УДК 902

НЕОЛИТИЗАЦИЯ ЕВРАЗИИ: АРХЕОЛОГИЧЕСКИЕ, АРХЕОГЕНЕТИЧЕСКИЕ И БИОМОЛЕКУЛЯРНЫЕ ПЕРСПЕКТИВЫ

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Аннотация: Переход мезолита к неолиту представлял собой более сложный и многообразный процесс по сравнению с раннее выдвинутой гипотезой. Введение гончарной технологии и первоначальное распространение керамики в Евразии демонстрируют появление различных методов ее изготовления и способов нанесения узоров в разных культурных и хронологических контекстах. Орнамент не может быть объяснен с помощью постепенного распространения людей и посуды в юго-восточном и северо-западном направлении через Европу в связи с миграционной моделью расселения народов. Данные свидетельствуют о появлении гончарной технологи и ее многократном изменении в различных палеолитических и неолитических контекстах, а также о сообществах охотников и собирателей, которые изготовляли керамические сосуды на территории Евразии. Древние генетические данные дают основание предположить, что процессы заселения Европы в доисторический период были значительно более сложными и многообразными, чем это предполагалось первоначально. Анализы палимпсеста отцовской Y-хромосомной и материнской митохондриальной родословных современного населения, а также древнего ДНК и древних демографических преобразований указывают на сложную картину разнообразных траекторий заселения на территории Европы. Археологические и биохимические данные показывают, что молочное хозяйство и потребление кисломолочных продуктов в Европе в эпоху неолита появилось до генетической адаптации к молочной культуре.

Ключевые слова: Евразия; неолитизация; расселение народов; керамика; человеческая ДНК и древняя ДНК; молочное хозяйство; переносимость лактазы.

Introduction

The appearance and diffusion of Neolithic cultures in Europe have long been studied in conjunction with migrations of prehistoric populations and pottery distribution, and became highly ideologised by the Lex Kossinae that equates ‘cultural province’ with ‘areas of particular people or tribes’ [1, p.3;]. Gordon Childe [2] agreed that Neolithic pottery was a universal indicator of both ‘cultural identities’ and ‘distributions of ethnic groups’, but he strongly disagreed that ceramic technology invention and its primary distribution can be found within Europe. It was “*the earliest conscious utilization by man of a chemical change... in the quality of the material*” that happened in the Near East in the context of Neolithic revolution, he suggested [3, p.76–77]. He stated that pottery arrived in Europe with Neolithic ‘immigrants from South-Western Asia’ who ‘were not full-time specialists, but had complete mastery over their material’. The ‘experienced farmers’ in the Peloponnese and the Balkans thus produced ‘extremely fine burnished and painted ware’, whereas the ‘Danubian I hoe-cultivators’ in the Carpathian Basin and Central Europe produced ‘unpainted and coarse and chaff-tempered vessels’. Beyond the agricultural frontier and pottery distribution on the North European plain, he recognised ‘scattered bands of food-gatherers’ [4p. 21, 25–26].

The linking of farming and pottery production gave rise to ‘centre and periphery’ perception of origin and dispersal of farming communities where pottery was used as proxy indicator of boundary between civilised and barbarian populations, and as a marker of gradual and unidirectional, southeast-north west oriented migration of both people and integrated ‘package’ of skills, technologies and languages across the Europe. However, the ‘package’ was never conceptualised although it relates to all aspects of ‘the Neolithic way of life’. A number of attempts have been made to ‘repack’ it, and it was suggested finally that such a uniform, stable, and complex entity of economic practises and material culture never existed [5, p.61-83; 6; 7 p.1-13; 8, p. 139-178; 9,p.291-305; 10, p. 35–58; 11, p. 237-252].

The ‘package’ still maintains a central position in determining movements of Levantine farmers, starting throughout Anatolia, sweeping over the Southeastern Europe, covering enormous areas, and leaving no gaps behind. However, Northeast and East Europe were marginalised for all the time, having no point of entry and remaining a blank through the (Early) Neolithic period [12, p. 177–189; 13, p. 150–160; 14, p. 371–384.; 15] (Fig. 1).

The application of physical anthropology and racial mapping in archaeology led Carleton Coon [16, p. 82–86, 104–107, Map 2]to relate Neolithic immigrants to ‘Danubian’ agriculturalists’, a ‘new branch of Mediterranean’ population in Europe that had originated in the Near East and was associated with the Natufian cultural context. He suggested that they migrated across Anatolia and/or the Aegean into Europe, and ‘up the Danube Valley’ into the Carpathian basin, Central Europe and farther to the west, to the Paris basin, where they met with the second group of ‘Mediterranean’ population, ‘which entered Europe from North Africa across the Straits of Gibraltar’. The first group brought ‘Danubian painted pottery’ that shows ‘definite Asiatic similarities’ into Europe. The second was associated with the dispersal of ‘incised pottery with banded decoration’. These streams have been recently recognised archaeogenetically [17, p. 2161–2167; 18, p. 24–37.], and re-actualised archaeologically as ‘Danubian’ and ‘Occidental’ groups [19, p. 59–88].

The geneticists shifted focus from phenotypes to genotypes, from cranial characteristics to classic genetic markers, from races to populations. The geographical correlation of the Early Neolithic painted pottery and ceramic female figurine distribution in Southeastern Europe and Anatolia, and the distribution of genetically identified Y-chromosome haplogroups in the modern paternal lineages of European and Near Eastern populations become recognized to be ‘the best material culture and genetic markers’ of ‘demic diffusion’ that radically reshaped the European population structure at the beginning of Neolithic [20, p. 707]. Ceramic female figurines were even suggested to mark the new ‘expansionist’ ideology that enabled the transition to the ‘agricultural way of life’ in the Near East first. Europe, however, did not become neolithicised until figurines reached the Balkans [21, p. 22–29, 204–205, 207–208].

The ‘demic diffusion migratory model

The rate of spread was calculated from a radiocarbon dates since Clark [22, p. 45-48; 23] introduce the first series of conventional 14C dates into archaeology. The dates that appeared to be arranged in a southeast-northwest cline he described as “*the gradual spread of farming culture and the Neolithic way of life from the Near East over Europe*”. Peter Breunig [24] allocated them to temporal zones of 500-year intervals, running from the Near East to Atlantic Europe and through the 7th millennium in Southeast Europe and the 6th millennium BC in Western Europe. The southeast-northwest temporal gradient of the ‘spread of the Neolithic way of life’ from the Near East across Europe was thus broadly accepted [25]. A less gradual movement was hypothesised in a demographic model suggesting migrations from one suitable environment to another. Van Andel and Runnels [26] suggested that Anatolian farmers first settled in small numbers on the Larissa Plain in Thessaly, as they thought this was the only region in the southern Balkans that could provide a secure and large enough harvest for significant population growth 'at the wave front' that led to the next migratory move (*i.e.*, 'leap-frog') towards the Danube and Carpathian Basin.

The geneticists Menozzi et al. [27], Ammerman and Cavalli-Sforza [28; 29], [30], and Cavalli-Sforza et al. [31] saw the same cline of radiocarbon dates and related, supposedly, initial Neolithic settlements dispersal as the marker of 'demic diffusion' and the Neolithic 'wave of advance'. They recognised the continuous displacements of farmers at an average of 1 km per year. The rate of displacement was calculated by the ratio between the time of departure from the Levant (Jericho was used as the starting point of diffusion), time of arrival in Europe, and the geographical distance between the two. There was not very much attention devoted to the discrepancy between the rates of advance of farmers on the continental and regional levels. Along with a continental average of 1,08 km/per year for all of Europe, the most extreme regional rates of 0,70 for Southeastern and 5,59 for Central and Western Europe were suggested. The authors believed, however, that such an average constant rate of diffusion must have been driven by permanent population growth, and that the continuous waves of population expansion must have been distinct from cultural diffusion.

Introducing the biological concept of 'deme' into archaeology they shifted the focus from phenotypes to genotypes, from cranial characteristics to classic genetic markers, from races to populations.They postulated that demic diffusion and the replacement of the indigenous European population are genetically and archaeologically grounded in the resemblance of a southeast-northwest gradient or cline of the first principal component of 95 gene frequencies of 'classic', non-DNA marker dispersal by modern European populations (allele frequencies for blood groups, the tissue antigen HLA system, and some enzymes), and the gradual distribution of Neolithic farming settlement as measured by radiocarbon dates. They sugested that the highest point of the first principal component centred in the Near East (Jericho) and then diminished with distance from that spot. The very lowest point was found in the Basque provinces of Alava, Biskaia, and Gipuzkoa on the Iberian Peninsula [32], and in Lapland in Scandinavia, and in general at the furthest distance from the Near East.

In the palimpsest of seven principal components and associated genetic landscapes, the first

was linked to the Near East, which was recognised as an ancestral homeland for the current population in Europe. The gradual changes in allele frequencies summarised on spatially interpolated 'synthetic maps' of allele-frequency distributions are due to the absorption of local hunter-gatherer populations into farming communities. It was hypothesised that the transition to farming in Europe correlates with the 'first demic event' and a massive movement of population from the Near East, without substantial contact with local Mesolithic populations. This demic event was believed to have significantly reshaped European population structure, and the current European gene pool was interpreted as consisting mainly of genetic variations originating in Near Eastern Neolithic populations, with only a small contribution from Mesolithic Europeans. It was suggested that 'demic diffusion' generated a genetic continuity between the Neolithic and modern populations of Europe [30; 31]. In this scenario, hunter-gatherers disappeared everywhere a few hundred of years after the arrival of the settled farmers. The elimination of the European hunter-gatherer population was assumed, despite only a 27 % total variation in classical marker frequencies attributed to Neolithic populations across Europe. Only some clear outliners, such as Basques and Lapps, have been shown to emerge from this homogeneous Neolithic entity as Palaeolithic hunter-gather relics.

The genetic landscapes of the first principal components corresponds well with the map of frequency distribution of morphological and anthropometric characteristics and associated physical types (races) identified by Coon [16] (Fig. 2). He related it with the Mesolithic-Neolithic transition and the great invasion of Mediterraneans in Europe which was followed by the process of 'Dinaricization'. The outcome of the process of mixing of reduced European hunter-gatherers, the Alpine race, and newcomers, the Mediterraneans, he suggested, was the hybrid Dinaric race to be marked by some morphological characteristics. He described the process in a way that, when the famers entered into the territory of hunter-gathers "*... the former were much more numerous than the latter, who either retired to environmental pockets economically unfavorable to the food producers, or were absorbed into the ethnic corpus of the latter. The adjustment of the earlier population element to the new conditions and their reemergence through the Mediterranean group made a combination of the two basic racial elements in a genetic sense necessary"* [16, p.647]. However, genetics labelled Coon's approach as 'scientific racism' and as the last gasp of an outdated scientific methodology [31, p. 267).

It is noteworthy that over the same period Renfrew [33, p.169-170, fig. 7. 9], relating the arrival of a Proto-Indo-European language in Europe to the arrival of farmers, objectified demic diffusion archaeologically through the catalogue of artefacts and symbols. It has become an icon perpetuating the legitimacy of both demic diffusion and great exodus in which Levantine and Anatolian farmers carried with them all the features of their cultures but, paradoxically, not the central authority and symbolic representations that maintained this power [34].

Since the revolution in the study of the human genome, studies have focussed on nuclear genetic DNA markers, *i.e.* mitochondrial (mt) and Y-chromosomal [35, 36]. The first is present in both sexes, but inherited only through the maternal line, while the latter is present only in males, and inherited exclusively through the male line [37]. Because they are non-recombinant and highly polymorphic, they are seen as ideal for reconstructing human population history and migration patterns. Thus different human nuclear DNA polymorphic markers (polymorphisms) of modern populations have been used to study genomic diversity, to define maternal and paternal lineage clusters (haplogroups), and to trace their (pre)historic genealogical trees, and chronological and spatial trajectories [38; 39; 40; 41; 42]. Particular attention has been drawn to the power of Y-chromosome biallelic markers, as they allow the construction of intact haplotypes and thus male-mediated migration can be readily recognised. We already mentioned above, it was hypothesised that the southeast-northwest cline of frequencies for selected Y-chromosome markers and related haplogroups indicates the movement of men with Levantine genetic ancestry, and that this coincides with the distribution of Early Neolithic painted pottery and ceramic female figurine distributions in Europe [20] . Recent genetic studies suggest that the modern peopling of Europe was a complex process, and that the view of a single demic event in the Early Neolithic is too simplistic [43]. The paternal heritage of the modern population of Southeast Europe reveals that the region was both an important source and recipient of continuous gene flows. The studies of the Y-chromosomal hg J1 (M267), J2 (M172), E (M78) and I (M423) strongly suggest continuous Mesolithic, Neolithic and post-Neolithic gene flows within Southeast Europe and between Europe and the Near East in both directions. In addition, the low frequency and variance associated with I and E clades in Anatolia and the Middle East support the European Mesolithic origin of these two haplogroups. The Neolithic and post-Neolithic components in the gene pool are most clearly marked by the presence of J lineages. Its frequency in Southeast European populations ranges from 2% to 20%, although some lineages may have arrived earlier than the Neolithic, which has led to the level of Neolithic immigration being overestimated [44; 45]. However, the mitochondrial genome dataset and timescale for lineages show that possible candidates for Neolithic immigration from the Near East would include hg J2a1a and K2a. It seems, however, that the immigration was minor [46].

The end of 'demic diffusion' population migratory model

The 'demic diffusion' model was criticised because the local features of the PC 'synthetic maps' are mathematical artefacts that "*do not necessarily indicate specific localized historical migration events*" [47, p. 646]. The PC gradients can occur even in the context of cultural diffusion, when there is no population expansion, and paradoxically, a 'very large level of Paleolithic ancestry' is necessary to produce the southeast-northwest gradient axis [48, p.60]. The highest haplotype diversity in European population is found not in Southeast Europe, but on the Iberian Peninsula, thus suggesting a south-north gradient and trans-Mediterranean gene flow with northern Africa [49, p.259–260].

Recent phylogenetic analyses of ancient mitochondrial and Y-chromosomal DNA (aDNA), extracted from Mesolithic and Neolithic human remains have revealed a genetic structure that cannot be explained by a southeast-northwest oriented 'wave of advance' or 'demic diffusion' of Near Eastern farmers and hunter-gatherer population replacements. Advances in aDNA methods and next-generation sequencing allow new approaches which can directly assess the genetic structure of past populations and related migration patterns. Mitochondrial aDNA analyses thus suggest variations in population trajectories in Europe. In central Europe, Neolithic farmers differed in various genetic markers from both Mesolithic hunter-gatherers and from modern European populations [50; 51; 52; 14]. The characteristic mtDNA type N1a, with a frequency distribution of 25% among Neolithic LBK farmers in Central Europe, is in contrast with the low frequency of 0.2% in modern mtDNA samples in the same area [50]. It was not observed in hunter-gatherer samples from Western and Northern Europe. On the contrary, hg H dominates (40%) present-day Central and Western European mitochondrial DNA variability. It was less common among Early Neolithic farmers and virtually absent in Mesolithic hunter-gatherers. Phylogeographic studies suggest that it arrived in Europe from the Near East before the Last Glacial Maximum, and survived in glacial refuges in Southwest Europe before undergoing a post-glacial re-expansion. Recently published analyses of the maternal population history of modern Europeans and hg H mitochondrial genomes from ancient human remains show that Early Neolithic lineages "*do not appear to have contributed significantly*" to present-day Central Europe's hg H diversity and distribution [53 p.7]. The hg H was associated with LBK culture, but lineages were lost during a short phase of population decline after 5000 calBC. The current diversity and distribution were largely established by the strong post-LBK population growth and by "*substantial genetic contributions from subsequent pan-European cultures such as the Bell Beakers expanding out of Iberia in the Late Neolithic, ... after which there appears to have been substantial genetic continuity to the present-day in Central Europe*" [53; 5, p.577].

A rather different picture emerges from the Iberian Peninsula, where the Neolithic composition of the haplogroup population (e.g., hg H, T2, J1c, I1, U4, W1) "is not significantly different from that found in the current population from the Iberian Peninsula", but differs from the Near Eastern groups [17, p.2165]. Interestingly, there is no evidence of the mt aDNA hg N1a in either Spain or France [55]. Two Mesolithic individuals, on the contrary, carried a mitochondrial U5b haplotype which does not cluster with modern populations from Southern Europe (including Basques), as suggested recently [56; 57]. The mt aDNA sequences from contemporary huntergatherer and farmer populations in Scandinavia and the Baltic differ significantly. These populations are unlikely to be the main ancestors of either modern Scandinavians or Saami, but indicate greater similarity between hunter-gatherers and modern eastern Baltic populations [58]. It has also been suggested that Scandinavian Neolithic huntergatherers shared most alleles with modern Finnish and northern Europeans, and the lowest allele sharing was with populations from Southeast Europe. In contrast, Neolithic farmers shared the greatest fraction of alleles with modern Southeast European populations, but were differentiated from Levantine populations and showed a pattern of decreasing genetic similarity to 'populations from the northwest and northeast extremes of Europe'[59, p. 469]. The most recent arhaeogenetic study reveals an extensive 'heterogeneity in the geographical, temporal and cultural distribution of the mtDNA diversity' in Northeast Europe. While some mt aDNA sequences from hunter-gatherer sites show a genetic continuity in some maternal lineages (e.g., hg U4, U5 and H) in Northeast Europe since the Mesolithic, and also genetic affinities with extant populations in Western Siberia, the precise genetic origins of the others is more difficult to identify. They all display clear haplotypic differences with contemporary Saami populations. The major prehistoric migration in the area was thought to have been associated with 'the spread of early pottery from the East' [60, p. 10-12].

Unfortunately, we still do not know what happened to the Mesolithic hunter-gatherer and Neolithic populations in Southeast Europe, as no aDNA studies have yet been carried out in the region.

The lactase persistence paradox

Dairying and lactose tolerance marked by the –13 910*T allele (lactase gene) in modern European populations are thought to have evolved in a relatively short period within the transition to farming and 'at the front of the demic diffusion' and were introduced to Europe by lactase-persistent farmers [61;62;14; 63; 64] for discussion see M.Budja [65].

All humans have the lactase gene, but only children produce lactase in sufficient amounts to break down lactose, the main sugar in milk. Fresh milk is a toxin to adults without lactase, and often causes symptoms such as abdominal pain, bloating, flatulence and diarrhoea. Lactase is an enzyme produced in the digestive system of mammalian infants, but is dramatically reduced after the weaning period. The ability to digest lactose found in fresh milk is called lactase persistence. However, the correlation between lactase persistence and fresh milk consumption is not yet fully understood.

The lactase persistence trait is found in approx. 35% of adults in human populations in the world, but varies widely between and within continents. The frequencies of lactase-persistent individuals are generally high in Europe, Central Asia and India but almost zero in Southeast Asia [62; 63]. In Europe, lactase persistence is at its highest frequency in the North, with a decreasing cline from the central and western (62–86%) to the southern and eastern regions (15–54%) [63, p.864]. On the Indian sub-continent the frequency of lactase persistence is higher in the North-West than elsewhere; further East, the lactase persistence frequency is generally low. In Africa and the Middle East, the distribution is patchy, with some pastoral nomadic tribes having high frequencies (92%) of lactase persistence compared with neighbouring groups living in the same region [66; 67; 63].

A number of single nucleotide polymorphisms that allow lactase to be produced into adulthood have different geographic distributions within the modern populations. The derived allelic variant –13 910*T of the first nucleotide cytosine to thymine transition is associated with lactase persistence in Europe, Central Asia and India [68; 69; 61]. This allele and associated selection for lactose tolerance seems to originate twice in ancestral populations (bearing haplotypes H) in regions north of the Caucasus and West of the Urals. The first origin is estimated at 12 000 to 5000 BP, and the second more recently at 3000 to 1400 years ago. It was suggested that the frequency gradient in modern populations shows that the allele migrated to the West [68, p.619–622]. Lactase persistence in Africa is linked to three single nucleotide polymorphisms, C–14 010, G–13 915 and G–13 907, close to the lactase gene [66]. They are linked to different ethnic groups with divergent haplotype backgrounds and geographic regions. However, some questions still remain unanswered. The Hadza people in Tanzania show a high level of lactase persistence despite having nothing to do with herding.

Several scenarios relating to the 'selection hypotheses on lactase persistence' and to 'the advantage of being lactase persistent' have been discussed recently for details see M.Budja [65]. The first 'gene - culture coevolution' or 'culture historical' hypothesis proposes that lactase persistence was selected among populations that consumed milk over generations and adopted animal breeding and dairying, thereby increasing the dependence of adults on milk. In opposition, the second, the 'reverse cause hypothesis', suggests that dairying was adapted by populations that were already lactase persistent. A mutation associated with lactase persistence within small human groups could have grown in frequency through genetic drift before milk was introduced into subsistence. The third, the 'calcium assimilation hypothesis', suggests that in high-latitude environments where lower sunlight produces less vitamin D (important for the absorption of calcium in bones) lactose in fresh milk promotes the uptake of calcium present in milk. In contrast to hunter-gatherers who had a vitamin D rich diet abundant in marine food, early agriculturalist might have had problems with vitamin D deficiency, and drinking milk could have been an advantage for lactase-persistent farmers. The fourth, the 'arid climate hypothesis', suggests that in regions where water was scarce, milk could be an uncontaminated source of fluid used by pastoralists. While lactase non-persistent individuals were at risk from diarrhoea and the dehydrating effects of drinking fresh milk, the selection may have been strong in lactase-persistent individuals.

We may assume that animal domestication in Neolithic brought milk into the diet, and that domestic animals were a more stable seasonal resource, which could became an alternative to hunter-gatherers' system of the seasonal exploitation of a broad spectrum of animal resources. Milk is a good source of calories, specifically an important source of protein and fat, and must have increased the quality of the diet. The milk production of a prehistoric cow has been estimated to range between 400 and 600kg per weaning period. Even when the milk necessary for the raising of the calves is subtracted, some 150–250kg remains. This is almost equivalent to the calorie gain from the meat of a whole cow. Over the years, milking thus may have resulted in a greater energy yield than the use of cattle for meat [63, p.865–866]. Dairying was especially important for children and adolescents as it prolongs the beneficial effects of milk (proteins, fats, but also calcium supply) long after weaning [70 p. 200; 71].

Archaeogenetic studies hypothesised that a single mutation (–13 910*T) in the human genome which allow adults to consume fresh milk evolved within a group(s) of Neolithic pioneer stockbreeders among whom lactase persistence was rare, but who initially practised dairying in Southeast Europe in the middle of 8th millennium BP and later migrated towards central and northern Europe to an area inhabited by foragers. They reached the northern Adriatic at c. 7400 BP [72; 63; 61; 62; 14; 73; 65].

Pascale Gerbault et al. [72; 63; 73] and Yuval Itan et al. [61;62] intensively studied the evolutionary processes that shaped the European lactase persistence patterns in modern populations. They ran computer simulations to test different selection hypotheses on lactase persistence in relation to demic diffusion and culture diffusion models. Their results are contrasting. Computer simulations showed that high lactase persistence frequencies observed in Northern and Western Europe can be explained by selective pressure, possibly increasing with latitude in a way that is highly compatible with the calcium assimilation hypothesis combined with the effect of demographic expansion (i.e. population growth) during the Neolithic transition. The much lower frequencies in Southeast Europe can be explained by genetic drift if this mutation was carried by Near-eastern pioneers. Keeping in mind that the demic diffusion model is based on the decreasing southeast-northwest cline of frequencies for selected Y-chromosome markers, indicating the movement of Neolithic men with Levantine genetic ancestry across Europe, it is important to note that the allelic variant –13 910*T cline travels in the opposite direction. However, computer modelling suggests that the centre of distribution of an allele can be far removed from its location of origin in the direction of population expansion, moving at the front of the demic diffusion. This process is called 'allele surfing' and is thought to have occurred with the spread of farmers in Europe [72, p.3, 7–8, Fig. 1; 63; 73, p.179–198, Fig. 4] thus hypothesised that strong selection for lactase persistence runs within the 'niche construction' at the front of the demic diffusion, where local environmental condition and subsistence strategies led to population increase and concentration on milk resources.

Itan et al. [61;62] see also Burger, Thomas [14] Leonardi et al. [64] suggest that natural selection began to act on a few lactase persistent individuals of the Starčevo and Körös cultures in the northern Balkans, and then rose rapidly in the gene-culture co-evolutionary process on the wave front of a demic diffusion to Central and Western Europe in the area of Linear Pottery culture at 'around 6256–8683 years BP' [61, p.7-8; 62; 64, p.95].

However, both scenarios, the demic diffusion of lactase-persistent farmers across Europe and the evolution of lactace persistence in Central Europe in the Neolithic, seem to be unrealistic. The archaeogenetic analysis of Neolithic skeletons suggests that "*lactase persistence frequency was significantly lower in early Neolithic Europeans than it is today, and may have been zero*" [64, p.93; 14]. Indeed, the analysis revealed an absence of the –13 910*T allele in Central Europe, in the Western Mediterranean and the Baltic in Mesolithic and Neolithic populations [14; 55; 58; 74]. The only exceptions are two post-Neolithic individuals in the Basque Country on the Iberian Peninsula [75].

Biomolecular analyses of dairy fats in Neolithic pottery suggest that milking, milk consumption and processing were widely adopted in the Neolithic in Europe before the lactase persistence arose or became frequent. It should be noted that lactose is progressively reduced by milk processing. The fermented milk products cause fewer or no mal-symptoms to lactase non-persistent individuals. While the lactose content of fresh milk ranges between 4.42–5.15 g/g% in cattle, 4.66–4.82 g/g% in goats and 4.57–5.40 g/g% in sheep, it can be reduced to 50–60% by bacterial fermentation. Some processed milk products (such as cheese and butter) have very low lactose content, ranging from 0–3.7 g/g% [74,p.267; 76, p.77]. The beginning of utilisation of lactic acid bacteria can be traced alongside the domestication of sheep, goat and cattle. In milking and milk processing, the lactococci and lactobacilli were manipulated to initiate the fermentation that converts milk into yogurt, buttermilk, butter and cheese. These certainly have advantages in storing and transporting dairy products and making them available in times of low milk production on one hand, and making milk available as a nutritional source throughout the entire life of the individuals on the other.

The analyses of dairy fats in pottery suggest that milking, milk consumption and processing were widely adopted in the Neolithic in Eurasia. Biomolecular analyses of the lipids present in food which become absorbed and trapped in the pores of clay vessels indeed show evidence of dairy production in southwest Asia as early as c. 7000 calBC. The apparent intensification of dairy processing in northwest Anatolia at 6500-5500 calBC was recognised as an early centre for milk processing, with cow's milk as the main source of dairy products in this region [77; 78; 79]. Degraded ruminant fatty acid in pottery suggest that milk products and milk processing (i.e. the heating of milk) in the Starčevo-

Criş culture began at c. 5950–5500 calBC and Körös culture at c. 5800-5700 calBC [80]. In Northern Adriatic in Vlaška culture context it was found that 30% of sampled pottery contain lipids characteristic of dairy fats thus indicating that the processing of dairy products in pottery vessels was quite extensive. The triacylglycerols (TAGs) distributions, the indicative lipids of degraded animal fats, suggest that residues of dairy products probably derived from goat milk. The pottery samples are well embedded in the time span 5467-5227 calBC [65, p.106-112]. In Northern Europe in the Early Neolithic LBK complex the milk processing is dated to c. 5200 and 4900-4800 calBC [81].

We may assume, therefore, that under normal circumstances lactase persistence is not necessarily to be under very strong selection in this population and fits with the hypothesis that dairying and milk consumption emerged before genetic adaptation.

The Pre-Neolithic ceramic technology (re)inventions and pottery distributions

Hunter-gatherers used diverse ceramic technologies long before the transition to farming began. The invention of ceramic technology in Western Eurasia and Northern Africa was associated with making of female and animal figurines within a period that ranges from c. 30 000 to 16 000 calBC (Figs. 3a, b). In Eastern Eurasia the invention was associated with the vessels making that appeared at c. 19 200-18 800 calBC at the earliest.

In Central Europe, an assemblage of 16 000 ceramic objects - more than 850 figural ceramics - have been found in Gravettian and Pavlovian hunter-gatherer camps at Dolní Věstonice, Předmostí, Pavlov I and Krems-Wachtberg. The assemblages are contextualized in Gravettian, Epigravettian and Pavlovian complexes and embedded within a period that ranges from c. 30 000 to 27 000 calBC. The ceramic distributions seem to be associated with the oven-like hearths. The available statistics indicate that almost all the figurines and statuettes were deliberately fragmented, although many of the pellets and balls which comprise a large quantity of the ceramic inventory were found intact [82, p.40, 56, 69, 95-100, Tab. 5.1; 83, p.39] (Fig. 4).

In Southeastern Europe the ceramics first appeared at c. 19 000 - 16 000 calBC. Thirty six ceramic artefacts (fragments of horse or deer figurines) have been found recently in Epigravettian context at the Vela Spila cave site on Korčula Island in the Adriatic [84, p.4–5]. The most eastern distribution of the ceramic figurines was found in Southern Siberia along the Yenisei River. The anthropomorphic ceramic figurine at Maininskaia (Maina) site was associated with the Upper Palaeolithic Afontova culture at c. 18 000 - 17 000 calBC [85, p.10].

The ceramic vessels making were suggested to occurred first at c. 19 200-18 800 calBC in Xianrendong Cave [86] and at c. 16 500-15 500 calBC in Yuchanyan Cave [87; 88] among small-scale sedentary or semi-sedentary hunter-gatherer communities south of the Yangtze River in Southeastern China. On the Japanese archipelago, it appeared at c. 14 000–13 100 calBC [89, p.38; 90]. In the Russian Far East, the time span is much broader and ranges from 15 990 to 7710 calBC [91; 92; 93].

In western Siberia in Tobol-Ishim forest zone, the initial distribution of pottery was hypothesised within the time span c. 8300-6400 calBC [94, p. 77]. Further to the west, across the Urals in the steppe and forest-steppe zone of Eastern Europe the oldest pottery was contextualised in small seasonal hunter-gatherers' sites scattered over a vast area. In the Lower Don River it was identified in Rakushechny Yar site at c. 7100-6500 cal BC. In the Lower Volga River it was contextualised in Kairshak-Tenteksor and Dzgangar-Varfolomeevka groups at c. 7100-6700 calBC in the Middle Volga River, and in Elshanian group in the Middle Volga River at 7200-6000 calBC [95; 96; 97]. Some of 14C dates are based on radiocarbon measurements of freshwater mollusc shells in the ceramic paste and on carbonised food residues on pottery. The radiocarbon values may thus be considered too old, as the reservoir effect leads to significant age offsets when the fresh water molluscs are dated. We may assume as well the radiocarbon dates of food residue can be influenced significantly by the freshwater reservoir effect stemming from fish and molluscs cooked in the pots. However, the bulk $\delta^{13}C$ and $\delta^{15}N$ analysis of charred surface residue allows us to discriminate between the terrestrial, freshwater and marine food resources, and thus make possible to identify the reservoir effect and associated age offsets in the interpretation of 14C dates and temporal patterns [98; 90; 99; 100; 101].

In the Near East the initial pottery production was embedded in farming social contexts. The vessels was painted and dated at 7066 – 6840 calBC [102; 103].

The earliest pottery distributions in Southeastern Europe are identified in time spans at c. 6500–6200 calBC in the southern Balkans and Peloponnese, and at c. 6440–6028 calBC in the northern and eastern Balkans [104; 105; 106; 107; 108; 109;110; 9; 111]. The southeast-northwest temporal gradient thus found no confirmation in the radiocarbon chronology of the initial Neolithic pottery distribution in Southeast Europe. The data suggest the contemporaneous appearance of pottery in regions where gradual colonisation was hypothesised. While pottery in the southern Balkans was found in farming settlement contexts, it appeared in the north at hunter-gatherers' sites as well [108; 110].

The pottery assemblages in Southeast Europe show local and regional differences in production techniques, vessel shapes and ornaments. The combined petrographic and chemical compositional analyses of clay matrix and ceramic fabrics clearly indicate differences in pottery production. Pottery in the northern Balkans was consistently manufactured according to a single recipe, using non-calcareous micaceous clay pastes, characterised by fine well-sorted alluvial quartz sand with feldspar, and heavily tempered with organic matter (i.e. chaff). In the Adriatic, however, pottery was heavily tempered with crushed calcite on the east coast, and with mineral resources (e.g., flint) and grog (recycled pottery) on the west coast [112; 113]. From the outset in the Aegean, pottery was made locally at a number of sites and exchanged regularly between neighbouring settlements. Some fine ware paste recipes show that pottery may have been transported over a distance of around 200km and that it may have been an item in maritime exchange networks. The unchanged ceramic matrix in some cases reflects significant continuity in pottery technology over the millennium [114; 115].

Two basic ornamental principles are recognised in the dispersal of pottery in Southeast Europe in the Early Neolithic. While painted motifs are limited to the Peloponnese, the Balkans and the southern Carpathian Basin, Cardium impressed ornaments mark the Adriatic coast. It is not before the Middle Neolithic that painted pottery appears on the east cost of the Adriatic [116; 117; 118].

The pottery assemblages in the earliest settlement contexts on the Peloponnese and the southernmost tip of the Balkan Peninsula consist of monochrome (red-slipped) pottery, and 'a very limited use of painting' [104, p. 112; 119, p.119]. Unpainted vessels were clearly the first to appear in settlements in the northern and eastern Balkans. They still prevail in the latter contexts, as painted vessels comprise from 0.2% to less than 10% of the total quantity of ceramics [108, p.126; 119, p. 122]. However, we cannot ignore the regionalisation evident in vessel forms [106] and ornamentation in later painted pottery [117; 120]. In southern parts of the region (Thessaly and the Peloponnese) ornaments appeared in red and black. Further to the north, in Macedonia, white was added. In northern and eastern regions of the Balkans, white ornamentation predominates in the earliest pottery assemblages. A similar pattern is seen in regional ornamental motifs distribution, as dots and grids predominate in the northern and eastern Balkans, and triangles, squares, zigzags and floral motifs in the southern Balkans and the Peloponnese.

All these data indicate that ceramic technology was invented and reinvented more than once in different Palaeolithic and Neolithic contexts, and that hunter-gatherer communities made ceramic vessels elsewhere in Eurasia. The various pottery-making techniques, vessel shaping and ornamentation reflect different, but parallel production methods and distributions before and after the transition to farming. Thus, in Western Eurasia, initial pottery distributions occurred in two almost contemporaneous, but geographically and culturally distinct areas. The northern distribution was embedded in mobile and semi-mobile hunter-gatherer contexts on the East European Plain; the southern is associated with subsistence farming in the Near East.

It is worth remembering that, while the southern was discussed constantly in both archaeological and archaeogenetic studies for review see M.Budja [110], the northern was ignored for much of the time [121; 122; 123; 124]. We already mentioned above that the southern Neolithic pottery distribution was suggested to be associated with the distribution of the genetically determined Y-chromosome haplogroup (hg) J in modern European populations. We may add however, that the northern correlates well with both, Y-chromosome hg N in modern [125]Derenko et al. 2007), and mitochondrial hg U4, U5 and H in ancient hunter-gatherers' and farmers' populations [60] (Figs. 5 and 6).

Instead of conclusions

The Mesolithic-Neolithic transformation was far more complex and variable process than previously hypothesised. The introduction of ceramic technology and initial pottery distributions in Eurasia show a wide-spread appearance of different pottery-making techniques and ornamental principles in different cultural and chronological contexts. The pattern cannot be explained by way of a narrow and gradual southeast - north west oriented spread of both people and vessels across Europe in a 'wave of advance' and within a 'first demic event'. We suggest that both were embedded in continuous social networks established long before the advent of the Neolithic in the Levant.

The data indicate that ceramic technology was invented and reinvented more than once in different Palaeolithic and Neolithic contexts, and that hunter-gatherer communities made ceramic vessels elsewhere in Eurasia. The various pottery-making techniques, vessel shaping and ornamentation reflect different, but parallel production methods and distributions before and after the transition to farming.

Initial pottery distribution in Europe shows two almost contemporary, but geographically distinct distributions. While the northern is embedded in hunter-gatherer contexts, it has been suggested that the southern was associated with the expansion of farming into the region. The pottery assemblages in both contexts differ in terms of vessel shapes, production techniques and decoration.

Archaeogeneticists suggest that the processes of peopling Europe in prehistory were far more complex and variable than was first thought. The palimpsest of Ychromosomal paternal and mitochondrial maternal lineages in modern populations reveals the signatures of several demographic expansions within Europe over millennia, and gene flows between Europe and western Asia in both directions. These processes have been suggested for the Mesolithic, Neolithic and Chalcolithic periods and seem to be more visible in the frequency of Y-chromosome markers in modern populations in the Balkans and Mediterranean than in other regions. Recent analyses of ancient DNA and palaeodemographic reconstructions show a complex picture of varied population trajectories elsewhere in Europe, and while such studies have yet to be conducted for Southeast Europe, a similar picture may be expected. Archaeological and biochemical data suggest that dairying was adopted in the Neolithic in Europe. Archaeogenetic data show, on the contrary, the absence of the lactase gene in Neolithic populations in Europe. Pastoralism and dairying thus appeared before lactase persistence arose or became frequent. We may assume, therefore, that dairying and fermented milk consumption in Europe emerged before the genetic adaptation to milk culture.

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FIGURE CAPTIONS

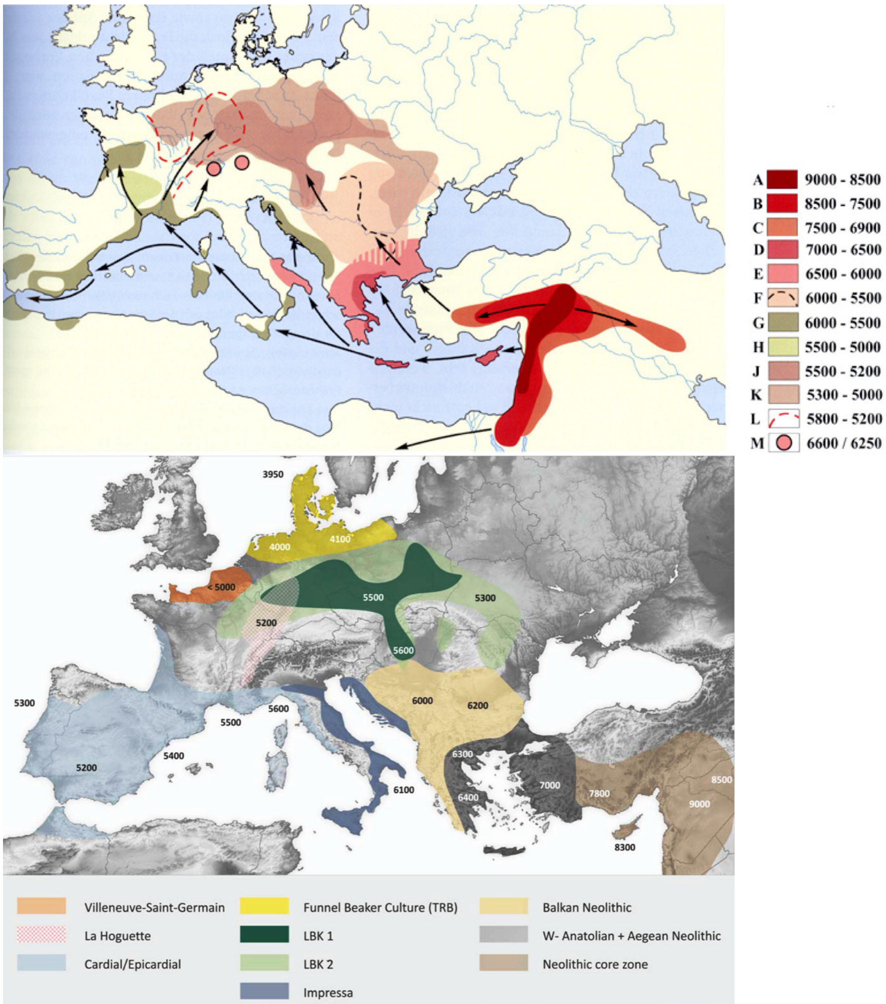

Fig. 1. The hypothesised southeast-northwest temporal gradient of the spread of the Neolithic package, cultural identities, 'demic diffusion' and genetic markers starting throughout Anatolia, crossing the Europe, covering enormous areas, and leaving no gaps behind. However, Northeast and East Europe were marginalised for all the time, having no point of entry and remaining a blank through the (Early) Neolithic period (from Budja 2013. Fig. 2)

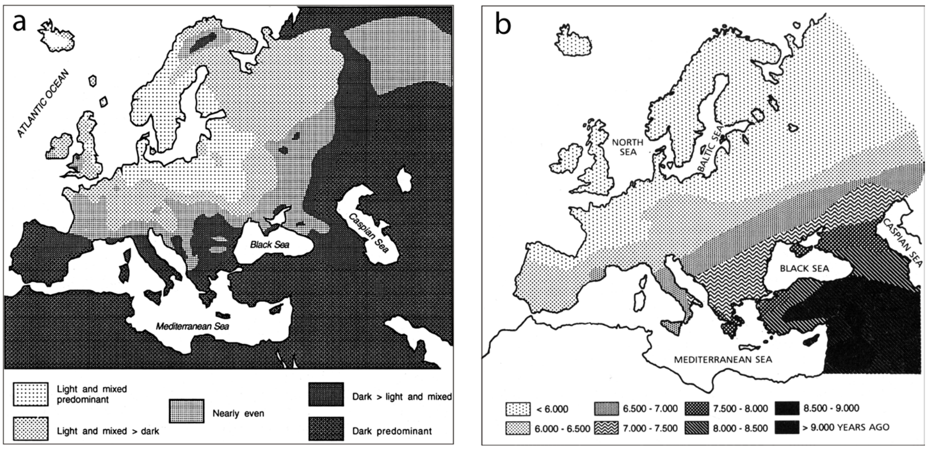

Fig. 2. Maps of (a) frequency distribution of morphological and anthropometric characteristics, and associated physical types races that was hypothesised to correspond with the Neolithic invasion of Mediterraneansin Europe and with the process of 'Dinaricization' (Coon 1939. 270-271, map 8), and (b) of genetic landscape of the first principal components that was hypothesised to correspond with Neolithic 'demic diffusion' (Cavalli-Sforza, Cavalli-Sforza 1995 fig. 6. 5)

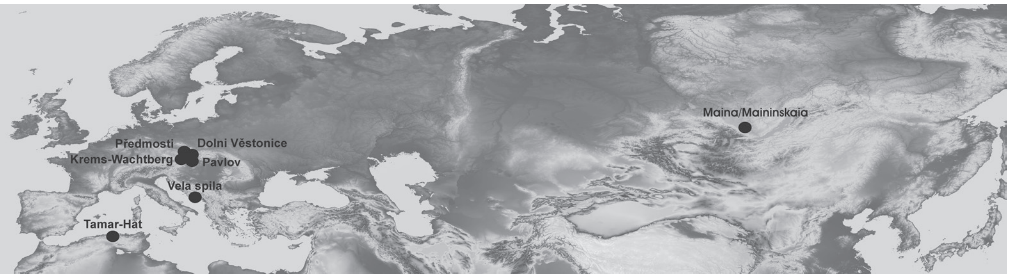

Fig. 3a. The 14C sum probability distribution of ceramic figurines in pre-Neolithic contexts in Eurasia. The sequence is based on 14C data sets from Dolní Věstonice, Pavlov I, Předmostí and Krems-Wachtberg in central Europe (Verpoorte 2001. 40,56, 59, 95-100; Einwögerer, Simon 2008. 39), from Vela spila on the Korčula Island in Adriatic (Farbstein et al. 2012. 4-5), from Tamar Hat in northern Africa and Maina in Siberia (Vasil'ev 2001.10, Fig.4; Farbstein et al. 2012. 11). The 14C dates are calibrated at 68.2% probability (2σ), using the OxCal 4.2.3 programme

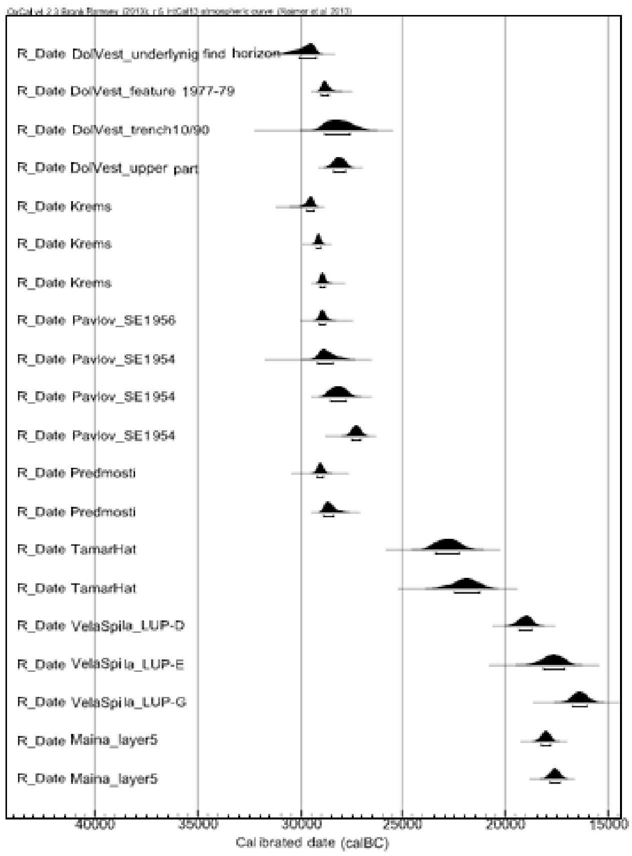

Fig. 3b. The geographic distribution of ceramic figurines deposited in Upper Palaeolithic contexts in Eurasia

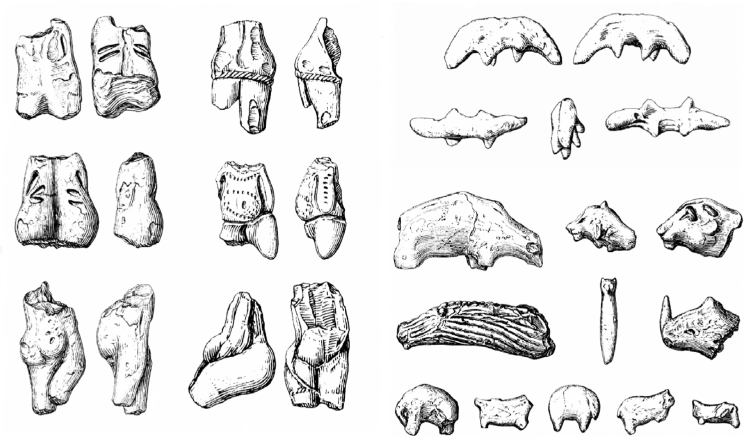

Fig 4. Anthropomorphic and zoomorphic ceramic figurines from the Upper Palaeolithic Pavlovian sites Dolní Věstonice, Pavlov, and Předmosti (after Verpoorte 2001 fig. 3. 6, 7, 8, 9, 46, 3.73, 8.1. 54)

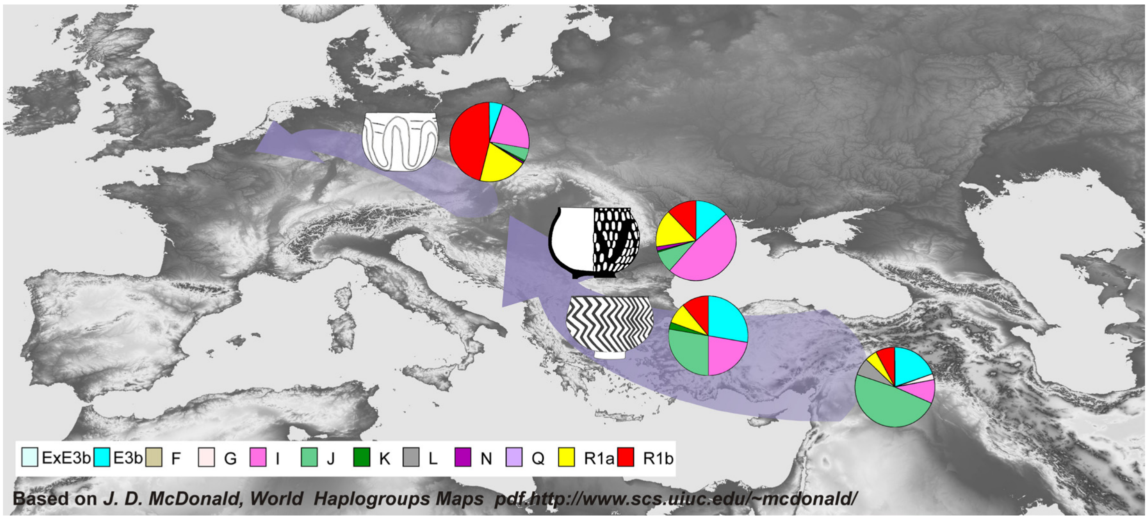

Fig.5. The southeast-northwest cline of frequencies for Y-chromosome haplogroups J and E within modern European populations were hypothesised to be associated with Levantine male contribution to the European Neolithic. It was suggested they geographically overlap with the distribution of Early Neolithic painted pottery and settlements distributions in Southestern Europe. The haplogroups distribution is based on McDonald's World Haplogroups Maps (McDonald 2005) (from Budja 2013. Fig. 5)

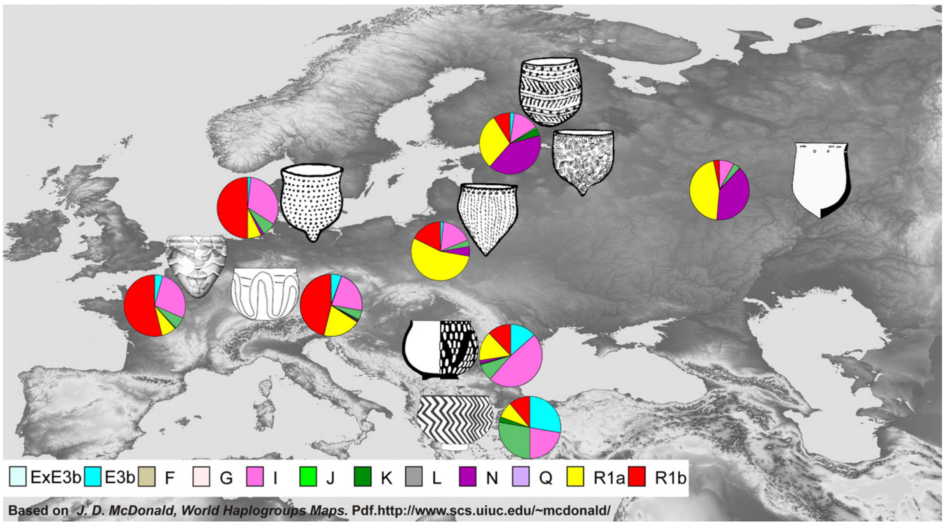

Fig. 6. The parallel clines of frequencies of Y-chromosome haplogroups J, E and N in modern populations in Europe and initial pottery distributions in Neolithic Europe. The haplogroup distribution is based on McDonald's World Haplogroups Maps (McDonald 2005) (from Budja 2013. Fig. 6)

THE NEOLITHISATION OF EURASIA: ARCHAEOLOGICAL, ARCHAEOGENTIC AND BIOMOLECULAR PERSPECTIVES

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Annotation: The Mesolithic-Neolithic transformation was far more complex and variable process than previously hypothesised. The introduction of ceramic technology and initial pottery distributions in Eurasia show a wide-spread appearance of different pottery-making techniques and ornamental principles in different cultural and chronological contexts. The pattern cannot be explained by way of a narrow and gradual southeast - north west oriented spread of both people and vessels across Europe in the context of demic diffusion migratory model. The data indicate that ceramic technology was invented and reinvented more than once in different Palaeolithic and Neolithic contexts, and that hunter-gatherer communities made ceramic vessels elsewhere in Eurasia. Archaeogenetic data suggest that the processes of peopling Europe in prehistory were far more complex and variable than was first thought. The analyses of palimpsest of Ychromosomal paternal and mitochondrial maternal lineages in modern populations and of ancient DNA and palaeodemographic reconstructions show a complex picture of varied population trajectories elsewhere in Europe. Archaeological and biochemical data suggest that dairying and fermented milk consumption in Europe in Neolithic emerged before the genetic adaptation to milk culture.

Keywords: Eurasia; neolithisation; demic diffusion; pottery; human DNA and aDNA; dairying; lactase persistence.