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NEOLITHIC TRANSITION IN EUROPE: EVOLUTIONARY ANTHROPOLOGY STUDY

ABSTRACT: The Neolithic transition in Europe was investigated. We have focused on the models of this transition already proposed in literature, and confronted them with our data. Our study is based on physical anthropology data that we have divided into five groups according to the economy and ecology of the human populations within. These groups are: hunter-gatherers, first farmers, late farmers, pastorial cultures and Bronze Age. We have documented a sharp dissimilarity between Mesolithic and Early Neolithic populations, but on the other hand a strong resemblance between hunter-gatherers, pastorial and Bronze Age cultures. This phenomenon was probably caused by migration of agricultural populations to Europe in the beginning of Neolithic and consequent absorption of these populations within the more numerous indigenous populations. We have also discovered a marked difference in the body stature between farmer males and females. Higher mobility of females' genes together with limited admixture of hunter-gatherers and first farmers' male part of population might possibly be responsible for this feature.

KEY WORDS: Neolithic – Mesolithic – Europe – Hunter gatherers – Farmers – Agriculture – Migration – Y chromosome – – Admixture

INTRODUCTION

The discussion about Neolithic transition in Europe and the influence of agriculture on human biology and culture has a long tradition in scientific literature (Ammerman, Cavalli-Sforza 1979, 1984, Barbujani *et al*. 1994, Bogucki 1988, Kruk, Milisauskas 1999, Milisauskas 1978, van Andel, Runnels 1995, Zvelebil, Rowley-Conwy 1984, Whittle 1992, Éry 1998, Fox 1996, Frayer 1981, Holliday 2002, Jacobs 1985, 1993, Krenz-Niedbała 2001, Larsen 1995, Molleson *et al*. 1993, Piontek *et al*. 2001, Szostek, Glab 2001, Vančata 1997, 2000, Vančata, Charvátová 2001). The focus has moved from classical physical anthropology more and more towards molecular genetics methods. In this article we would like to discuss advantages and disadvantages of Y chromosome molecular genetic analysis and in the second part, we would like to introduce our study of Central European Neolithic. It consists of a mixture of classical anthropology methods and models based on molecular and archeological data. This allowed us to verify some earlier presented theories about population movements and admixture in European Neolithic, and also to neglect the others.

In this article, we use the term Neolithic or farmer societies for populations that clearly used cultivating crops and breeding domesticated animals as a main source of their living. Information about the way of life of Mesolithic and Neolithic populations was acquired from archeological literature (Bogucki 1988, 1996, 1999, Bogucki, Grygiel 1993, Kruk, Milisauskas 1999, Milisauskas 1978, Whittle 1992, 1996). Neolithic period can be divided into several stages that are marked by population movements and spread of agriculture to previously Mesolithic regions. We will use following nomenclature in this article. (i) Early Neolithic for the initial phase of Neolithic, approximately 5500 – 4500 BC for Central Europe. This stage was marked by the appearance of agriculture in this area and the farmer societies consist mainly of Linear Band Pottery (LBP)

cultures that inhabited the loess soils in lowlands. (ii) In Middle Neolithic (4500 – 3200 BC) agriculture has spread northwards and westwards from Central Europe. More noticeable diversification can be seen in the farmer populations. Cultural complexes of Middle Neolithic are Lengyel, Tiszapolgár, Stroke Ornamented Pottery (SOP) and Funnel Beaker Culture (FBC). (iii) Late Neolithic (3200 – 2100 BC) is a time full of changes in Europe. Although cultures like Baden and FBC-Baden still resemble the older farmer societies of Early and Middle Neolithic, new cultural complexes of Corded Ware Culture (CWC) and Bell Beaker Culture (BBC) appear. These (semi-) pastorial cultures seem to dominate over farmer ones in the end of Neolithic and in the beginning of Bronze Age.

Several models have been proposed to describe the appearance of agriculture in Europe. They can be divided into two groups. The first one contains the models that were created by geneticists and based on genetic data as a primary source, and afterwards also verified by cultural data (linguistics, material culture, human etiology). Second group of models was established by archeologists and they were based on archeological data-sets. Some of these models are often presented in the literature as standing against each other, but if we take a closer look, we can see, that they describe different phases of the same problem. In this case, it shouldn't have been unrealistic, if several situations from different models have arisen in our history or even coexisted in the same time in different geographic regions of Late Mesolithic/Early Neolithic Europe.

First group contains 3 models based foremost on genetic data: Wave of Advance (WoA) (Ammerman, Cavalli-Sforza 1979, 1984), Neolithic Demic Diffusion (NDD) (Barbujani *et al.* 1994, Cavalli-Sforza *et al.* 1994) and Staged Population-Interaction Wave of Advance (Renfrew 2001). The basics of WoA model are in Wright's model of spread of advantageous feature in population. There are three essential variables in this model: population growth, migrational activity and migration speed. WoA presumes migration of Neolithic farmer populations from Anatolia to Europe and significant Mesolithic-Neolithic interactions that could lead to several ends ranging from admixture to replacement. Migration of farmer populations is supposed to have numerous features, in particular a steady continual spread in all directions, which is caused by random short distance movements in every generation. This model was based on phenotypic data first (protein form frequencies), later also gene allele frequencies have been examined. Genetic data were combined with linguistic data that support migration of Neolithic populations from SE to NW Europe in the beginning of Neolithic. As with the new techniques in molecular genetics new data are available, they are being incorporated into the old WoA model. This progress is quite remarkable in NDD model, which is the second improved stage of WoA. In NDD model there was multiple times increased the genetic support for farmers' migration (Cavalli-Sforza *et al.* 1994), as well as a linguistic data has been added (Cavalli-Sforza *et al.* 1992, Renfrew 1991) together with more theoretical framework (Barbujani *et al.* 1995, Edmonds *et al.* 2004). In the third stage (SPIWA model) also genetic data from sex markers (Y chromosome, mtDNA) have been included, together with more cultural markers (Renfrew 2001).

Second group of models contains 2 models: Cultural Diffusion Model (CDM) (Zvelebil, Rowley-Conwy 1984, 1986, Zvelebil 1986, Zvelebil 1995, Zvelebil 1998, Whittle 1992, 1996) and Adjusted Wave of Advance (van Andel, Runnels 1995). CDM is based solely on archeological data only and criticizes the WoA line of models. However, this model is not as consistent as WoA based models. While Whittle (1992, 1996) is convinced of European Neolithic transformation taking place without any population influence from Anatolia, Zvelebil and Rowley-Conwy (1984) describes the situation of hunter-gatherers populations being transformed to agriculture. Despite Zvelebil and Rowley-Conwy (1984) prefers the transformation of indigenous populations to agriculture, it does not reject the possibility of migration and admixture with farmer populations. WoA model is criticized mostly because of its simplicity. Adjusted Wave of Advance was introduced by archeologists, and is in agreement with some WoA presumptions, albeit only in geographically limited area of southern Europe.

MATERIALS AND METHODS

In our study we explored the differences of male and female parts of Mesolithic, Neolithic and Bronze Age population from Central Europe. Our goal was to test several hypotheses that were presented in introduction of this article on available skeletal material. *Table 1* shows the samples that were used in our research. Maximum number of 86 metric traits was measured on long bones (femur, tibia, fibula, humerus, radius and ulna). Please note, that this number was usually lower, because of the fragmentation of skeletal material, or some requested traits were not published in original articles. Set of equations for calculation of body height (8 equations) and body mass (25 equations) was applied to all samples (the set of equations could be seen in Piontek, Vančata 2002). Afterwards, skeletal ponderal indices – Body Mass Index (BMI) and Rohrer Index (RI) – were computed. As we can see from *Table 1*, samples were divided into five groups depending on their economy and ecology according to archeological literature. These groups were: hunter-gatherers for Mesolithic populations, first farmers for Linear Band Pottery cultures, late farmers for post-Early Neolithic agricultural populations (mostly Lengyel-Polgar cultural complex), pastorial cultures for distinct herders' populations from Middle and Late Neolithic (mostly Bell Beaker Culture and Corded Ware Culture), and Bronze Age cultures. Parametric (t-test), non-parametric (Mann-Whitney U test) tests and Principal Component analysis (PC) were used for evaluating the relations between these economy-based population groups using Statistica 6.0 software.

TABLE 1. Number and origin of our samples.

Period	Culture	Number of samples			Reference	Type of economy
		men	women	total		
Mesolithic –5500 BC	**hunter-gatherers**	13	3	16	Vančata 1997	hunter-gatherers
EN 5500–4500 BC	**LBP**, Elbesaalegebiet (Germany)	13	19	32	Vančata 1997, Bach and Bach 1981	first farmers
	LBP, Panonia (Hungary)	24	13	37	Éry 1998	first farmers
	Körös, Panonia (Hungary)	7	12	19	Éry 1998	first farmers
MN 4500–3200 BC	**Lengyel-Polgár**, Panonia (Hungary)	46	64	110	Éry 1998	late farmers
LN 3200–2100 BC	**BBC**, Prague (Czech Republic)	10	6	16	Vančata 1997	pastorial cultures
	CWC, Zlota (Poland)	34	35	69	Krenz-Niedbala 2000, 2001	pastorial cultures
	CWC, Eastern Europe	19	12	31	Éry 1998	pastorial cultures
Bronze Age 2100–900 BC	**Vatya**, Panonia (Hungary)	11	14	25	Éry 1998	Bronze Age
	Maros-Perjámos, Panonia (Hungary)	65	69	134	Éry 1998	Bronze Age
	Tumulus, Panonia (Hungary)	112	102	214	Éry 1998	Bronze Age
	Únětice, Bajč a Vepřek (Czech Republic, Slovak Republic)	22	19	41	Charvátová 1999 Mottl *et al.* unpublished data	Bronze Age

EN – Early Neolithic, MN – Middle Neolithic, LN – Late Neolithic, LBP – Linear Band Pottery, BBC – Bell Beaker Culture, CWC – Corded Ware Culture

RESULTS

Firstly we were testing the differences in body shape and size between Mesolithic hunter-gatherers and the Neolithic populations. Our results show that there is a strong disparity between Mesolithic people and first farmers of LBP cultural complex. On the other hand, the differences in measured variables between hunter-gatherers and other Neolithic and Bronze Age populations are diminishing in post-Early Neolithic period. What this could mean and what are our assumptions about this discrepancy will be discussed in next chapters. Valuable overview of our results could be seen in *Table 2.* Two distinctive features have appeared after Principal Component analysis has been performed. i) Our results show a strong difference between males and females, ii) we can identify two clusters in our data set. In the first one, there are economy-based groups of First Farmers and Late Farmers. The second group is formed by the remaining groups of Hunter-gatherers, Pastorial Cultures and Bronze Age cultures. While the disparity was found more or less in all measured variables, it is best seen in the summative variables of body height and body mass or in the derived variables of BMI or RI. As we can see in *Table 2.*, mean body height hunter-gatherers males is 168.73 ± 8.36, in females 155.47 ± 8.04, which is very similar to body height of pastorial cultures (males: 168.07 ± 8.38, females: 155.65 ± 7.28) and Bronze Age cultures (males: 166.82 ± 7.09, females: 154.82 ± 5.81). Differences between these values were statistically insignificant. On the other hand, body heights of cluster first farmers (males: 162.86 ± 5.00, females: 150.22 ± 7.19) and late farmers (males: 163.11 ± 6.70, females: 151.37 ± 6.94) were significantly different from the first cluster while at the same time statistically insignificantly different against each other. But not only in body height there were differences between our sample groups. It was the body stature or robusticity, which was expressed by body weight, BMI and RI values, which was characteristic for our populations. And it was our first farmers' data group that has extreme values of these three variables in comparison with other groups. In particular the males of first farmers were clearly divergent, as was confirmed by statistical analyses. Our results are further discussed in next chapter.

TABLE 2. Results.

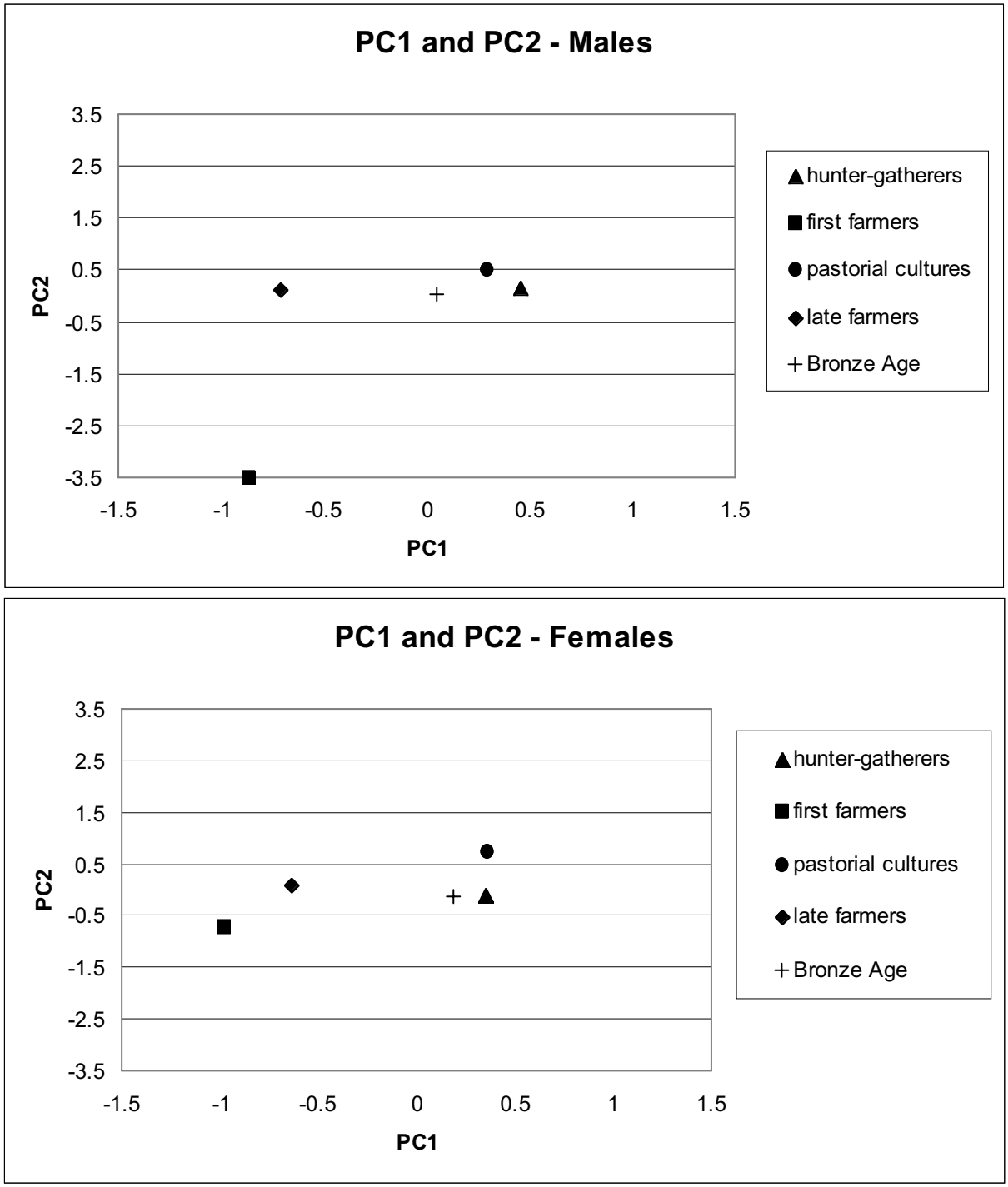
MALES	Body Height Mean (cm)	Body Height n	Body Height Std.Dev.	Body Mass Mean (kg)	Body Mass n	Body Mass Std.Dev.
hunter-gatherers	168.74	12	8.36	63.26	13	7.67
first farmers	162.86	42	5.00	64.10	42	3.58
late farmers	163.11	45	6.70	58.50	45	5.49
pastorial cultures	168.07	55	8.38	61.74	56	6.79
Bronz Age	166.82	171	7.09	61.71	175	6.07
FEMALES						
hunter-gatherers	155.47	3	8.04	52.28	3	10.55
first farmers	150.22	41	7.19	49.19	41	4.29
late farmers	151.37	59	6.94	49.16	59	5.30
pastorial cultures	155.65	43	7.28	49.25	49	7.86
Bronz Age	154.82	171	5.81	51.82	174	4.60
MALES	**BMI Mean**	**BMI n**	**BMI Std.Dev.**	**RI Mean**	**RI n**	**RI Std.Dev.**
hunter-gatherers	22.02	12	0.6890	1.31	12	0.0498
first farmers	24.19	42	1.4426	1.49	42	0.1221
late farmers	21.93	45	0.2991	1.35	45	0.0380
pastorial cultures	21.78	55	1.1424	1.30	55	0.0985
Bronz Age	22.07	171	0.3308	1.32	171	0.0415
FEMALES						
hunter-gatherers	21.55	3	1.9833	1.39	3	0.0773
first farmers	21.79	41	1.0969	1.46	41	0.1224
late farmers	21.38	59	0.3491	1.41	59	0.0418
pastorial cultures	21.10	43	1.2164	1.36	43	0.1217
Bronz Age	21.56	171	0.4018	1.39	171	0.0394

n – number of samples, Std.Dev. – standard deviation, BMI – body mass index, RI – Rohrer index

DISCUSSION

First, we would like to concentrate on the role of Mesolithic hunter-gatherers in Neolithic populations. As was introduced in the beginning of this article, there are two distinct theories about their role. The more traditional one views them as founders of agricultural society in Europe. While the transformation process was either initiated by some external factor (cultural influence from southeastern Europe), or it was a process that started in the Mesolithic society itself. Second view of them was outlined by geneticists and population biologists in 70's of 20th century. This idea is connected with the migration of farmer populations from Near East to Europe and consequential replacement of majority of indigenous hunters-gatherers with the incoming farmers in the conditions of limited admixture (Ammerman, Cavalli-Sforza 1984, Barbujani, Bertorelle 2001). Our research gives us some more insight into processes in the European Neolithic. First and foremost, Mesolithic hunter-gatherers and first farmers are two biologically distinct populations. But our hunter-gatherers sample and samples of pastorial cultures and Bronze Age cultures are very similar to each other. This can be very clearly seen on the *Figure 1*, where are two graphs of PC analysis results. Even though our study can not reveal, whether this similarities are based on descent, or the contrast between hunter-gatherers and first farmers was found because these two populations were of dissimilar origin, but the results are very presumptive. Our assumption about the results is validated by this PC analysis. There could be seen two distinct population clusters. First of them is formed by first farmers and late farmers. The second one includes hunter-gatherers, pastorial cultures and Bronze Age cultures. Although these two graphs were generated using body height, mass, BMI and RI variables, we could argue, that those four variables encompass the variability from all long bones that were measured, both longitudinal and circumference measures. Our idea about Neolithic transition

in Europe is now more comprehensible. While Mesolithic and early agricultural populations were both culturally and biologically different, this fact was caused, from our point of view, by migration of farmer populations to Central Europe about 5500 BC. This fact was already proposed in literature (Ammerman, Cavalli-Sforza 1979, van Andels, Runnels 1995, Semino *et al.* 2000, 2004, Chikhi *et al.* 2002), but argument exists about the number or proportion of first farmers to indigenous populations and about the admixture rate. We can also bring some new insights to this argument. In spite of the robust difference between hunter-gatherers and first farmers, in later phases of Neolithic the differences in measured features between post-Early Neolithic populations begin to unify. So, the first farmers in particular and late farmers in minor way are distinct from both preceding and following populations. This feature could be



PC1 plotted against PC2 for body height, body mass, BMI and RI variable

FIGURE 1. Principal component analysis results.

TABLE 3. Apportionment of PC analysis variability.

PC1 and PC2 Height, Mass, BMI, RI Males		**PC1 and PC2 Height, Mass , BMI, RI Females**	
principal component	% from total variability	principal component	% from total variability
PC1	61.53	PC1	63.38
PC2	38.36	PC2	36.52
total	**99.89**	**total**	**99.90**

interpreted in several ways. It is a well known fact, that agriculture is connected with some negative effects on the population health level. This is predominantly caused by the increase of population in farmer societies, together with more sedental way of life. The negative effects might include added workload per person with the consequent change of stature, dependence on one of few species of plants or animal, which can bring insufficient intake of vital nutritional elements, transition of animal parasites on humans, larger settlements allow infectious diseases to remain prevalent in population with the infinite supply of sensitive individuals, change from K- to r-reproducing strategy with increased infant death rates and lower lifetime expectation of females (Larsen 1995). All these features could lead to diminishing the welfare of the population and lifespan expectancy as well. From our point of view, even if this could clarify the change of stature in Mesolithic hunter-gatherers after a shift to agriculture way of life, this alone can not explain so strong differences between first and late farmers and successive populations. In that case, late farmers should be even more divergent from hunter-gatherers and Late Neolithic populations. But they are not. The results show, that biological features of late farmers are somewhere between first farmers and the cluster of hunter-gatherers. pastorial cultures and Bronze age cultures. Our idea about the role of Mesolithic hunter-gatherers in Neolithic is following. Our data shows, that there was a migration of agricultural populations in the beginning of Neolithic together with little or no admixture with indigenous populations in the first phase. Probably, the numbers of incoming farmers were small in comparison with hunter-gatherers. In that case, it is possible to view such a results as we have from the analysis of pastorial and Bronze Age cultures. We expect that after establishing a settled Neolithic society in lowlands of Central Europe in Early Neolithic, the cultural complex of agriculture moved northwards and to higher latitude areas (Bogucki 1988, Kruk, Milisauskas 1999). This might have been connected with incorporating of local hunters to the farmers' society, or more precisely, incorporation of farmers' society and their culture into the Mesolithic population. Our data illustrate this process as a strong resemblance between Mesolithic, Late Neolithic and Bronze Age cultures.

But was there any difference between males and females in these population movements? We assume there was. First of all, it's our own data that show the disproportion between male and female part of the first farmers. As we can see from *Figure 1*, there is a pronounced difference between males and females in this population. Such differences are not common in hunter-gatherers, pastorial cultures and Bronze Age cultures, but neither in late farmers. It might be the effect or relatively small data set, or a bias of used methods. Or this feature might be caused by the agricultural way of life, where the workload was divided unequal between males and females. Other explanation could be in different dispersal patterns of both sexes. Patrilocality has already been described in humans (Cavalli-Sforza, Minch 1997, Seielstadt *et al.* 1998, Oota *et al.* 2001), as well as in other contemporary primates (Utami *et al.* 2002). A situation where females would be more similar to indigenous populations could also arise, if there would exist a one-way females gene flow from these local populations to the incoming one. This idea might be also supported by genetic studies of Y chromosome and mtDNA. It has been already proposed in a study supporting WoA model that among farmer populations and indigenous hunter-gatherers there must have been only a limited admixture in the initial period of time (Barbujani 1994, Barbujani, Bertorelle 2001, Bertranpetit 2000). Also studies of Y chromosome agree with our research with the massive migration of farmers in the beginning of Neolithic (Underhill *et al.* 2000, 2001, Hammer *et al.* 2001, Hammer, Zegura 2002, Wells *et al.* 2001, Poloni *et al.* 1997, Jobling, Tyler-Smith 2003, Rosser *et al.* 2000, Pereira *et al.* 2001, King, Underhill 2002). Some Y chromosome specific markers in modern European gene pool have been identified as of Neolithic origin. These are binary markers haplogroups Eu4, Eu9, Eu10 a Eu11 (Semino *et al.* 2000), today in the unified nomenclature of Y chromosomal haplogroups they are marked as E3b, J2, F* a J*, G (YCC 2002). While there is still a discussion going on about the ratio between incoming and indigenous populations (for more detailed information see Semino et al. 2000, Chikhi *et al.* 2002). As the previous genetic studies have demonstrated, the representation of Neolithic markers in today's European gene pool is diminishing from southeast to northwest direction. Despite the fact that the representation of Neolithic markers in Greece and on Balkans could be as high as 50% or more, it has decreased to 10% or less in northwest Europe and Scandinavia. It is clear from our data that even in Central Europe, the number of incoming farmers wasn't that high, to influence the body stature after they were absorbed by the indigenous populations.

However, situation that can be said about Neolithic from the results of mtDNA research in much less obvious. Variability of European human mtDNA is very limited. Two main characteristics of this variability are clinal distribution in the Mediterranean region and essentially homogenous area

north from clinal distribution with the exception of Saami population (Simoni *et al.* 2000). It is supposed, that this situation could arise in three different ways, Paleolithic colonization of Europe with modern Homo sapiens, Mesolithic recolonization from glacial refugia, or Neolithic farmers migration (Richards *et al.* 1997). As we have mentioned earlier, the homogeneity of European mtDNA variation could have been caused by higher mobility of females genetic markers, either by supposed patrilocality of farmers, or/and by cultural-based ability of females genes to infiltrate extraneous populations. This phenomenon is sometimes referred to as hypergamy (Cavalli-Sforza, Minch 1997).

Although our results seem to be robust, they can be influenced by several factors. First of all, it is the sample size. Especially the sample size of hunter-gatherers is too low, with females having only 3 valid samples and males only 12 for most tests. Also sample size of first farmers could be higher. Second potential problem could arise with the origin of samples. In spite of all anthropological measurements should be standardized, as there are several sources of our data set, different researchers taking those data might cause some bias on our results. But still, even with those dangers, our results are suggestive and are in accordance with some already published studies.

CONCLUSION

In our research of population movements during European Neolithic, we have confirmed some already proposed theories and refused some others. From our point of view, the most important role in forming modern European population was played by the indigenous hunter-gatherers. While our data show that the European population was almost indisputably influenced by a migration of first agriculturalists, presumably from southeast direction, their proportion in Central European region was so small that it has not influenced body stature of Late Neolithic and Bronze Age populations.

But to what extend have the first farmers influenced modern European gene pool could not been examined in detail by this research. Post-Early Neolithic populations were predominantly composed of local Mesolithic populations that accepted the Neolithic agricultural way of life and altered it for their needs.

Some of our tests indicate that there might be inequality in the gene flow between local populations and incoming farmer populations. While Early Neolithic males are more different from their Mesolithic counterparts then females, we propose, that there was an increased one-way gene drift from Mesolithic to Neolithic population, most probably in the form of females exchange.

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