	A	A	G	G	G	G	a	C	g	
MECE10		a	T	C	-	-	T	c	A	A	A	G	G	G	G	A	C	G	
MEKÖ01		a	T	C	C	c	T	-	A	A	A	G	G	G	G	A	C	G	
MEMO04	H7	A	C	C	C	C	T	c	A	A	A	G	G	G	G	A	C	G	
MEMO08		A	T	C	C	c	T	-	A	A	A	G	G	G	G	A	C	G	
MEMO13	H7	A	t/C	C/t	C	C	T	C	A	A	A	G	G	G	G	A	C	G	T
MEMO16		A	T	C	C	C	T	C	A	A	A	G	G	G	G	A	C	G	T
PULE1.2	H7	A	C	C	C	C	T	C	A	a	A	G	G	G	G	A	C	G	
PULE1.23	H1	A	T	T	C	C	T	c	A	A	A	G	G	G	G	A	C	G	
TIBO01		a	T	C	C	c	T	C	A	A	A	G	G	G	G	A	C	G	
TIBO02		A	T	C	C	C	T	c	A	A	A	G	G	G	G	A	C	G	
TIDO05		A	T	C	-	-	T	-	A	A	A	G	G	G	G	A	C	G	
TISO01	H7	a	C	C	C	c	T	-	A	A	A	G	G	G	G	A	C	G	
TISO09	H7	-	C	C	C	C	T	C	A	A	a	G	G	G	G	A	C	G	
TISO12	J1c*	a	t	t	c	c	t	c	a	-	a	g	g	g	g	a	c	g	
TISO17		-	t	c	c	c	t	c	a	a	a	g	g	g	g	a	c	g	
TITE04	H7	a	C	C	C	C	T	C	A	A	A	G	G	G	G	A	C	G	
TOPE07		a	T	C	C	c	T	-	A	A	A	G	G	G	G	A	C	G	
TOPE11		A	T	C	C	c	T	c	A	A	A	G	G	G	G	A	C	G	
TÖSM01		-	T	C	C	c	T	c	A	A	A	G	G	G	G	a	C	G	
VSM03		A	T	C	C	c	T	c	A	A	A	G	G	G	G	A	C	G	
VSM11	H1	a	T	T	C	c	T	-	A	A	A	G	G	G	G	A	C	G	T
VSM13	H1	a	T	T	C	c	T	-	A	A	A	G	G	G	G	A	C	G	T
VSM15	H1	a	T	T	C	-	T	-	A	A	A	G	G	G	G	A	C	G	T
VSM21		a	T	C	C	c	T	-	A	A	A	G	G	G	G	A	C	G	

* TISO12 belongs to hg J1c, but was erroneously analysed with the HPLEX17. The marker for H1 (np 3010) is also diagnostic for J1, hence the result

U-Plex and T1/T2

		U2_16051	U3_16343	U4_4646	U5_3197	U5a_14793	U5b_14182	U8_9698
		G	C	G	G	C	C	G
Individual	HG	A	T	A	A	T	T	A
ABO12	U5b	a	T	A	G	T	C	A
ABO19	U5b	a	T	A	G	-	C	-
CEG01	U4	a	T	a/G	a	T	T	A
GAEL01	U5a	a	T	A	G	C	T	A
GAEL07	U3	a	C	A	A	T	T	A
HAJE11	U4	a	T	a/G	A	T	T	A
HELI01	U5a	A	T	A	G	t/C	T	A
HELI02	U8	A	T	A	A	T	T	G
HELI09	U5a	a	T	A	G	c	T	A
HMG02	U5b	A	T	A	G	t	C	a
MEKÖ02	U4	a	T	a/G	A	-	T	a
MEMO12	U5a	A	T	A	G	C	T	A
MEMO14	U4	A	T	G	A	t	T	A
MEMO17	U4	A	T	G	A	T	T	A
MEMO23	U5b	a	T	A	G	T	C	A
PULE1.17	U8	a	T	A	A	T	T	G
TIBO03	U5b	a	T	A	G	T	C	A
TISO02	U5b	A	T	A	G	T	C	a
TISO03	U5b	a	T	A	G	T	C	A
TOPE08	U5a	a	T	A	G	C	T	A
TOPE12	U8	a	T	A	A	T	T	a/G
VSM17	U8	a	T	A	A	T	T	G
VSM18	U8	A	T	A	A	-	T	G
VSM19	U8	a	T	A	A	t	T	G

		T1_12633	T2_11812
		A	G
Individual	HG	C	A
MAP01	T2	C	G
MAP02	T2	c	G
HMG06	T2	C	G
HMG07 B	t2	c	g
HMG01	n.d.	C	a/g
MEKÖ03	T2	c	G
ABO11	T2	C	G
FUGU09	T2	C	G
PULE1.10	T2	-	G
HAJE09	T2	c	G
FUGU04 A	t2	c	g
PULE1.18 A	t2	c	G
TIBO05 A	t1	a	a
VSM16 A	t1	a	a
BEP04	T2	c	G

D: Additional information prehistoric comparison data

Hunter-gatherer metapopulations (HG):

Time Period	Metapop.	Country	Site	SampleID	Age (as given in publication)	n	Haplogroup	References
Paleolithic		Russia	Kostenki		33000-30000 BP (stratigraphy)	1	U2	Krause et al. 2010
		Russia	Mal'ta		24,423–23,891 cal BP	1	U	Raghavan et al. 2014
Mesolithic	HGE	Russia	Chekalino	ChekalinoIVa	7800 calBC	1	U5a	Bramanti et al. 2009
		Russia	Lebyazhinka	LebyazhinkaIV	8000-7000calBC	1	U5a1	Bramanti et al. 2009
		Russia	Yuzhnyy Oleni Ostrov	UZOO43	7500 BP	9	U2e	Der Sarkissian et al 2013
		Russia	Yuzhnyy Oleni Ostrov	UZOO46			U2e	Der Sarkissian et al 2013
		Russia	Yuzhnyy Oleni Ostrov	UZOO16			U4	Der Sarkissian et al 2014
		Russia	Yuzhnyy Oleni Ostrov	UZOO40			U4	Der Sarkissian et al 2015
		Russia	Yuzhnyy Oleni Ostrov	UZOO70			U5a	Der Sarkissian et al 2016
		Russia	Yuzhnyy Oleni Ostrov	UZOO77			H	Der Sarkissian et al 2017
		Russia	Yuzhnyy Oleni Ostrov	UZOO7			C1	Der Sarkissian et al 2018
		Russia	Yuzhnyy Oleni Ostrov	UZOO8			C1	Der Sarkissian et al 2019
		Russia	Yuzhnyy Oleni Ostrov	UZOO74			C1	Der Sarkissian et al 2020
		Russia	Popovo	PO4	7000 BP	2	U4	Der Sarkissian et al 2021
		Russia	Popovo	PO2			U4	Der Sarkissian et al 2022
Paleolithic	HGC	Czech Republic	Dolni-Vestonice	DOV13	31155 +- 85 calBP	3	U8	Fu et al. 2013
		Czech Republic	Dolni-Vestonice	DOV14			U	Fu et al. 2013
		Czech Republic	Dolni-Vestonice	DOV15			U	Fu et al. 2013
		Germany	Oberkassel	OBK998	14020+-151 calBP	1	U5b1	Fu et al. 2013
		Germany	Hohler Fels	HohlerFels49	13400 calBC	1	U	Bramanti et al. 2009
Mesolithic		Germany	Blätterhöhle	Bla3	9210 +- 29	4	U2e	Bollongino et al 2013
		Germany	Blätterhöhle	Bla6	8796 +- 90 calBC		U5b2a2	Bollongino et al 2013
		Germany	Blätterhöhle	Bla19	8638 +- 56 calBC		U5a	Bollongino et al 2013
		Germany	Blätterhöhle	Bla20	8652 +- 58 calBC		U5a2c3	Bollongino et al 2013
		Luxemburg	Loschbour	LOS	8054 +- 127 cal BP	1	U5b1a	Fu et al. 2013
		Germany	Bad Dürrenberg	BadDürrenberg2	6850 cal BC	1	U4	Bramanti et al. 2009

		Germany	Hohlenstein-Stadel	Hohlenstein-Stadel5830a	6700 cal BC	2	U5a2a	Bramanti et al. 2009
		Germany	Hohlenstein-Stadel	Hohlenstein-Stadel5830b			U5b2	Bramanti et al. 2009
		Sweden	Motala	MOT1	(6,361-5,516 cal BC), one outlier (7,212 ± 109 BP)	7	U5a1	Lazaridis et al 2013
		Sweden	Motala	MOT2			U2e1	Lazaridis et al 2013
		Sweden	Motala	MOT3			U5a1	Lazaridis et al 2013
		Sweden	Motala	MOT4			U5a2d	Lazaridis et al 2013
		Sweden	Motala	MOT6			U5a2d	Lazaridis et al 2013
		Sweden	Motala	MOT9			U5a2	Lazaridis et al 2013
		Sweden	Motala	MOT12			U2e1	Lazaridis et al 2013
		Poland	Dudka	Dudka3	4000-3000 cal BC	1	U5b	Bramanti et al. 2009
		Lithunia	Kretuonas	Kretuonas3	4450 cal BC	2	U5b	Bramanti et al. 2009
		Lithunia	Kretuonas	Kretuonas1	4200 cal BC		U5b	Bramanti et al. 2009
		Lithunia	Spiginas	Spiginas4	6350 cal BC	1	U4	Bramanti et al. 2009
		Poland	Dudka	Dudka2	3650 calBC	1	U5b	Bramanti et al. 2009
		Lithuania	Donkalnis	Donkalnis1	mesolithic (context)	1	U5b	Bramanti et al. 2009
		Poland	Drestwo	Drestwo2	2250 cal BC	1	U5a	Bramanti et al. 2009
		Croatia	Vela Spila	STANKO	7200±30 BP (layer)	1	U5b	Szécsényi-Nagy et al. 2014
Paleolithic		Spain	La Chora	CH.1	Magdalenian	1	H	Hervella et al. 2012
		Spain	La Pasiega	PS.1	Magdalenian	1	H	Hervella et al. 2012
		Spain	Erralla	ERR.1	Magdalenian (12310 BP)	1	U5b	Hervella et al. 2012
		Italy	Paglicci cave	PAG12	24,720 +- 429 BP	2	N*	Caramelli et al. 2003
		Italy	Paglicci cave	PAG25	23,000 +- 350 BP		HV	Caramelli et al. 2003
		Italy	Grotta d´Oriente	ORIB	10,680-10,520 cal BP	1	HV1	Mannino et al.2012
	HGS	Portugal	Toledo	Tol1	8028-6411 cal BC	1	H1b1a'c'd'h	Chandler et al. 2005, Chandler 2003
		Spain	La Braña	Bra1	6,980±50 BP	2	U5b2c1	Sánchez-Quinto et al. 2012
Mesolithic		Spain	La Braña	Bra2	7,030±50 BP		U5b2c1	Sánchez-Quinto et al. 2012
		Spain	Aizpea	AIZ	6600+-65BP	1	U5b	Hervella et al. 2012
		Portugal	Concheiro da Moita do Sebastão	Seba1		1	U5b	Roth 2014, unpublished
		Portugal	Arapouco	Ara7	5992-5715 cal BC	2	U5b1c2	Chandler et al. 2005, Chandler 2003
		Portugal	Arapouco	Ara10			N*	Chandler et al. 2005, Chandler 2003
		Portugal	Poças de São Bento	PSB2	5770-5229 cal BC	1	H	Chandler et al. 2005, Chandler 2003

	Portugal	Cabeço de Pez	CdP3	5214-4805 cal BC	3	H	Chandler et al. 2005, Chandler 2003
	Portugal	Cabeço de Pez	CdP4			H1b1a'c'd'h	Chandler et al. 2005, Chandler 2003
	Portugal	Cabeço de Pez	CdP5			N*	Chandler et al. 2005, Chandler 2003
	Portugal	Cabeço das Amoreiras	CdA3	5064-4715 cal BC	1	U4	Chandler et al. 2005, Chandler 2003

Neolithic Ukraine (NUK):

Six out of seven individuals from the original study (Nikitin et al. 2012) were considered in this study: Ni94, Ya19, Ya34, Ya36, Ya36, Ya 45, Ya64. One sample (Ni58) was excluded due to dating issues.

Early Neolithic Northern Spain (NSE)

The original study by Hervella et al. (2012) featured 27 individuals from the site of Los Cascajos. The individuals CAS-21, CAS-33, CAS-193 and CAS257 were younger than 4500 cal BC. Twelve of the remaining individuals had to be excluded because of insufficient sequence reproduction: (CAS-48, CAS-90, CAS-148, CAS-173, CA-S179, CAS-180, CAS-181, CAS-191, CAS-202, CAS-216, CAS-254, CA-S341).

Cardial Catalonia (CARcat):

Two individuals from the Can Sadurní (CSA0511 and CSA24) site (Gamba et al. 2012) were excluded from this study due to insufficient reproduction of the HVS-I.

E: Haplogroup frequencies Alföld and comparison data

Values are given in %.

NSE= early Neolithic northern Spain, CPE= Central Portugal early Neolihtic NUK= Neolithic Ukraine

	n	C	N*	N1a	N1b	I	W	X	R	HV	V	H	T1	T2	J	U	U2	U3	U4	U5	U5a	U5b	U8	K
Alföld												*												
Körös	16	0	0	0	0	0	0	6.25	0	0	6.25	18.75	0	25	6.25	0	0	0	0	0	0	0	0	37.5
ALBK early	35	0	0	8.57	0	0	0	2.86	2.86	5.71	2.86	22.86	0	11.43	2.86	0	0	0	5.71	0	5.71	2.86	2.86	22.86
ALBK later	144	0	0	6.94	0	0	0.69	4.17	0.69	3.47	3.47	16.67	3.47	15.28	18.06	0	0	0.69	2.08	0	3.47	3.47	1.39	15.97
Esztár	20	0	0	0	0	0	0	0	5	10	10	20	0	5	10	0	0	0	0	0	5	0	5	30
Szakálhát	51	0	0	3.92	0	0	1.96	0	0	1.96	3.92	17.65	3.92	21.57	27.45	0	0	0	1.96	0	0	3.92	0	11.76
North	14	0	0	0	0	0	0	0	0	7.14	14.29	28.57	7.14	28.57	7.14	0	0	0	0	0	0	0	0	7.14
South	37	0	0	5.41	0	0	2.7	0	0	0	0	13.51	2.7	18.92	35.14	0	0	0	2.7	0	0	5.41	0	13.51
Tiszadob/ Bükk	44	0	0	9.09	0	0	0	13.64	0	2.27	2.27	11.36	2.27	15.91	13.64	0	0	2.27	2.27	0	6.82	4.55	2.27	9.09
Tisza	48	0	0	4.17	2.08	0	0	2.08	0	8.33	0	10.42	2.08	18.75	29.17	0	0	0	0	0	0	2.08	8.33	12.5
Tisza East	26	0	0	7.69	3.85	0	0	3.85	0	7.69	0	19.23	3.85	11.54	23.08	0	0	0	0	0	0	0	11.54	7.69
Tisza River	22	0	0	0	0	0	0	0	0	9.09	0	0	0	27.27	36.36	0	0	0	0	0	0	4.55	4.55	18.18
Transdanubia																								
Starčevo	44	0	0	6.82	0	0	4.55	6.82	0	2.27	6.82	6.82	2.27	20.45	11.36	0	0	2.27	2.27	0	0	0	0	27.27
TLBK	52	0	0	7.69	0	0	0	0	0	1.92	5.77	26.92	1.92	19.23	11.54	0	3.85	0	0	0	1.92	0	0	19.23
Vinča	31	0	0	12.9	0	0	0	0	0	3.23	0	3.23	0	19.35	9.68	0	3.23	9.68	0	0	6.45	3.23	0	29.03
Lengyel	82	0	0	12.2	0	0	1.22	1.22	0	7.32	0	21.95	0	18.29	7.32	0	0	0	0	1.22	1.22	3.66	6.1	18.29
Sopot	37	0	0	10.81	0	0	0	2.7	0	10.81	0	27.03	0	13.51	13.51	0	0	2.7	0	0	2.7	0	2.7	13.51
Central Europe																								
LBK	109	0	0	11.93	0	0	2.75	0.92	0	4.59	4.59	16.51	0	22.94	11.93	0	0	0.92	0	0	1.83	0.92	0	20.18
Rössen Culture	17	0	0	5.88	0	0	0	5.88	0	23.53	5.88	29.41	0	11.76	0	0	0	0	0	0	0	5.88	0	11.76

	n	C	N*	N1a	N1b	I	W	X	R	HV	V	H	T1	T2	J	U	U2	U3	U4	U5	U5a	U5b	U8	K
Southwestern Europe																								
Cardial Catalonia	12	0	16.67	0	0	0	0	8.33	0	0	0	16.67	0	16.67	0	0	0	0	0	0	0	8.33	0	33.33
NSE	23	0	0	0	0	4.35	0	0	0	4.35	0	52.17	0	0	4.35	21.74	0	0	0	0	0	4.35	0	8.7
CPE	9	0	0	0	0	0	0	0	0	0	11.11	66.67	0	0	0	11.11	0	0	0	0	0	11.11	0	0
Ukraine		0	0	6.82	0	0	4.55	6.82	0	2.27	6.82	6.82	2.27	20.45	11.36	0	0	2.27	2.27	0	0	0	0	27.27
NUK	6	33.33	0	0	0	0	0	0	0	0	0	33.33	0	0	0	0	0	16.67	0	0	16.67	0	0	0
Hunter-gatherers																								
Centraul Europe	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10.71	10.71	0	7.14	0	32.14	35.71	3.57	0
Eastern Europe	15	20	0	0	0	0	0	0	0	0	0	6.67	0	0	0	6.67	20	0	26.67	0	20	0	0	0
Southwestern Europe	18	0	16.67	0	0	0	0	0	0	11.11	0	33.33	0	0	0	0	0	0	5.56	0	0	33.33	0	0

* Frequencies of subclades of H in the Alföld dataset

Culture/ group	n	H1	H5	H7	other H
Körös	16	6.25	0	0	12.5
ALBK early	35	0	8.57	5.71	8.57
ALBK later	144	0.69	3.47	3.47	9.03
Esztár	20	0	5	0	15
Szakálhát	51	1.96	3.92	5.88	5.88
North	14	7.14	0	14.29	7.14
South	37	0	5.41	2.7	5.41
Tiszadob/Bükk	44	0	0	4.55	6.82
Tisza	48	6.25	0	0	4.17
Tisza East	26	11.54	0	0	7.69
Tisza River	22	0	0	0	0

Groups and frequencies of the subclades of H used in the pan-European analyses

Group	n	H1	H2	H3	H4	H5	H7	H10	H11	H13	H14	H16	H23	other H
ENH	11	9.09	0	0	0	27.27	18.18	0	0	0	0	0	0	45.45
MNH	24	4.17	0	0	0	20.83	20.83	0	0	0	0	0	0	54.17
LNH	5	60	0	0	0	0	0	0	0	0	0	0	0	40
ENC	16	31.25	0	0	0	12.5	0	6.25	0	0	0	6.25	6.25	37.5
MNC	9	11.11	0	22.22	0	55.56	11.11	0	0	0	0	0	0	0
BBC	10	30	0	20	20	20	0	0	0	0	0	0	0	10
UC	7	0	14.29	28.57	14.29	0	14.29	0	14.29	0	0	0	0	14.29
TRE	6	50	0	50	0	0	0	0	0	0	0	0	0	0
NEOI	11	45.45	0	45.45	0	0	0	0	0	0	0	0	0	9.09
CHI	31	64.52	0	16.13	0	0	0	0	0	0	0	0	0	19.35
BAI	8	75	0	0	0	0	0	0	0	0	0	0	0	25

ENH= Early Neolithic Hungary (Körös & ALBK early), MNH= Middle Neolithic Hungary, LNH= Late Neolithic Hungary, ENC= Early Neolithic Central Europe, MNC= Middle Neolithic Central Europe, BBC= Bell Beaker Central Europe, UC= Unetice Culture Central Europe, TRE= Treilles, NEOI= Neolithic Iberian Peninsula, CHI= Chalcolithic Iberian Peninsula, BAI= Bronze Age Iberian Peninsula

F: Models tested in the AMOVA

The five best models of each setup (three and four groups, respectively) are highlighted in grey

		Among groups					Within populations					Among populations within groups				
	Model	sum of squares	variance components	% of variation	Fct	p	sum of squares	variance components	% of variation	Fst	p	sum of squares	variance components	% of variation	Fsc	p
	3 groups															
1	(KÖR_ALBKearly) + (SzakN_SzakS_ALBKtb_ALBKe) + (TiszaRiver_TiszaEast)	11200119	0.01014	0.37	0.00368	0.36559+-0.01859	535200733	2.66534	96.60	0.03396	0.00000+-0.00000	23200760	0.08357	3.03	0.03040	0.00489+-0.00247
2	(KÖR_SzakN) + (ALBKearly_SzakS_ALBKtb_ALBKe) + (TiszaRiver_TiszaEast)	8200699	-0.00708	-0.26	-0.00257	0.53666+-0.01652	535200733	2.66534	96.81	0.03191	0.00098+-0.00098	26200180	0.09494	3.45	0.03440	0.00196+-0.00136
3	(KÖR_SzakS) + (ALBKearly_SzakN_ALBKtb_ALBKe) + (TiszaRiver_TiszaEast)	11200217	0.00925	0.34	0.00335	0.39883+-0.01687	535200733	2.66534	96.62	0.03383	0.00000+-0.00000	23200662	0.08407	3.05	0.03058	0.00293+-0.00164
4	(KÖR_ALBKtb) + (ALBKearly_SzakN_SzakS_ALBKe) + (TiszaRiver_TiszaEast)	7200145	-0.03998	-1.46	-0.01456	0.85826+-0.01154	535200733	2.66534	97.09	0.02905	0.00000+-0.00000	27200734	0.11974	4.36	0.04299	0.00000+-0.00000
5	(KÖR_ALBKe) + (ALBKearly_SzakN_SzakS_ALBKtb) + (TiszaRiver_TiszaEast)	10200771	0.01410	0.51	0.00511	0.35851+-0.00461	535200733	2.66534	96.53	0.03466	0.00050+-0.00026	24200108	0.08159	2.96	0.02970	0.00218+-0.00046
6	(KÖR_TiszaRiver) + (SzakN_SzakS_ALBKtb_ALBKe) + (ALBKearly_TiszaEast)	9200872	-0.00163	-0.06	-0.00059	0.52624+-0.00487	535200733	2.66534	96.73	0.03271	0.00020+-0.00014	25200007	0.09175	3.33	0.03328	0.00020+-0.00014
7	(KÖR_TiszaEast) + (SzakN_SzakS_ALBKtb_ALBKe) + (ALBKearly_TiszaRiver)	4200702	-0.06288	-2.30	-0.02298	0.99545+-0.00068	535200733	2.66534	97.39	0.02609	0.00040+-0.00019	30200177	0.13427	4.91	0.04796	0.00000+-0.00000
	variations of model no.5															
8	(KÖR_ALBKe) + (SzakN_SzakS_ALBKtb) + (ALBKearly_TiszaRiver_TiszaEast)	11200545	0.01607	0.58	0.00582	0.34050+-0.00460	535200733	2.66534	96.56	0.03441	0.00040+-0.00019	23200334	0.07891	2.86	0.02876	0.00505+-0.00072
9	(KÖR_ALBKe) + (ALBKearly_SzakS_ALBKtb) + (SzakN_TiszaRiver_TiszaEast)	11200183	0.01703	0.62	0.00617	0.33624+-0.00509	535200733	2.66534	96.53	0.03472	0.00040+-0.00019	23200696	0.07883	2.85	0.02873	0.00218+-0.00046
10	(KÖR_ALBKe) + (ALBKearly_SzakN_ALBKtb) + (SzakS_TiszaRiver_TiszaEast)	15200718	0.06066	2.19	0.02188	0.06059+-0.00241	535200733	2.66534	96.14	0.03856	0.00050+-0.00026	19200161	0.04623	1.67	0.01705	0.03752+-0.00193
11	(KÖR_ALBKe) + (ALBKearly_SzakN_SzakS) + (ALBKtb_TiszaRiver_TiszaEast)	11200244	0.01196	0.43	0.00433	0.39752+-0.00473	535200733	2.66534	96.60	0.03400	0.00030+-0.00017	23200634	0.08186	2.97	0.02980	0.00386+-0.00061
12	(KÖR_ALBKe) + (TiszaRiver_SzakN_SzakS_ALBKtb) + (ALBKearly_TiszaEast)	13200698	0.04195	1.52	0.01515	0.15218+-0.00360	535200733	2.66534	96.26	0.03743	0.00030+-0.00017	21200181	0.06170	2.23	0.02262	0.01653+-0.00134
13	(KÖR_ALBKe) + (TiszaEast_SzakN_SzakS_ALBKtb) + (ALBKearly_TiszaRiver)	12200133	0.02557	0.93	0.00925	0.27376+-0.00450	535200733	2.66534	96.42	0.03581	0.00030+-0.00017	22200746	0.07342	2.66	0.02681	0.00554+-0.00079

		Among groups					Within populations					Among populations within groups				
	Model	sum of squares	variance components	% of variation	Fct	p	sum of squares	variance components	% of variation	Fst	p	sum of squares	variance components	% of variation	Fsc	p
14	(KÖR_ALBKe) + (TiszaRiver_ALBKearly_SzakS_ALBKtb) + (SzakN_TiszaEast)	9201370	-0.00052	-0.02	-0.00019	0.50574+-0.00455	535201733	2.66534	96.72	0.03281	0.00050+-0.00022	25201509	0.09095	3.30	0.03300	0.00099+-0.00039
15	(KÖR_ALBKe) + (TiszaEast_ALBKearly_SzakS_ALBKtb) + (SzakN_TiszaRiver)	12201754	0.04520	1.63	0.01629	0.11238+-0.00370	535201733	2.66534	96.06	0.03941	0.00059+-0.00024	22201125	0.06415	2.31	0.02350	0.00634+-0.00084
16	(KÖR_ALBKe) + (TiszaRiver_ALBKearly_SzakN_ALBKtb) + (SzakS_TiszaEast)	12201480	0.02656	0.96	0.00961	0.26970+-0.00466	535201733	2.66534	96.43	0.03566	0.00040+-0.00019	22201399	0.07201	2.61	0.02631	0.00762+-0.00084
17	(KÖR_ALBKe) + (TiszaEast_ALBKearly_SzakN_ALBKtb) + (SzakS_TiszaRiver)	17201183	0.08174	2.94	0.02939	0.01911+-0.00134	535201733	2.66534	95.82	0.04179	0.00040+-0.00019	17201696	0.03452	1.24	0.01278	0.08396+-0.00299
18	(KÖR_ALBKe) + (TiszaRiver_SzakN_SzakS_ALBKearly) + (TiszaEast_ALBKtb)	13201662	0.03789	1.37	0.01369	0.20743+-0.00377	535201733	2.66534	96.34	0.03664	0.00020+-0.00014	21201217	0.06348	2.29	0.02326	0.01267+-0.00100
19	(KÖR_ALBKe) + (TiszaEast_SzakN_SzakS_ALBKearly) + (TiszaRiver_ALBKtb)	10201210	-0.00099	-0.04	-0.00036	0.52446+-0.00512	535201733	2.66534	96.72	0.03278	0.00030+-0.00017	24201668	0.09132	3.31	0.03313	0.00149+-0.00038
	variations of model no. 10															
20	(KÖR_ALBKe) + (ALBKearly_ALBKtb) + (SzakN_SzakS_TiszaRiver_TiszaEast)	17201029	0.07457	2.69	0.02686	0.03376+-0.00158	535201733	2.66534	96.01	0.03995	0.00030+-0.00017	17201850	0.03633	1.31	0.01345	0.05554+-0.00201
21	(KÖR_ALBKe) + (SzakN_ALBKtb) + (ALBKearly_SzakS_TiszaRiver_TiszaEast)	12201074	0.02033	0.74	0.00736	0.31723+-0.00429	535201733	2.66534	96.49	0.03509	0.00020+-0.00014	22201805	0.07661	2.77	0.02794	0.00505+-0.00072
22	(KÖR_ALBKe) + (SzakN_ALBKearly) + (ALBKtb_SzakS_TiszaRiver_TiszaEast)	13201223	0.04017	1.45	0.01450	0.16069+-0.00364	535201733	2.66534	96.22	0.03780	0.00030+-0.00017	21201656	0.06453	2.33	0.02364	0.00990+-0.00100
	variations of model no. 17, third group unchanged															
23	(KÖR_ALBKe_TiszaEast) + (ALBKearly_SzakN_ALBKtb) + (SzakS_TiszaRiver)	13201819	0.03555	1.29	0.01286	0.17366+-0.00387	535201733	2.66534	96.41	0.03587	0.00059+-0.00024	21201059	0.06361	2.30	0.02331	0.01366+-0.00129
24	(KÖR_ALBKe_ALBKearly) + (TiszaEast_SzakN_ALBKtb) + (SzakS_TiszaRiver)	21201001	0.11179	4.02	0.04019	0.00703+-0.00076	535201733	2.66534	95.82	0.04185	0.00020+-0.00014	13201878	0.00462	0.17	0.00173	0.37842+-0.00471
25	(KÖR_ALBKe_SzakN) + (ALBKearly_TiszaEast_ALBKtb) + (SzakS_TiszaRiver)	16201805	0.07161	2.58	0.02581	0.03663+-0.00188	535201733	2.66534	96.05	0.03948	0.00099+-0.00030	18201074	0.03793	1.37	0.01403	0.05871+-0.00223
26	(KÖR_ALBKe_ALBKtb) + (ALBKearly_TiszaEast_SzakN) + (SzakS_TiszaRiver)	11201851	0.01184	0.43	0.00429	0.40515+-0.00429	535201733	2.66534	96.62	0.03383	0.00069+-0.00025	23201028	0.08150	2.95	0.02967	0.00495+-0.00070
27	(KÖR_TiszaEast) + (ALBKe_ALBKearly_SzakN_ALBKtb) + (SzakS_TiszaRiver)	13201097	0.03165	1.14	0.01144	0.23178+-0.00407	535201733	2.66534	96.39	0.03613	0.00050+-0.00022	21201782	0.06827	2.47	0.02497	0.00941+-0.00100

		Among groups					Within populations					Among populations within groups				
	Model	sum of squares	variance components	% of variation	Fct	p	sum of squares	variance components	% of variation	Fst	p	sum of squares	variance components	% of variation	Fsc	p
28	(KÖR_ALBKearly) + (ALBKe_TiszaEast_SzakN_ALBKtb) + (SzakS_TiszaRiver)	17202044	0.07233	2.61	0.02606	0.04178+-0.00197	535202733	2.66534	96.04	0.03961	0.00030+-0.00017	17202835	0.03761	1.36	0.01391	0.08119+-0.00268
29	(KÖR_SzakN) + (ALBKe_TiszaEast_ALBKearly_ALBKtb) + (SzakS_TiszaRiver)	16202655	0.08024	2.88	0.02883	0.02366+-0.00136	535202733	2.66534	95.76	0.04239	0.00010+-0.00010	18202224	0.03776	1.36	0.01397	0.06851+-0.00240
30	(KÖR_ALBKtb) + (ALBKe_TiszaEast_ALBKearly_SzakN) + (SzakS_TiszaRiver)	13202445	0.02761	1.00	0.00999	0.24465+-0.00455	535202733	2.66534	96.48	0.03522	0.00069+-0.00025	21202433	0.06969	2.52	0.02548	0.00941+-0.00101
	variations of model no. 24, changing positions of Körös culture															
31	(ALBKe_ALBKearly) + (KÖR_TiszaEast_SzakN_ALBKtb) + (SzakS_TiszaRiver)	17202366	0.07473	2.69	0.02693	0.03257+-0.00159	535202733	2.66534	96.04	0.03956	0.00040+-0.00019	17202512	0.03505	1.26	0.01298	0.10663+-0.00273
32	(ALBKe_ALBKearly) + (TiszaEast_SzakN_ALBKtb) + (KÖR_SzakS_TiszaRiver)	18202279	0.08269	2.98	0.02980	0.02040+-0.00138	535202733	2.66534	96.04	0.03963	0.00010+-0.00010	16202600	0.02729	0.98	0.01013	0.15119+-0.00328
	variations of model no. 32															
33	(ALBKe_ALBKearly_SzakN) + (TiszaEast_ALBKtb) + (KÖR_SzakS_TiszaRiver)	16202625	0.06327	2.28	0.02284	0.04634+-0.00189	535202733	2.66534	96.22	0.03779	0.00050+-0.00022	18202254	0.04141	1.49	0.01530	0.05406+-0.00220
34	(ALBKe_ALBKearly) + (TiszaEast_ALBKtb) + (KÖR_SzakS_TiszaRiver_SzakN)	19202556	0.09666	3.48	0.03478	0.01188+-0.00117	535202733	2.66534	95.91	0.04086	0.00020+-0.00014	15202323	0.01688	0.61	0.00629	0.21337+-0.00428
	variations of model no. 24															
35	(KÖR_ALBKe_ALBKearly) + (TiszaEast_ALBKtb) + (SzakS_TiszaRiver_SzakN)	21202959	0.12083	4.34	0.04342	0.00307+-0.00059	535202733	2.66534	95.78	0.04219	0.00040+-0.00019	12202920	-0.00342	-0.12	-0.00128	0.44495+-0.00407
36	(KÖR_ALBKe_ALBKearly_SzakN) + (TiszaEast_ALBKtb) + (SzakS_TiszaRiver)	19202725	0.09758	3.51	0.03512	0.00554+-0.00075	535202733	2.66534	95.93	0.04072	0.00030+-0.00017	15202154	0.01555	0.56	0.00580	0.19842+-0.00409
	variations of model no. 35															
37	(ALBKe_ALBKearly) + (KÖR_TiszaEast_ALBKtb) + (SzakS_TiszaRiver_SzakN)	17202668	0.07621	2.75	0.02748	0.03307+-0.00180	535202733	2.66534	96.09	0.03914	0.00000+-0.00000	17202211	0.03235	1.17	0.01199	0.10703+-0.00326
38	(KÖR_ALBKearly) + (ALBKe_TiszaEast_ALBKtb) + (SzakS_TiszaRiver_SzakN)	17202917	0.07990	2.88	0.02879	0.03703+-0.00163	535202733	2.66534	96.03	0.03965	0.00030+-0.00017	16202962	0.03014	1.09	0.01118	0.11248+-0.00290
39	(KÖR_ALBKearly) + (TiszaEast_ALBKtb) + (ALBKe_SzakS_TiszaRiver_SzakN)	15202960	0.05751	2.08	0.02076	0.07762+-0.00285	535202733	2.66534	96.22	0.03781	0.00040+-0.00019	18202919	0.04721	1.70	0.01741	0.03683+-0.00194
40	(KÖR_ALBKe) + (TiszaEast_ALBKtb_ALBKearly) + (SzakS_TiszaRiver_SzakN)	18202361	0.09104	3.27	0.03273	0.01337+-0.00117	535202733	2.66534	95.83	0.04174	0.00020+-0.00014	16202517	0.02506	0.90	0.00932	0.12931+-0.00343

		Among groups					Within populations					Among populations within groups				
	Model	sum of squares	variance components	% of variation	Fct	p	sum of squares	variance components	% of variation	Fst	p	sum of squares	variance components	% of variation	Fsc	p
41	(KÖR_ALBKe) + (TiszaEast_ALBKtb) + (SzakS_TiszaRiver_SzakN_ALBKearly)	13203662	0.03789	1.37	0.01369	0.20812+-0.00414	535203733	2.66534	96.34	0.03664	0.00030+-0.00017	21203217	0.06348	2.29	0.02326	0.01396+-0.00102
42	(KÖR_ALBKe_TiszaEast) + (ALBKearly_ALBKtb) + (SzakS_TiszaRiver_SzakN)	15203123	0.04840	1.75	0.01749	0.10881+-0.00297	535203733	2.66534	96.33	0.03669	0.00030+-0.00017	19203756	0.05312	1.92	0.01954	0.01950+-0.00121
43	(KÖR_ALBKe_ALBKtb) + (TiszaEast_ALBKearly) + (SzakS_TiszaRiver_SzakN)	13203235	0.02715	0.98	0.00983	0.23822+-0.00438	535203733	2.66534	96.49	0.03505	0.00050+-0.00022	21203643	0.06967	2.52	0.02547	0.01178+-0.00106
44	(KÖR_ALBKe_SzakS) + (TiszaEast_ALBKtb) + (ALBKearly_TiszaRiver_SzakN)	9203233	-0.01659	-0.60	-0.00603	0.68842+-0.00460	535203733	2.66534	96.84	0.03159	0.00089+-0.00028	25203646	0.10353	3.76	0.03739	0.00129+-0.00033
45	(KÖR_ALBKe_TiszaRiver) + (TiszaEast_ALBKtb) + (ALBKearly_SzakS_SzakN)	11203812	0.01356	0.49	0.00491	0.36604+-0.00444	535203733	2.66534	96.6	0.03399	0.00030+-0.00017	23203067	0.08021	2.91	0.02922	0.00475+-0.00068
46	(KÖR_ALBKe_SzakN) + (TiszaEast_ALBKtb) + (ALBKearly_SzakS_TiszaRiver)	12203011	0.01732	0.63	0.00627	0.32921+-0.00448	535203733	2.66534	96.56	0.03436	0.00030+-0.00017	22203868	0.07752	2.81	0.07752	0.00505+-0.00067
47	(KÖR_TiszaEast_ALBKearly_SzakN) + (ALBKe_ALBKtb) + (SzakS_TiszaRiver)	13203404	0.02734	0.99	0.00990	0.25604+-0.00430	535203733	2.66534	96.49	0.03514	0.00040+-0.00019	21203475	0.06973	2.52	0.02550	0.01079+-0.00117
48	(KÖR_TiszaEast_ALBKearly) + (ALBKe_ALBKtb) + (SzakS_TiszaRiver_SzakN)	14203487	0.03971	1.44	0.01436	0.15277+-0.00367	535203733	2.66534	96.4	0.03598	0.00030+-0.00017	20203392	0.05977	2.16	0.02193	0.02020+-0.00145
49	(KÖR_ALBKtb_ALBKearly) + (ALBKe_TiszaEast) + (SzakS_TiszaRiver_SzakN)	14203308	0.04262	1.54	0.01540	0.13990+-0.00362	535203733	2.66534	96.34	0.03664	0.00040+-0.00019	20203571	0.05877	2.12	0.02157	0.02020+-0.00144
50	(KÖR_SzakS_ALBKearly) + (ALBKtb_TiszaEast) + (ALBKe_TiszaRiver_SzakN)	10203420	-0.00093	-0.03	-0.00034	0.52535+-0.00507	535203733	2.66534	96.72	0.03281	0.00040+-0.00019	24203459	0.09134	3.31	0.03313	0.00198+-0.00042
51	(KÖR_TiszaRiver_ALBKearly) + (ALBKtb_TiszaEast) + (ALBKe_SzakS_SzakN)	11203868	0.01181	0.43	0.00428	0.40743+-0.00504	535203733	2.66534	96.62	0.03380	0.00040+-0.00019	23203010	0.08143	2.95	0.02965	0.00475+-0.00076
52	(KÖR_SzakN_ALBKearly) + (ALBKtb_TiszaEast) + (ALBKe_SzakS_TiszaRiver)	13203860	0.03367	1.22	0.01218	0.18525+-0.00367	535203733	2.66534	96.45	0.03553	0.00050+-0.00022	21203019	0.06451	2.33	0.06451	0.01287+-0.00112
53	(KÖR_ALBKe_ALBKearly) + (SzakS_TiszaEast_ALBKtb) + (TiszaRiver_SzakN)	17203836	0.08720	3.14	0.03135	0.01663+-0.00122	535203733	2.66534	95.83	0.04170	0.00010+-0.00010	17203043	0.02879	1.04	0.01069	0.09614+-0.00326
54	(KÖR_ALBKe_ALBKearly) + (TiszaRiver_TiszaEast_ALBKtb) + (SzakS_SzakN)	18203404	0.08476	3.05	0.03053	0.02178+-0.00146	535203733	2.66534	96.00	0.04000	0.00040+-0.00019	16203474	0.02629	0.95	0.00977	0.13287+-0.00397
55	(KÖR_ALBKe_ALBKearly) + (SzakS_ALBKtb) + (TiszaEast_TiszaRiver_SzakN)	16203227	0.06096	2.2	0.02201	0.05970+-0.00229	535203733	2.66534	96.23	0.03774	0.00030+-0.00017	18203652	0.04357	1.57	0.01608	0.03089+-0.00158
56	(KÖR_ALBKe_ALBKearly) + (TiszaRiver_ALBKtb) + (TiszaEast_SzakS_SzakN)	16203423	0.06091	2.2	0.02199	0.06307+-0.00260	535203733	2.66534	96.24	0.03764	0.00020+-0.00014	18203456	0.04333	1.56	0.01600	0.04337+-0.00184

		Among groups					Within populations					Among populations within groups				
	Model	sum of squares	variance components	% of variation	Fct	p	sum of squares	variance components	% of variation	Fst	p	sum of squares	variance components	% of variation	Fsc	p
57	(KÖR_ALBKe_ALBKearly) + (SzakN_ALBKtb) + (TiszaEast_SzakS_TiszaRiver)	19204214	0.09182	3.31	0.03306	0.01109+-0.00103	535204733	2.66534	95.98	0.04022	0.00059+-0.00028	15204665	0.01986	0.72	0.00740	0.18050+-0.00378
58	(KÖR_ALBKe_ALBKearly) + (TiszaEast_SzakS) + (ALBKtb_TiszaRiver_SzakN)	16204831	0.06579	2.37	0.02374	0.04198+-0.00202	535204733	2.66534	96.19	0.03805	0.00059+-0.00024	18204048	0.03964	1.43	0.01466	0.06485+-0.00281
59	(KÖR_ALBKe_ALBKearly) + (TiszaEast_TiszaRiver) + (ALBKtb_SzakS_SzakN)	16204094	0.06260	2.26	0.02258	0.04901+-0.00214	535204733	2.66534	96.15	0.03845	0.00109+-0.00034	18204785	0.04399	1.59	0.01624	0.04218+-0.00195
60	(KÖR_ALBKe_ALBKearly) + (TiszaEast_SzakN) + (ALBKtb_SzakS_TiszaRiver)	15204186	0.05514	1.99	0.01990	0.09347+-0.00275	535204733	2.66534	96.19	0.03814	0.00010+-0.00010	19204693	0.05054	1.82	0.01861	0.02535+-0.00174
	variations of model no.34															
61	(ALBKe_ALBKearly) + (KÖR_TiszaEast_ALBKtb) + (SzakS_TiszaRiver_SzakN)	17204668	0.07621	2.75	0.02748	0.03614+-0.00164	535204733	2.66534	96.09	0.03914	0.00040+-0.00019	17204211	0.03235	1.17	0.01199	0.10733+-0.00307
62	(ALBKe_ALBKearly) + (SzakS_TiszaEast_ALBKtb) + (KÖR_TiszaRiver_SzakN)	17204506	0.08094	2.91	0.02914	0.02901+-0.00152	535204733	2.66534	95.94	0.04062	0.00059+-0.00024	17204373	0.03191	1.15	0.01183	0.04495+-0.00199
63	(ALBKe_ALBKearly) + (TiszaRiver_TiszaEast_ALBKtb) + (SzakS_KÖR_SzakN)	15204703	0.05530	2.00	0.01997	0.08752+-0.00282	535204733	2.66534	96.25	0.03750	0.00010+-0.00010	19204176	0.04856	1.75	0.01789	0.04495+-0.00199
64	(ALBKe_TiszaEast) + (ALBKearly_ALBKtb) + (KÖR_SzakS_TiszaRiver_SzakN)	14204022	0.03800	1.37	0.01374	0.19911+-0.00386	535204733	2.66534	96.38	0.03617	0.00040+-0.00019	20204857	0.06203	2.24	0.02274	0.01683+-0.00118
65	(ALBKe_ALBKtb) + (TiszaEast_ALBKearly) + (KÖR_SzakS_TiszaRiver_SzakN)	13204136	0.02474	0.9	0.00896	0.27465+-0.00485	535204733	2.66534	96.51	0.03491	0.27465+-0.00485	21204743	0.07168	2.60	0.02619	0.01228+-0.00107
66	(ALBKe_SzakS) + (TiszaEast_ALBKtb) + (KÖR_ALBKearly_TiszaRiver_SzakN)	11204252	0.00381	0.14	0.00138	0.44634+-0.00440	535204733	2.66534	96.68	0.03319	0.00079+-0.00030	23204627	0.08769	3.18	0.03185	0.00396+-0.00056
67	(ALBKe_TiszaRiver) + (TiszaEast_ALBKtb) + (KÖR_ALBKearly_SzakS_SzakN)	10204269	-0.00174	-0.06	-0.00063	0.52980+-0.00462	535204733	2.66534	96.73	0.03272	0.00040+-0.00019	24204610	0.09190	3.34	0.03333	0.00168+-0.00045
68	(ALBKe_SzakN) + (TiszaEast_ALBKtb) + (KÖR_ALBKearly_SzakS_TiszaRiver)	10204547	0.00363	0.13	0.00132	0.44812+-0.00478	535204733	2.66534	96.67	0.03325	0.00030+-0.00017	24204332	0.08805	3.19	0.03198	0.00267+-0.00056
69	(SzakS_ALBKearly) + (TiszaEast_ALBKtb) + (KÖR_ALBKe_TiszaRiver_SzakN)	11204731	0.01029	0.37	0.00373	0.39287+-0.00520	535204733	2.66534	96.63	0.03368	0.00050+-0.00022	23204148	0.08261	3.00	0.03006	0.00337+-0.00057
70	(TiszaRiver_ALBKearly) + (TiszaEast_ALBKtb) + (KÖR_ALBKe_SzakS_SzakN)	9204688	-0.01271	-0.46	-0.00462	0.61386+-0.00523	535204733	2.66534	96.82	0.03183	0.00030+-0.00017	25204191	0.10032	3.64	0.03627	0.00109+-0.00031
71	(SzakN_ALBKearly) + (TiszaEast_ALBKtb) + (KÖR_ALBKe_TiszaRiver_SzakS)	11204945	0.01271	0.46	0.00461	0.36752+-0.00505	535204733	2.66534	96.6	0.03400	0.00020+-0.00014	22204933	0.08109	2.94	0.02953	0.00485+-0.00067
72	(ALBKe_ALBKearly) + (KÖR_ALBKtb) + (TiszaEast_SzakS_TiszaRiver_SzakN)	16204235	0.06045	2.18	0.02181	0.06337+-0.00232	535204733	2.66534	96.18	0.03816	0.00030+-0.00017	18204644	0.04529	1.63	0.01671	0.04317+-0.00172

		Among groups					Within populations					Among populations within groups				
	Model	sum of squares	variance components	% of variation	Fct	p	sum of squares	variance components	% of variation	Fst	p	sum of squares	variance components	% of variation	Fsc	p
73	(ALBKe_ALBKearly) + (SzakS_ALBKtb) + (TiszaEast_KÖR_TiszaRiver_SzakN)	14205594	0.04283	1.55	0.0154	0.13030+-0.00334	535205733	2.66534	96.36	0.0363	0.00040+-0.00019	20205285	0.05779	2.09	0.02122	0.01822+-0.00130
74	(ALBKe_ALBKearly) + (TiszaRiver_ALBKtb) + (TiszaEast_KÖR_SzakS_SzakN)	13205317	0.02739	0.99	0.0099	0.25208+-0.00423	535205733	2.66534	96.48	0.0352	0.00010+-0.00010	21205562	0.06990	2.53	0.02556	0.01069+-0.00097
75	(ALBKe_ALBKearly) + (SzakN_ALBKtb) + (TiszaEast_KÖR_SzakS_TiszaRiver)	16205166	0.05984	2.16	0.0215	0.07149+-0.00234	535205733	2.66534	96.18	0.0381	0.00040+-0.00019	18205713	0.04599	1.66	0.04599	0.04941+-0.00211
76	(ALBKe_ALBKearly) + (TiszaEast_KÖR) + (ALBKtb_SzakS_TiszaRiver_SzakN)	13205558	0.03879	1.40	0.0140	0.17703+-0.00354	535205733	2.66534	96.30	0.0370	0.00010+-0.00010	21205321	0.06370	2.30	0.02334	0.01604+-0.00123
77	(ALBKe_ALBKearly) + (TiszaEast_SzakS) + (ALBKtb_KÖR_TiszaRiver_SzakN)	14205570	0.04246	1.53	0.0153	0.13564+-0.00312	535205733	2.66534	96.35	0.0365	0.00020+-0.00014	20205309	0.05863	2.12	0.02152	0.02703+-0.00151
78	(ALBKe_ALBKearly) + (TiszaEast_TiszaRiver) + (ALBKtb_KÖR_SzakS_SzakN)	12205766	0.02811	1.02	0.0101	0.23614+-0.00455	535205733	2.66534	96.43	0.0357	0.00040+-0.00019	22205113	0.07070	2.56	0.02584	0.00950+-0.00101
79	(ALBKe_ALBKearly) + (TiszaEast_SzakN) + (ALBKtb_KÖR_SzakS_TiszaRiver)	12205109	0.02285	0.83	0.0082	0.29515+-0.00416	535205733	2.66534	96.46	0.0354	0.00040+-0.00019	22205770	0.07495	2.71	0.02735	0.00733+-0.00085
	variations of model no. 24															
80	(TiszaEast_ALBKe_ALBKearly) + (KÖR_SzakN_ALBKtb) + (SzakS_TiszaRiver)	15205042	0.04629	1.67	0.0167	0.12020+-0.00328	535205733	2.66534	96.34	0.0365	0.00050+-0.00022	19205837	0.05490	1.98	0.02018	0.03396+-0.00187
81	(SzakN_ALBKe_ALBKearly) + (KÖR_TiszaEast_ALBKtb) + (SzakS_TiszaRiver)	15205055	0.04734	1.71	0.0171	0.10604+-0.00311	535205733	2.66534	96.33	0.0367	0.00040+-0.00019	19205823	0.05429	1.96	0.01996	0.02743+-0.00151
82	(ALBKtb_ALBKe_ALBKearly) + (KÖR_TiszaEast_SzakN) + (SzakS_TiszaRiver)	14205534	0.04490	1.62	0.0162	0.12881+-0.00340	535205733	2.66534	96.32	0.0368	0.12881+-0.00340	20205345	0.05703	2.06	0.02095	0.01980+-0.00139
83	(SzakS_ALBKe_ALBKearly) + (ALBKtb_TiszaEast_SzakN) + (KÖR_TiszaRiver)	11205808	0.01799	0.65	0.0065	0.32653+-0.00445	535205733	2.66534	96.54	0.0345	0.00020+-0.00014	23205070	0.07745	2.81	0.02824	0.00693+-0.00080
84	(TiszaRiver_ALBKe_ALBKearly) + (ALBKtb_TiszaEast_SzakN) + (KÖR_SzakS)	12205511	0.01933	0.7	0.0070	0.31762+-0.00430	535205733	2.66534	96.55	0.0344	0.00040+-0.00019	22205368	0.07582	2.75	0.02766	0.00713+-0.00081
85	(KÖR_TiszaEast_ALBKearly) + (ALBKe_SzakN_ALBKtb) + (SzakS_TiszaRiver)	13205654	0.03134	1.13	0.0113	0.20158+-0.00378	535205733	2.66534	96.46	0.0353	0.00010+-0.00010	21205225	0.06644	2.40	0.02432	0.01386+-0.00106
86	(KÖR_SzakN_ALBKearly) + (ALBKe_TiszaEast_ALBKtb) + (SzakS_TiszaRiver)	16205038	0.05867	2.12	0.0211	0.06703+-0.00230	535205733	2.66534	96.23	0.0377	0.00059+-0.00024	18205841	0.04587	1.66	0.01692	0.05248+-0.00221
87	(KÖR_ALBKtb_ALBKearly) + (ALBKe_TiszaEast_SzakN) + (SzakS_TiszaRiver)	13205318	0.03057	1.11	0.0110	0.20297+-0.00379	535205733	2.66534	96.45	0.0354	0.00059+-0.00024	21205561	0.06750	2.44	0.02470	0.00812+-0.00086
88	(KÖR_SzakS_ALBKearly) + (ALBKtb_TiszaEast_SzakN) + (ALBKe_TiszaRiver)	9205524	-0.00835	-0.30	-0.0030	0.61020+-0.00443	535205733	2.66534	96.79	0.0321	0.00020+-0.00014	25205355	0.09683	3.52	0.03505	0.00208+-0.00049
89	(KÖR_TiszaRiver_ALBKearly) + (ALBKtb_TiszaEast_SzakN) + (ALBKe_SzakS)	10205860	0.00145	0.05	0.0005	0.50020+-0.00520	535205733	2.66534	96.70	0.0330	0.00030+-0.00017	24205019	0.08951	3.25	0.03249	0.00535+-0.00076

		Among groups					Within populations					Among populations within groups				
	Model	sum of squares	variance components	% of variation	Fct	p	sum of squares	variance components	% of variation	Fst	p	sum of squares	variance components	% of variation	Fsc	p
90	(KÖR_ALBKe_ALBKtb) + (TiszaEast_SzakN_ALBKearly) + (SzakS_TiszaRiver)	11206851	0.01184	0.43	0.0042 9	0.40238+-0.00461	535206733	2.66534	96.62	0.0338 3	0.00030+-0.00017	23206028	0.08150	2.95	0.02967	0.00545+-0.00074
91	(KÖR_ALBKe_SzakS) + (TiszaEast_SzakN_ALBKtb) + (ALBKearly_TiszaRiver)	8206609	-0.02256	-0.82	-0.0082 0	0.73267+-0.00471	535206733	2.66534	96.9	0.0310 3	0.00040+-0.00019	26206270	0.10790	3.92	0.03891	0.00178+-0.00043
92	(KÖR_ALBKe_TiszaRiver) + (TiszaEast_SzakN_ALBKtb) + (ALBKearly_SzakS)	11206123	0.00651	0.24	0.0023 6	0.00236	535206733	2.66534	96.66	0.0334 1	0.00050+-0.00022	23206756	0.08562	3.11	0.03112	0.00396+-0.00060
	variations of model no. 36															
93	(SzakS_ALBKe_ALBKearly_SzakN) + (ALBKtb_TiszaEast) + (KÖR_TiszaRiver)	12206180	0.02124	0.77	0.0076 9	0.30515+-0.00411	535206733	2.66534	96.5	0.0349 9	0.00050+-0.00022	22206699	0.07541	2.73	0.02751	0.00762+-0.00085
94	(TiszaRiver_ALBKe_ALBKearly_SzakN) + (ALBKtb_TiszaEast) + (KÖR_SzakS)	12206473	0.01729	0.63	0.0062 7	0.34119+-0.00426	535206733	2.66534	96.57	0.0343 2	0.00020+-0.00014	22206406	0.07743	2.81	0.02823	0.00545+-0.00071
95	(KÖR_ALBKtb_ALBKearly_SzakN) + (ALBKe_TiszaEast) + (SzakS_TiszaRiver)	13206380	0.03333	1.21	0.0120 5	0.23099+-0.00420	535206733	2.66534	96.39	0.0361 4	0.00030+-0.00017	21206499	0.06661	2.41	0.02438	0.01366+-0.00106
96	(KÖR_ALBKe_TiszaEast_SzakN) + (ALBKearly_ALBKtb) + (SzakS_TiszaRiver)	14206449	0.04006	1.45	0.0144 9	0.16703+-0.00384	535206733	2.66534	96.39	0.0360 8	0.00050+-0.00022	20206430	0.05970	2.16	0.02191	0.01426+-0.00126
97	(KÖR_ALBKe_ALBKtb_SzakN) + (ALBKearly_TiszaEast) + (SzakS_TiszaRiver)	12206777	0.02217	0.80	0.0080 3	0.29861+-0.00448	535206733	2.66534	96.52	0.0347 9	0.00050+-0.00022	22206102	0.07389	2.68	0.02698	0.00941+-0.00100
98	(KÖR_ALBKe_ALBKearly_TiszaEast)) + (SzakN_ALBKtb + (SzakS_TiszaRiver)	17206281	0.07129	2.57	0.0257 1	0.04822+-0.00233	535206733	2.66534	96.10	0.0389 8	0.00050+-0.00022	17206598	0.03682	1.33	0.01363	0.07515+-0.00257
99	(KÖR_ALBKe_ALBKearly_ALBKtb) + (SzakN_TiszaEast) + (SzakS_TiszaRiver)	14206844	0.05248	1.89	0.0189 3	0.08178+-0.00273	535206733	2.66534	96.16	0.0384 0	0.00059+-0.00024	20206035	0.05395	1.95	0.01984	0.02713+-0.00182
100	(KÖR_ALBKe_ALBKearly_SzakS) + (ALBKtb_TiszaEast) + (SzakN_TiszaRiver)	12206691	0.02781	1.01	0.0100 6	0.24446+-0.00373	535206733	2.66534	96.43	0.0357 1	0.00040+-0.00019	22206188	0.07090	2.57	0.02591	0.00802+-0.00094
101	(KÖR_ALBKe_ALBKearly_TiszaRiver) + (ALBKtb_TiszaEast) + (SzakN_SzakS)	17206142	0.06977	2.52	0.0251 6	0.05515+-0.00198	535206733	2.66534	96.13	0.0387 5	0.00059+-0.00024	17206737	0.03766	1.36	0.01393	0.06297+-0.00235
102	(KÖR_ALBKe_ALBKearly_SzakN) + (SzakS_ALBKtb) + (TiszaEast_TiszaRiver)	13206898	0.03701	1.34	0.0133 9	0.21267+-0.00394	535206733	2.66534	96.39	0.0360 7	0.00040+-0.00019	20206981	0.06272	2.27	0.02299	0.00911+-0.00083
103	(KÖR_ALBKe_ALBKearly_SzakN) + (TiszaRiver_ALBKtb) + (TiszaEast_SzakS)	14206431	0.03856	1.39	0.0139 5	0.18891+-0.00402	535206733	2.66534	96.4	0.0359 7	0.00030+-0.00017	20206448	0.06089	2.2	0.02233	0.01475+-0.00116
	4 groups (based on results of 3-group models)															

		Among groups					Within populations					Among populations within groups				
	Model	sum of squares	variance components	% of variation	Fct	p	sum of squares	variance components	% of variation	Fst	p	sum of squares	variance components	% of variation	Fsc	p
1	(ALBKe_ALBKearly) + (TiszaEast_ALBKtb) + (SzakS_TiszaRiver) + (KÖR_SzakN)	24207866	0.11384	4.11	0.04106	0.00960+-0.00103	535207733	2.66534	96.13	0.03867	0.00040+-0.00019	10207013	-0.00663	-0.24	-0.00250	0.50950+-0.00506
2	(TiszaEast_ALBKearly) + (ALBKe_ALBKtb) + (SzakS_TiszaRiver) + (KÖR_SzakN)	18207445	0.03619	1.31	0.01311	0.26366+-0.00410	535207733	2.66534	96.53	0.03469	0.00059+-0.00024	16207434	0.05960	2.16	0.02187	0.03356+-0.00178
3	(ALBKtb_ALBKearly) + (ALBKe_TiszaEast) + (SzakS_TiszaRiver) + (KÖR_SzakN)	19207331	0.04996	1.81	0.01808	0.15109+-0.00336	535207733	2.66534	96.44	0.03561	0.00030+-0.00017	15207548	0.04846	1.75	0.01786	0.04644+-0.00198
4	(SzakS_ALBKearly) + (ALBKtb_TiszaEast) + (ALBKe_TiszaRiver) + (KÖR_SzakN)	14207219	-0.00912	-0.33	-0.00331	0.62832+-0.00473	535207733	2.66534	96.76	0.03238	0.00030+-0.00017	20207660	0.09831	3.57	0.03557	0.00356+-0.00059
5	(TiszaRiver_ALBKearly) + (ALBKtb_TiszaEast) + (ALBKe_SzakS) + (KÖR_SzakN)	13207710	-0.01983	-0.72	-0.00720	0.70366+-0.00434	535207733	2.66534	96.81	0.03187	0.00030+-0.00017	21207169	0.10756	3.91	0.03879	0.00089+-0.00028
6	(KÖR_ALBKearly) + (ALBKtb_TiszaEast) + (TiszaRiver_SzakS) + (ALBKe_SzakN)	14207950	-0.00132	-0.05	-0.00048	0.51386+-0.00506	535207733	2.66534	96.72	0.03281	0.00069+-0.00025	19207929	0.09174	3.33	0.03327	0.00515+-0.00067
7	(SzakN_ALBKearly) + (ALBKtb_TiszaEast) + (TiszaRiver_SzakS) + (ALBKe_KÖR)	21207830	0.07626	2.76	0.02756	0.04762+-0.00230	535207733	2.66534	96.34	0.03662	0.04762+-0.00230	13207049	0.02506	0.91	0.00931	0.14208+-0.00390
8	(ALBKe_ALBKearly) + (SzakS_ALBKtb) + (TiszaEast_TiszaRiver) + (KÖR_SzakN)	19207038	0.04765	1.72	0.01724	0.16515+-0.00432	535207733	2.66534	96.44	0.03557	0.00050+-0.00022	15207840	0.05065	1.83	0.01865	0.03772+-0.00189
9	(ALBKe_ALBKearly) + (TiszaRiver_ALBKtb) + (TiszaEast_SzakS) + (KÖR_SzakN)	19207571	0.05000	1.81	0.01810	0.14376+-0.00347	535207733	2.66534	96.46	0.03540	0.00020+-0.00014	15207308	0.04781	1.73	0.01762	0.05465+-0.00216
10	(ALBKe_ALBKearly) + (SzakS_ALBKtb) + (TiszaEast_TiszaRiver) + (KÖR_SzakN)	19207038	0.04765	1.72	0.01724	0.17257+-0.00361	535207733	2.66534	96.44	0.03557	0.00040+-0.00019	15207840	0.05065	1.83	0.01865	0.03703+-0.00175
11	(ALBKe_ALBKearly) + (KÖR_ALBKtb) + (SzakS_TiszaRiver) + (TiszaEast_SzakN)	19207900	0.05046	1.83	0.01826	0.13436+-0.00366	535207733	2.66534	96.48	0.03520	0.00030+-0.00017	14207979	0.04679	1.69	0.01725	0.06347+-0.00245
12	(ALBKe_ALBKearly) + (SzakN_ALBKtb) + (SzakS_TiszaRiver) + (TiszaEast_KÖR)	20207978	0.06346	2.30	0.02296	0.09495+-0.00274	535207733	2.66534	96.42	0.03575	0.00040+-0.00019	13207901	0.03536	1.28	0.01309	0.11010+-0.00316
13	(ALBKe_ALBKearly) + (TiszaEast_ALBKtb) + (KÖR_TiszaRiver) + (SzakS_SzakN)	24207149	0.10441	3.77	0.03769	0.02040+-0.00141	535207733	2.66534	96.21	0.03795	0.00020+-0.00014	10207730	0.00072	0.03	0.00027	0.40386+-0.00557
	variations of model no. 13															
14	(TiszaEast_ALBKearly) + (ALBKe_ALBKtb) + (KÖR_TiszaRiver) + (SzakS_SzakN)	17207729	0.02503	0.91	0.00907	0.36604+-0.00466	535207733	2.66534	96.59	0.03408	0.00040+-0.00019	17207150	0.06900	2.5	0.02523	0.02495+-0.00155
15	(TiszaEast_ALBKe) + (ALBKearly_ALBKtb) + (KÖR_TiszaRiver) + (SzakS_SzakN)	18207615	0.03934	1.42	0.01424	0.23050+-0.00376	535207733	2.66534	96.51	0.03494	0.00050+-0.00022	16207264	0.05715	2.07	0.02099	0.03604+-0.00187
16	(ALBKe_ALBKearly) + (KÖR_ALBKtb) + (TiszaEast_TiszaRiver) + (SzakS_SzakN)	19207115	0.03953	1.43	0.01432	0.22218+-0.00375	535207733	2.66534	96.54	0.03465	0.00030+-0.00017	15207764	0.05613	2.03	0.02063	0.03743+-0.00175

		Among groups					Within populations					Among populations within groups				
	Model	sum of squares	variance components	% of variation	Fct	p	sum of squares	variance components	% of variation	Fst	p	sum of squares	variance components	% of variation	Fsc	p
17	(ALBKe_ALBKearly) + (TiszaRiver_ALBKtb) + (TiszaEast_KÖR) + (SzakS_SzakN)	17208889	0.02534	0.92	0.0091 8	0.35149+-0.00446	535208733	2.66534	96.59	0.0340 5	0.00030+-0.00017	16208990	0.06862	2.49	0.02510	0.01782+-0.00117
18	(KÖR_ALBKearly) + (TiszaEast_ALBKtb) + (ALBKe_TiszaRiver) + (SzakS_SzakN)	20208658	0.06095	2.20	0.0220 5	0.09733+-0.00272	535208733	2.66534	96.42	0.0357 9	0.00050+-0.00022	14208221	0.03797	1.37	0.01405	0.09317+-0.00274
19	(TiszaRiver_ALBKearly) + (TiszaEast_ALBKtb) + (ALBKe_KÖR) + (SzakS_SzakN)	19208119	0.04283	1.55	0.0155 1	0.21059+-0.00355	535208733	2.66534	96.5	0.0349 7	0.00040+-0.00019	15208760	0.05374	1.95	0.01976	0.03861+-0.00170
21	(ALBKe_ALBKearly) + (SzakS_ALBKtb) + (KÖR_TiszaRiver) + (TiszaEast_SzakN)	19208107	0.04744	1.72	0.0171 7	0.17673+-0.00345	535208733	2.66534	96.45	0.0355 1	0.00040+-0.00019	15208772	0.05069	1.83	0.01866	0.04000+-0.00185
22	(ALBKe_ALBKearly) + (SzakS_TiszaEast) + (KÖR_TiszaRiver) + (ALBKtb_SzakN)	21208944	0.07672	2.77	0.0277 3	0.03663+-0.00189	535208733	2.66534	96.35	0.0365 0	0.00020+-0.00014	12208935	0.02425	0.88	0.00902	0.17822+-0.00394
23	(SzakS_ALBKearly) + (TiszaEast_ALBKtb) + (KÖR_TiszaRiver) + (ALBKe_SzakN)	14208950	-0.00132	-0.05	-0.0004 8	0.51030+-0.00490	535208733	2.66534	96.72	0.0328 1	0.00010+-0.00010	19208929	0.09174	3.33	0.03327	0.00465+-0.00064
24	(SzakN_ALBKearly) + (TiszaEast_ALBKtb) + (KÖR_TiszaRiver) + (ALBKe_SzakS)	15208705	0.00150	0.05	0.0005 4	0.50604+-0.00471	535208733	2.66534	96.70	0.0329 6	0.00050+-0.00022	19208174	0.08934	3.24	0.03243	0.00614+-0.00078
26	(ALBKe_ALBKearly) + (TiszaEast_ALBKtb) + (SzakN_TiszaRiver) + (KÖR_SzakS)	21208563	0.07316	2.64	0.0264 5	0.05545+-0.00211	535208733	2.66534	96.35	0.0364 8	0.00020+-0.00014	12208935	0.02425	0.88	0.00902	0.17822+-0.00394
	variations of model no. 22															
27	(SzakS_ALBKearly) + (ALBKe_TiszaEast) + (KÖR_TiszaRiver) + (ALBKtb_SzakN)	13208916	-0.01928	-0.70	-0.0070 0	0.69248+-0.00486	535208733	2.66534	96.81	0.0319 2	0.00059+-0.00024	20208963	0.10717	3.89	0.03865	0.00406+-0.00065
28	(TiszaEast_ALBKearly) + (ALBKe_SzakS) + (KÖR_TiszaRiver) + (ALBKtb_SzakN)	14208992	-0.00937	-0.34	-0.0034 0	0.63515+-0.00448	535208733	2.66534	96.76	0.0324 4	0.00020+-0.00014	19208887	0.09874	3.58	0.03572	0.00545+-0.00075
29	(ALBKe_ALBKearly) + (TiszaRiver_TiszaEast) + (SzakS_KÖR) + (ALBKtb_SzakN)	19208098	0.03914	1.42	0.0141 8	0.23693+-0.00404	535208733	2.66534	96.54	0.0346 2	0.00030+-0.00017	15208781	0.05644	2.04	0.02074	0.04515+-0.00207
30	(ALBKe_ALBKearly) + (SzakS_TiszaEast) + (SzakN_TiszaRiver) + (KÖR_ALBKtb)	19208375	0.04577	1.66	0.0165 7	0.19535+-0.00347	535208733	2.66534	96.49	0.0350 8	0.00040+-0.00019	15208504	0.05114	1.85	0.01883	0.04564+-0.00212
31	(KÖR_ALBKearly) + (SzakS_TiszaEast) + (ALBKe_TiszaRiver) + (ALBKtb_SzakN)	18208452	0.03271	1.18	0.0118 5	0.28139+-0.00475	535208733	2.66534	96.56	0.0344 0	0.00030+-0.00017	16208426	0.06224	2.25	0.02282	0.02861+-0.00193
32	(TiszaRiver_ALBKearly) + (SzakS_TiszaEast) + (ALBKe_KÖR) + (ALBKtb_SzakN)	16208913	0.01471	0.53	0.0053 3	0.40554+-0.00497	535208733	2.66534	96.64	0.0335 8	0.00010+-0.00010	17208966	0.07790	2.82	0.07790	0.01040+-0.00102
33	(ALBKtb_ALBKearly) + (SzakS_TiszaEast) + (KÖR_TiszaRiver) + (ALBKe_SzakN)	17208444	0.02865	1.04	0.0103 8	0.32832+-0.00427	535208733	2.66534	96.55	0.0344 8	0.00040+-0.00019	17208435	0.06653	2.41	0.02435	0.01554+-0.00119

		Among groups					Within populations					Among populations within groups				
	Model	sum of squares	variance components	% of variation	Fct	p	sum of squares	variance components	% of variation	Fst	p	sum of squares	variance components	% of variation	Fsc	p
34	(SzakN_ALBKearly) + (SzakS_TiszaEast) + (KÖR_TiszaRiver) + (ALBKe_ALBKtb)	16209236	0.00744	0.27	0.00270	0.44832+-0.00492	535209733	2.66534	96.68	0.03324	0.00030+-0.00017	18209643	0.08421	3.05	0.03063	0.00891+-0.00090
	variations of model no. 7															
35	(ALBKtb_ALBKearly) + (SzakN_TiszaEast) + (TiszaRiver_SzakS) + (ALBKe_KÖR)	20209693	0.06514	2.35	0.02355	0.07327+-0.00230	535209733	2.66534	96.36	0.03637	0.00050+-0.00022	14209186	0.03318	1.28	0.01313	0.08228+-0.00288
36	(TiszaEast_ALBKearly) + (SzakN_ALBKtb) + (TiszaRiver_SzakS) + (ALBKe_KÖR)	21209117	0.06631	2.40	0.02398	0.06515+-0.00219	535209733	2.66534	96.40	0.03598	0.00040+-0.00019	13209762	0.03318	1.20	0.01230	0.11376+-0.00325
37	(SzakS_ALBKearly) + (ALBKtb_TiszaEast) + (SzakN_TiszaRiver) + (ALBKe_KÖR)	17209675	0.03064	1.11	0.01110	0.29356+-0.00483	535209733	2.66534	96.54	0.03456	0.00040+-0.00019	17209204	0.06477	2.35	0.02372	0.01802+-0.00137
38	(KÖR_ALBKearly) + (ALBKtb_TiszaEast) + (TiszaRiver_SzakS) + (ALBKe_SzakN)	22209105	0.07991	2.89	0.02888	0.02624+-0.00151	535209733	2.66534	96.32	0.03684	0.00079+-0.00027	12209774	0.02203	0.80	0.00820	0.15535+-0.00397
39	(SzakN_ALBKearly) + (TiszaRiver_TiszaEast) + (ALBKtb_SzakS) + (ALBKe_KÖR)	16209003	0.00990	0.36	0.00359	0.44287+-0.00500	535209733	2.66534	96.66	0.03342	0.00059+-0.00024	18209876	0.08227	2.98	0.02994	0.00059+-0.00024
40	(SzakN_ALBKearly) + (SzakS_TiszaEast) + (TiszaRiver_ALBKtb) + (ALBKe_KÖR)	16209536	0.01111	0.4	0.00403	0.42733+-0.00510	535209733	2.66534	96.66	0.03342	0.00010+-0.00010	18209343	0.08105	2.94	0.02951	0.00634+-0.00071
41	(SzakN_ALBKearly) + (ALBKe_TiszaEast) + (TiszaRiver_SzakS) + (ALBKtb_KÖR)	15209502	-0.00553	-0.20	-0.00201	0.55178+-0.00475	535209733	2.66534	96.74	0.03263	0.00030+-0.00017	19209377	0.09544	3.46	0.03457	0.00515+-0.00085
42	(SzakN_ALBKearly) + (KÖR_TiszaEast) + (TiszaRiver_SzakS) + (ALBKe_ALBKtb)	15209270	-0.00687	-0.25	-0.00250	0.59158+-0.00455	535209733	2.66534	96.74	0.03256	0.00109+-0.00031	19209609	0.09659	3.51	0.03497	0.00386+-0.00058
43	(SzakN_ALBKearly) + (ALBKtb_TiszaEast) + (KÖR_SzakS) + (ALBKe_TiszaRiver)	15209072	-0.00786	-0.29	-0.00285	0.61030+-0.00423	535209733	2.66534	96.75	0.03251	0.00040+-0.00019	19209807	0.09741	3.54	0.03526	0.00525+-0.00072

G: p-values of the genetic distances (FST-values)

Alföld

	HGC	**Körös**	**ALBK early**	**ALBK later**	Szakálhát	*North*	*South*	**Tiszadob/Bükk**	**Esztár**	**Tisza Total**	*Tisza East*	*Tisza River*
Körös	0.00000+-0.0000	*										
ALBK early	0.00000+-0.0000	0.19275+-0.0037	*									
ALBK later	0.00000+-0.0000	0.03208+-0.0017	0.12078+-0.0030	*								
Szakálhát	0.00000+-0.0000	0.01792+-0.0013	0.00158+-0.0004	*	*							
North	0.00000+-0.0000	0.17365+-0.0040	0.06395+-0.0022	*	*	*						
South	0.00000+-0.0000	0.01515+-0.0012	0.00238+-0.0005	*	*	0.37590+-0.0051	*					
Tiszadob/Bükk	0.00000+-0.0000	0.01396+-0.0011	0.08979+-0.0032	*	0.01772+-0.0012	0.33729+-0.0048	0.02030+-0.0012	*				
Esztár	0.00000+-0.0000	0.12415+-0.0035	0.78527+-0.0038	*	0.00426+-0.0006	0.03475+-0.0020	0.00505+-0.0007	0.03851+-0.0020	*			
Tisza Total	0.00000+-0.0000	0.03297+-0.0018	0.01396+-0.0011	0.43322+-0.0049	0.31165+-0.0050	0.45530+-0.0050	0.25582+-0.0042	0.12494+-0.0032	0.02871+-0.0016	*		
Tisza East	0.00000+-0.0000	0.01297+-0.0012	0.09088+-0.0028	0.61895+-0.0051	0.12326+-0.0034	0.23532+-0.0042	0.13118+-0.0035	0.60598+-0.0053	0.04089+-0.0021	*	*	
Tisza River	0.00000+-0.0000	0.14276+-0.0037	0.01198+-0.0011	0.16295+-0.0030	0.50599+-0.0050	0.51629+-0.0047	0.42590+-0.0044	0.03891+-0.0021	0.02851+-0.0017	*	0.15751+-0.0037	*

Carpathian Basin

	Starčevo	**TLBK**	**Vinča**	**Sopot**	**Lengyel**
Körös	0.54618+-0.0046	0.05544+-0.0024	0.22265+-0.0041	0.04415+-0.0019	0.15909+-0.0037
ALBK early	0.56113+-0.0050	0.09653+-0.0028	0.65696+-0.0047	0.44807+-0.0042	0.82962+-0.0037
ALBK later	0.28423+-0.0052	0.15890+-0.0039	0.08663+-0.0028	0.65627+-0.0053	0.04980+-0.0022
Szakálhát					

North	0.46025+-0.0048	0.49332+-0.0046	0.15107+-0.0035	0.36224+-0.0051	0.16523+-0.0036
South	0.03069+-0.0016	0.10375+-0.0029	0.02267+-0.0017	0.08465+-0.0027	0.00287+-0.0006
Tiszadob/Bükk	0.15187+-0.0034	0.08306+-0.0026	0.06425+-0.0024	0.30660+-0.0044	0.04643+-0.0022
Esztár	0.24443+-0.0041	0.02653+-0.0015	0.28047+-0.0046	0.13830+-0.0037	0.23453+-0.0039
Tisza	0.17038+-0.0039	0.08494+-0.0027	0.04802+-0.0021	0.14375+-0.0036	0.02732+-0.0016
Tisza East	0.22711+-0.0041	0.24344+-0.0049	0.20543+-0.0038	0.55212+-0.0053	0.18572+-0.0035
Tisza River	0.19533+-0.0041	0.06821+-0.0024	0.05316+-0.0020	0.04138+-0.0017	0.02416+-0.0016

Europe

Additional F_{ST} values

(The Late Neolithic Transdanubian data and the Vinca data were not included, because the data were unpublished by the time of the thesis)

	LBK	RSC	NUK	CPE	CARcat	NSE	HGS	HGC	HGE
Körös	0.02087	0.07018	0.19474	0.15083	-0.03919	0.13913	0.16385	0.32351	0.13733
ALBK early	0.00623	-0.00583	0.09926	0.03102	0.0011	0.01306	0.0607	0.21272	0.07364
ALBK later	0.00933	0.0053	0.09632	0.02562	0.03242	0.03036	0.07113	0.18668	0.08949
Tisza	0.01645	0.04459	0.14402	0.07913	0.04836	0.07628	0.12574	0.26673	0.1336
Starčevo	0.00103	0.00691	0.11516	0.04761	-0.00792	0.05187	0.08905	0.23631	0.09097

	LBK	RSC	NUK	CPE	CARcat	NSE	HGS	HGC	HGE
TLBK	-0.00553	0.01119	0.09967	0.04542	0.05261	0.06428	0.11329	0.23320	0.12159
LBK	*	0.01561	0.10862	0.04574	0.02050	0.04009	0.10662	0.22465	0.11771
RSC		*	0.05148	-0.00215	0.04320	0.03773	0.05801	0.23362	0.04686
NUK			*	0.12811	0.15201	0.18911	0.10235	0.21577	-0.00177
CPE				*	0.05436	0.09501	0.02159	0.23479	0.02587
CARcat					*	0.06073	0.07719	0.27662	0.07361
NSE						*	0.10681	0.29372	0.12703
HGS							*	0.10505	-0.00552
HGC								*	0.12589
HGE									*

	LBK	RSC	NUK	CPE	CARcat	NSE	HGS	HGC	HGE
Körös	0.13702+-0.0033	0.03980+-0.0020	0.00624+-0.0009	0.01693+-0.0013	0.75676+-0.0036	0.00129+-0.0003	0.00000+-0.0000	0.00000+-0.0000	0.00149+-0.0004
ALBK early	0.22057+-0.0044	0.54717+-0.0053	0.02891+-0.0017	0.14642+-0.0034	0.37323+-0.0049	0.17959+-0.0038	0.00673+-0.0008	0.00000+-0.0000	0.00297+-0.0006
ALBK later	0.03683+-0.0019	0.28898+-0.0049	0.02980+-0.0015	0.14880+-0.0037	0.07752+-0.0026	0.02346+-0.0015	0.00257+-0.0005	0.00000+-0.0000	0.00149+-0.0004
Tisza	0.05653+-0.0024	0.03257+-0.0015	0.01129+-0.0010	0.02930+-0.0016	0.05920+-0.0022	0.00228+-0.0005	0.00000+-0.0000	0.00000+-0.0000	0.00000+-0.0000
Starčevo	0.35501+-0.0044	0.28918+-0.0045	0.02148+-0.0015	0.08722+-0.0028	0.51698+-0.0053	0.01168+-0.0012	0.00069+-0.0003	0.00000+-0.0000	0.00208+-0.0005
TLBK	0.64132+-0.0048	0.23691+-0.0044	0.04851+-0.0018	0.09732+-0.0028	0.06316+-0.0018	0.00822+-0.0009	0.00089+-0.0003	0.00000+-0.0000	0.00020+-0.0001

	LBK	RSC	NUK	CPE	CARcat	NSE	HGS	HGC	HGE
LBK	*	0.17147+-0.0037	0.03277+-0.0017	0.09207+-0.0024	0.17127+-0.0036	0.02336+-0.0014	0.00119+-0.0003	0.00000+-0.0000	0.00119+-0.0004
RSC		*	0.13335+-0.0037	0.46451+-0.0048	0.11435+-0.0031	0.04287+-0.0021	0.01218+-0.0012	0.00000+-0.0000	0.05158+-0.0021
NUK			*	0.05594+-0.0026	0.01624+-0.0013	0.00238+-0.0006	0.03693+-0.0016	0.00327+-0.0005	0.44124+-0.0055
CPE				*	0.15642+-0.0034	0.01931+-0.0013	0.24166+-0.0043	0.00109+-0.0004	0.25295+-0.0046
CARcat					*	0.05297+-0.0024	0.02663+-0.0015	0.00000+-0.0000	0.03980+-0.0017
NSE						*	0.00030+-0.0002	0.00000+-0.0000	0.00020+-0.0001
HGS							*	0.00624+-0.0008	0.48837+-0.0055
HGC								*	0.00495+-0.0007
HGE									*

Declaration of previous (partial) publication

Part of the data from this dissertation was presented as a poster at the Conference "Early Farmers - The View from Archaeology and Science" held at Cardiff University, UK, 14.-16.05.2012 and subequently published as:
Szécsényi-Nagy A., Keerl V. *et al.* „Ancient DNA Evidence for a Homogeneous Maternal Gene Pool in Sixth Millennium cal BC Hungary and the Central European LBK" in the conference volume *Early Farmers- The View from Archaeology and Science* (eds. A. Whittle, P. Bickle), Proceedings of the British Academy 198, 71-93, Oxford University Press/British Academy, London, UK (2014)

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Berufserfahrung

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Ausbildung

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