News and views

Current Knowledge of the Neolithisation Process:
a Central European Perspective

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1. Introduction

At the end of the 19th century, it was generally accepted that a hiatus occurred between the Palaeolithic and the Neolithic. Therefore, the appearance of the Neolithic in Europe was associated with the arrival of new people, colonists from the south-east (Vencl 2007, 124–125). Since that time, the Mesolithic period and the emergence of farming in the Near East and its spread to Europe has received broad attention among researchers, particularly in the English-speaking world (Zvelebil, ed. 1986; Gronenborn 2007, 73–75). Thus, a large number of hypotheses regarding the process of Neolithisation have been suggested, which can be divided into three main groups, based on the relative contribution of local hunter-gatherers and newcomers, early farming communities, to the European Neolithic.

The first group of models consists of migration hypotheses which argue that the Neolithic arrived in Central Europe along with the first farmers from the Near East and south-eastern Europe. The second group, in contrast, explains the arrival of the Neolithic through the acculturation theories suggesting that the local hunter-gatherers played the decisive role and accepted the Neolithic way of life themselves only through the spread of information and the plant-animal package. Finally, the most recent group of models, the integrationist view, suggests that both the indigenous Mesolithic population and the neighbouring Neolithic societies played an important role in the Neolithisation of Central Europe.

1.1 The migration theories

According to Marek Zvelebil, the notion of farmers as our ancestors is one of the pervading claims regarding national and European identity. He argues that there was traditionally a tendency for European prehistorians to place a major emphasis on the Neolithic. Zvelebil considers three particular reasons for this tendency. The first is the prejudice against savage, primitive and barbarian foragers, particularly in contrast to civilised, ordered and cultured farming communities. The second arose from the rise of urbanism which resulted in the idealization of the pastoral and rural way of life. The last one is the need on the part of certain nation-states, including...
former Czechoslovakia, to construct a national identity. Apart from archaeology, this theme, which Zvelebil calls “farmers or ancestors”, can also be found in literature or in popular culture (Zvelebil 1995a, 145–147).

In archaeology, these views were supported by Vere Gordon Childe, who offers the ex oriente lux interpretation of agricultural dispersal. In his book The Dawn of European Civilisation, published in London in 1925, he argues that the transition from foraging to farming in Europe was the result of immigration of populations from the Near East, who brought with them advanced and superior technology and culture, and replaced the indigenous Mesolithic hunter-gatherers. He believes that this process was a major turning point in human history and referred to it as the “Neolithic revolution”. On the other hand, he emphasises that the term “Neolithic revolution” amounts to a gradual, rather than radical, but transformative process (Childe 1925; 1936).

An entire series of authors have substantiated these diffusionist and migration models (e.g. Clark 1966; Tringham 1971; Runnels, van Andel 1995; Bogucki 2003). Furthermore, these hypotheses have been supported by genetic studies. The pioneering works of Albert Ammerman, an archaeologist, and L. L. Cavalli-Sforza, a population geneticist (1984), are well-known, however, their model has been intensely criticised (see below). A special contribution to this hypothesis has been provided by Colin Renfrew, who has added a linguistic aspect to the discussion and linked the Neolithic colonisation of Europe to the advent of the first agrarian populations speaking Indo-European languages (Renfrew 1987, 145–152).

Traditionally, the spread of farming across Central Europe has been accepted as an example of agricultural colonisation by farmers of LBK (Vencl 1986; Bogucki 2001; Neustupný 2004). In the Czech Republic, one of the most notable studies of the Neolithisation of Central Europe has been carried out by Slavomil Vencl (1982). On the basis of anthropological, demographic, botanical, ecological and last but not least archaeological evidence, he has supported the notion that the Neolithisation of Central Europe involved several waves of colonisation, in which the colonists settled in practically unoccupied land. Vencl assumes that the indigenous Mesolithic population played a negligible role in the transition, apart from certain peripheral regions, where the quality of the environment was insufficient for the advancing agriculture societies. Vencl has also considered certain parallels from ethnography and antique sources and has pointed out that the first farmers were mentally more advanced than the indigenous hunter-gatherers and that such a difference could lead to some hostile violent conflicts (Vencl 1982, 665–678; Vencl 1986). In terms of the further development of research into the nature of the transition to agriculture, a special offshoot of the models has been applied by Petr Květina (2007). On the basis of anthropological and ethnographic evidence, Květina makes an attempt to reconstruct the encounter between early farmers and local hunter-gatherers and suggests possible violent clashes between the domestic and incoming populations. Květina, however, considers only the first contact between the communities.

Despite the fact that the migration theories appeared to be compatible with the rate of the spread of the Neolithic measured from radiocarbon dates (Ammerman, Cavalli-Sforza 1984), there are several implications for this immigrationist explanation. The first is that this process had to be driven by the rapid population growth experienced by the emergence of Neolithic farming populations (e.g.
Renfrew 1987). However, such a population growth as an explanation for agriculture transition has been criticised for a lack of evidence by a number of scholars (e.g. Zvelebil 2002). Secondly, this approach fails to consider the role of the original hunter-gatherer population. Unfortunately, extremely sparse evidence concerning late Mesolithic settlement in Central Europe may support these hypotheses (Mateiciucová 2008, 34–36; Zvelebil 1986a, 9).

1.2 The acculturation theories
The acculturation theories represent the opposite perspective to the migration hypotheses. The adoption of farming in Europe and the origins of the Neolithic are viewed exclusively as the uptake of the so-called “Neolithic package”, including a sedentary way of life, the first permanent villages, domesticated crops and animals, and new skills such as polished stone production and pottery, by local forager populations. These hypotheses do not credit that migration from the Near East played any important role. Consequently, the transition of hunters and gatherers to agriculture is primarily explained by the reduction of available resources with an emphasis on the fact that hunter-gatherers adopted farming under pressure. A further emphasis is placed on the sedentary way of life, which is perceived as the crucial aspect leading to the farming (Binford 1968; Zvelebil 1981; 1986a; Rowley-Conwy 1983; Mateiciucová 2008). Authors such as Dennel (1983), Barker (1985), Tillmann (1993), Pavík (1994), Kind (1998), or the later work of Tringham (2000) may be placed in this group.

These authors argue that domesticated animals and plants were acquired via trade with the Neolithic population of the Near East, and subsequently with agriculturalists living in the Balkans and the Mediterranean area. This idea is supported by accumulating archaeobotanical evidence pointing out agricultural activity in Central and Northern Europe well before the onset of the Neolithic (Enry-Rodmann et al. 1997; Gehlen, Schön 2003; Innes et al. 2003; Poska, Saarse 2006; Behre 2007; Tinner et al. 2007). On the basis of these results, the authors suggest that agriculture developed locally throughout the late Mesolithic and Neolithic.

Mention should also be made of A. Whittle (1996), who provides a view of the acculturation process from a social perspective and suggests the local adoption of non-local resources and technologies, facilitated through contacts and interactions outside of Central Europe. In his view, however, the original forager population was motivated by existing social ethics, instead of accepting the notion of population growth leading to the colonisation of new territories.

1.3 The integrationism theories
Apart from the previous two groups of hypotheses, a number of scholars have regarded both types of processes, involving migration and acculturation, as playing an important role in the transition to farming in Central Europe. This intermediate model, described by Zvelebil (2002) as “integrationism”, sees the agricultural transition in terms of selective colonisation by fairly small groups through mechanisms such as “leapfrog colonisation”, frontier mobility, and contact (Zvelebil 1986a; 1986b; Gronenborn 1994; Mateiciucová 2004; 2008). The availability model, suggested by Zvelebil and Rowley-Conwy (1984; 1986; Zvelebil 1986a; Zvelebil 1986b), placed a great deal of emphasis, in contrast to the earlier ones, on the members of the Mesolithic societies. Therefore, this theory is based on the assumption that there is not a substantial difference between Mesolithic foragers and the early farming population. Consequently, the entire zone of foraging-farming interactions is assumed as the frontier, rather than as merely the line of forager-farmer contact. The availability model is divided into three phases depending on the relationship between incoming farmers and indigenous Mesolithic populations within a region and on the intensity of farming practises:

1. the availability phase
The availability phase exists in the early stages of the agricultural frontier, when farmers and foragers are developing contacts but are still two culturally and economically independent units. During this phase, the agricultural way of life is known to the Mesolithic population through a certain exchange of materials and information. The availability phase ends with the adoption of some elements of farming by foragers or with the settlement of farmers in the territory used by hunter-gatherers.

2. the substitution phase
The substitution phase is divided into two forms: external, in which farmers settled in the forager territory and competed with the remaining hunter-gatherers for land and resources, and internal, in which the foragers add certain elements of farming into their range of subsistence strategies. In both cases, the key concept is the competition between two mutually incompatible ways of life.

3. the consolidation phase
This consolidation phase, the final stage in the transition to farming, is the first phase with a predominantly Neolithic economy, marked by extensive and intensive growth of food production: having occupied the best soils, extending to new, secondary areas, and having exhausted, the possibilities of the extensive form of land-use, more intensive farming practices are employed. The use of wild resources is merely complementary, and its role increases only as an emergency strategy. This phase ends when the socio-economic conditions in the area become indistinguishable from those in areas settled earlier and the effects of the transition disappear (Zvelebil 1986a, 10–13).

This third group of hypotheses is supported by an analysis of the isotope of strontium and sulphur contained in the bones and teeth of early farmers, revealing that not all the people buried within the same place spent their childhood or adulthood there. Thus, they are likely to have been immigrants from an area where the isotopic values correspond to those found in the previously hunting-gathering regions (Bentley et al. 2002; Richards et al. 2008). Arguments supporting
the integrationist model of the transition to agriculture have also been provided by genetic researchers discussing the ancestry of Europeans (Richards 2003), and an analysis of chipped stone artefacts, indicating that early farmers of Central Europe partly continued in the traditions of the local forager populations (Tillmann 1993; Mateiuciová 2004; 2008). Excellent evidence for interaction between farming communities and adjacent groups practising hunting and gathering is also offered from prehistoric Poland. According to this evidence, many hunter-gatherers had produced and used pottery long before they took up farming. Moreover, these hunter-gatherer groups appeared to have incorporated some elements of Neolithic group’s technology into their existing ceramic traditions (Nowak 2009).

The availability model introduced space, time, and regional variability into the transition and this model has been widely referred to. However, there are also certain problems related to this complex view of the Neolithisation process. Firstly, the transition is basically seen as a one-way process, populations are defined within it according to the stage they have reached towards a pre-defined end, farming. Thus, particular difficulties derive from the application of the general model in certain areas. Another problem involves the fact that the model assumes both the general process and the end result as constant, despite the huge diversity in space and time, which the transition from foraging to farming represents (Pluciennik 1998, 68–69; Pavlík 2005, 295).

Turning now to the nature of the transition to farming, it is worth pointing out that a number of authors have also considered contacts that took place within the farmer/forager transition on the social level (Zvelebil, Dolukhanov 1991; Zvelebil 1995b). Certain models even stress the significance of deeper symbolic meanings in the process of Neolithisation. Previous factors leading to the Neolithisation such as climate, environment, and population pressure have been relegate to the background. Instead, an emphasis is placed on the study of the social and ideological components of the “Neolithic package”. According to J. Cauvin, the Neolithisation process led to a shift in human thinking, culminating in the increasing sophistication of human symbolic and ritual behaviour (Cauvin 2003). Similarly, I. Hodder (1990) draws attention to the transition to farming as a process, in which the wild and natural was transformed into the domesticated. This means that the transition from a society living in the wild (agrios) to a domestic economy (domus), which he calls the domestication of society.

2. The Neolithisation process: various approaches

Apart from the models and hypotheses, further aspects of the transition to farming and the origin of the LBK such as genetics, stable isotope analysis, lithic studies, and demography are also considered and presented. In addition to trying to answer questions such as how farming was introduced to Europe, they aim at increased exploration of the nature of the agricultural transition.

2.1 Genetic aspects of the transition to farming

The nature of agricultural transition is a matter of continuing debates not only in archaeology, but also in population genetics. The genetic history of past populations has mostly been drawn from modern-day Eurasian populations. Recently, however, ancient DNA studies, which allow for the direct comparison of archaeological and modern populations, have also enabled the answering of the question as to whether early European farmers were immigrants or descendants of resident hunter-gatherers who had adopted farming (Richards 2003; Haak et al. 2005). These methods are still being verified and tested, however, and are, as yet, not extensive enough to provide conclusive results regarding the genetic contribution of SW Asian farmers to the European gene pool. Thus, they cannot solve this question themselves (Bellwood 2001).

2.1.1 Modern human DNA

The subject of the genetic history of Europe was primarily created by Luca Cavalli-Sforza and his colleagues in the 1970s. His pioneering work, carried out in collaboration with the archaeologist Albert Ammerman, was the first sustained attempt to apply genetic data to a question of archaeological interest. Their work The Neolithic Transition and the Genetics of Population in Europe, published in 1984, offered a scientific model explaining the origins and spread of farming in western Eurasia, accepting the central role of sedentism, population growth, and resource pressure in the early farming communities. Cavalli-Sforza and Ammerman measured the rate of spread of farming into Europe, drawing on radiocarbon dates provided by Clark (1965), and concluded that the entire process of the spread of the Neolithic, from Greece to the British Isles, took place over about 2500 years, at a uniform rate of approximately one kilometre per year. They compiled synthetic gene maps which demonstrate geographic clines by principal component analysis. The genetic map produced by the first principal component, accounts for 27% of the total variation in classical marker frequencies across Europe and the Near East, indicating a gradient from the south-east to the north-west. They thus introduced the expression “demic diffusion” to illustrate the immigration of farmers themselves, in contrast to “cultural diffusion”, the spread of farming as an idea through the indigenous hunter-gatherers (Ammerman, Cavalli-Sforza 1973; 1984; Cavalli-Sforza et al. 1994).

Moreover, they suggested a different model known as “wave of advance”, instead of the traditional model of migration and colonization. The wave of the advance model assumes the population growth resulting from agricultural surpluses, and either displacing or absorbing the less numerous Mesolithic hunter-gatherer population. This process leads to a radial expanding population wave, in which the culture spreads with the expansion of people. Not only did the wave of the advance model seem to be compatible with the available radiocarbon dates from Neolithic sites, but also the introduction of genetic data including allele frequencies for blood groups, the tissue antigen HLA system, and certain enzymes, into
the question of agricultural transition supported this notion (Ammerman, Cavalli-Sforza 1973; 1984; Richards 2003). It is worth pointing out that although Ammerman and Cavalli-Sforza (1984) predict that a major component of the modern European gene pool is derived from Near-Eastern farmers, they acknowledge the role of indigenous people in the spread of the Neolithic. A number of recent publications (Barbujani, Dupanloup 2002; Chikhi 2002), however, seem to not credit any role to local foragers and argue that the Neolithic must have spread into the continent exclusively by population movement (Thomas 2006, 52).

Nevertheless, the wave of the advance model introduced by Ammerman and Cavalli-Sforza (1984) has been substantially criticised (e.g. Zvelebil 1986a; 1989; 1998; 2002; Thomas 1996; Pluciennik 1998; Price 2000). Firstly, there has been no evidence for identifying the first principal component with the Neolithic expansion. Instead, the gradients might have be the result of numerous other dispersals. Another problem derives from the fact that the items of the Neolithic package, used by Ammerman and Cavalli-Sforza to identify a settlement as the Neolithic, might often be exchanged into Mesolithic communities. Finally, there is broad agreement among archaeologists that there is no evidence for large scale continent-wide migration. Also, 25 years later at a conference in Venice in 1998, one of the authors, A. Ammerman, looked back and debated how his and Cavalli-Sforza’s ideas developed and influenced further research (see Ammerman, Biagi 2003).

In the 1980s, apart from the principal component analysis of the classical markers such as blood groups, HLA antigens, and enzymes, it became possible to analyse the DNA sequences of the genes themselves. In particular, attention has been drawn to the two non-recombining loci in humans: the mitochondrial DNA (mtDNA), which is inherited only down the maternal line, and the Y chromosome, which is only present in males and inherited from father to son. The mitochondrial genome and the Y chromosome are ideal for reconstructing evolutionary trees or networks, which can be put into a time frame, and the age of the molecules at their nodes can be estimated (Richards 2003, 144–145).

Mitochondrial DNA analysis indicates a similar trend as the principal component analysis of the classical markers but accounts for only 10–20% of the mitochondrial sequences all throughout Europe (Richards et al. 1996; 1998). The first results from European mtDNA concluded that the ancestors of the great majority of modern lineages entered Europe during the Upper Palaeolithic, whereas the incoming lineages were in the minority (Richards et al. 1996; 1998). These results have been further supported by numerous studies (Torroni et al. 1998; Richards et al. 2000; Richards 2003) also indicating that on the maternal line of descent, only a minority of European ancestors were Near Eastern farmers. The majority, however, were indigenous European hunter-gatherers, who adopted farming at a later point. It is also worth mentioning that these results provide information about female heritage, therefore, men could be of foreign origin (Ammerman et al. 2006). Nevertheless, the mtDNA work has been criticised by a number of authors in the field of traditional population genetics, using a different methodological protocol (Cavalli-Sforza, Minch 1997; Barbujani et al. 1998; Chikhi et al. 2002; Barbujani, Bertorelle 2001).

Y-chromosomal DNA analysis suggests that the frequency of haplotypes originating in the Near East averages about 20–25%, similar to the estimates from mtDNA (Semino et al. 1996; 2000; Underhill et al. 2000; but see Chikhi et al. 2002). The contribution of Palaeolithic hunter-gatherers as opposed to Neolithic agriculturalists to the colonisation of Europe has also been recently studied in the Czech population (Kračmarová et al. 2006). The results indicate that the haplogroups (I, R1a, R1b) linked to the post-glacial recolonisation of Europe reached frequencies of 80.6%. In contrast, haplogroups (E3b, G, J2) likely brought to Europe by agriculturalists from the Near East occurred in 15% of the test sample. (Kračmarová et al. 2006; see Zvelebil, Pettit 2006 for further discussion).

In spite of the fact that the above-mentioned genetic studies have led to conflicting results, it is possible to see a congruence in the results of all three systems (autosomal, mtDNA, Y-chromosome) in relation to the demic expansion of Neolithic Near Eastern farmers into Europe (Lell, Wallace 2000). All would suggest the contribution of south-west Asian populations into the European gene pool and report similar south-east-north-west clines across Europe. On a continental scale, the above-mentioned genetic evidence can be summarised as follows (Table 1).

Table 1. Summarised genetic evidence.

<table>
<thead>
<tr>
<th>Source</th>
<th>Contribution of Near Eastern farmers to the European gene pool</th>
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</thead>
<tbody>
<tr>
<td>Ammermann, Cavalli-Sforza 1984</td>
<td>75–90%</td>
</tr>
<tr>
<td>Chikhi et al. 2002</td>
<td>50–65%</td>
</tr>
<tr>
<td>King, Underhill 2002</td>
<td>2–40%</td>
</tr>
<tr>
<td>Richards et al. 1996; 2000</td>
<td>20–25%</td>
</tr>
<tr>
<td>Semino et al. 2000</td>
<td>20–25%</td>
</tr>
</tbody>
</table>

To sum up, the authors of recent studies of modern human DNA tend to support the integrationist view that the first farmers of Central Europe made only a small contribution to the genetic heritage of present-day Europeans (Richards et al. 1996; 1998; 2000; Semino et al. 1996; 2000; Torroni et al. 1998; Simoni et al. 2000; Underhill et al. 2000; 2001; Richards 2003; Kračmarová et al. 2006). Furthermore, the difference between greater male (Y-chromosomal DNA) and lesser female (mtDNA) genetic contribution to the Neolithisation process might indicate male exogamy and long-distance travel on the one hand, and female matrilocality and regional endogamy on the other (Zvelebil 2002).

According to Marek Zvelebil (2002), four major processes are involved with the arrival of the Neolithic and contributed to the generation of south-east-north-west genetic gradient patterns:
1. The pattern of small-scale population movements progressing from south-east Europe to the north-west over millennia.
2. At the onset of the Neolithic, “targeted”, “leapfrog” or “pioneer” settlement of selected and targeted optimal areas by small numbers of incoming farmers from the Near East/Anatolia to south-east, Central and Mediterranean Europe, resulting in the foundation of agricultural “enclaves” within landscapes occupied by hunter-gatherers.
3. The adoption of farming by indigenous foragers through contact, intermarriage, and socially regulated mobility between hunter-gatherers and farmers within frontier zones.

2.1.2 Ancient human DNA

Genetic studies carried out on modern European populations have led to conflicting results (see above). Ancient DNA studies, however, seem to support gene admixture on a regional scale (Haak et al. 2005; Ammerman et al. 2005; Bramanti 2008; Bramanti et al. 2009). Haak et al. (2005) analysed mtDNA of Neolithic skeletons from Central Europe and concluded that those first farmers did not have a strong genetic influence on modern European female lineages. The likely explanation for these results offered by authors suggests that the female early Neolithic farmers could have been genetically diluted by resident native hunter-gatherers, since a particular mtDNA haplotype (N1a) found in early Neolithic skeletons is comparatively rare among modern Europeans (see Ammerman et al. 2006; Burger et al. 2006 for further discussion). This conclusion is supported by the above-mentioned studies of modern human DNA, archaeologically (e.g. Gronenborn 1999; 2007), and also by stable isotope studies (Bentley et al. 2002).

In contrast, a number of recent ancient mtDNA studies (Bramanti et al. 2009; Haak et al. 2010) have suggested that the LBK populations shared an affinity with the modern-day Near East and Anatolia, supporting a major genetic input from this area during the advent of farming in Europe. These data are compatible with a model of Central Europe in the early Neolithic of indigenous populations plus major genetic inputs from expanding populations in the Near East. Thus, on a regional scale, these results support the “leapfrog” colonization model, where early farmers initially targeted the economically favourable loess plains in Central Europe. Nevertheless, the LBK populations also showed unique genetic characteristics including a clearly distinct distribution of mitochondrial haplogroup frequencies, implying that further significant genetic changes took place in Europe after the early Neolithic (Haak et al. 2010).

Moreover, despite the fact that discontinuity seems to be an important feature of the prehistoric mitochondrial record of Central Europe, one should bear in mind that there are major problems with sample size, population substructure, and, of course, the danger of sample contamination (Soares et al. 2010). In the Czech Republic, Bramanti (2008) has carried out ancient mtDNA analysis of an early LBK population from Vedrovice (see below).

2.2. Stable isotope analysis

Stable isotope analysis helps directly answer frequently discussed questions concerning former diet, demography, residence patterns, and diseases. Stable isotopes find their way into organisms through diet, and are consequently gradually integrated into the tissue of bones and teeth. Bioarchaeology primarily uses the following isotopes and their ratios: 13C/12C, 14N/15N, 87Sr/86Sr, 18O/16O, and 34S/32S. Their natural sources are atmosphere, water, and a geological base, from where they enter the plant and animal bodies and participate in their tissue building. To analyse for stable isotopes, collagen or hydroxyapatite is extracted from the bone with the resulting material providing a relative abundance of the different isotopes present (Mays 1998, 182; Kovačíková, Brůžek 2008). In order to investigate the nature of the agricultural transition, an emphasis is placed on analysis concerning mobility and dietary patterns carried out by examining human skeletons from Mesolithic and early Neolithic Central Europe.

2.2.1 Mobility patterns

Measuring of strontium and sulphur isotopes in human skeletons can directly, in contrast to DNA analysis, examine human mobility on a regional and local scale. Migrant individuals who moved between geologic regions can be identified by comparing the isolate signature in adult teeth, composed over the first years of life, with that in the bones, which preserve the isotopic profile corresponding to the last years of life. Therefore, if the teeth and bones of an adult have different signatures, then that individual spent his or her final years in different geological areas. These ratios are further compared with the values from the local geology and indicate whether an individual moved into the region during later life (Bentley et al. 2002; Bentley 2007; Bickle, Hofmann 2007; Katzenberg 2008; Richards et al. 2008).

A strontium isotope analysis of skeletal remains from LBK sites in south-west Germany has indicated a high incidence of migration in these Neolithic communities (Price et al. 2001; Bentley et al. 2002; 2003a; 2003b; Bentley 2006; Bickle, Hofmann 2007). A high incidence of non-locals was revealed, for example, at LBK cemeteries of Flomborn (64%) and Schweizlingen (25%) in the Rhine Valley, Dillingen (65%) along the Danube Valley, and Vaihingen (30%) in the Neckar Valley. The authors have dealt with the pattern of migration of farmers into Central Europe at the beginning of the Neolithic and have offered a derivation from or interaction with hunter-gatherers as a likely explanation. In addition, the results from Schweizlingen have demonstrated that migration was dominated by females having grown up in the uplands on either side of the Rhine Valley and joining the agricultural community through marriage (Price et al. 2001; Bentley et al. 2002; Bentley 2007; Zvelebil, Pettitt 2008). This is a common pattern observed
and discussed in ethnographic and anthropological literature (Zvelebil 1986a; Zvelebil, Pettit 2008).

2.2.2 Dietary patterns
Stable carbon, nitrogen, and sulphur isotope analysis has been successfully applied to address questions of subsistence and diet during the transition to farming (e.g. Richards, Hedges 1999; Bocherens et al. 2007; Fischer et al. 2007; Nehlich et al. 2010). It is based on the assumption that differences in the isotope ratios of elements reflect the fact that each organism is a component of global geochemical cycles and the concentration of isotopes deposited in human and animal bones and teeth during life inform us about climate and food web position by means of the isotope ratios which increase at each trophic level. Consequently, the ratio of $^{13}$C/$^{12}$C ($\delta^{13}$C) can be used to distinguish between marine and terrestrial ecosystems or $C_3$ (a number of temperate plant species) and $C_4$ (e.g. maize, sorghum, millet, sugar cane) plants, which fix carbon by different photosynthetic pathways. In combination with the stable nitrogen isotope ratio ($\delta^{15}$N), it is possible to identify categories of plants and separate herbivores from carnivores. The ratio of $^{34}$S/$^{32}$S ($\delta^{34}$S) provides evidence of the proportion of terrestrial, freshwater, and marine sources in a diet, and is complementary to that of the carbon and nitrogen ratios (Mays 1998, 183; Sealy 2001, 270–271; Katzenberg 2008, 423–424; Kovačíková, Brůžek 2008).

As mentioned above, recent research has focused on stable isotope analysis, which provides strong evidence of a sharp shift in subsistence practice during the transition to farming from various corners of the continent such as Denmark (Tauber 1981; Fischer et al. 2007), Portugal (Lubell et al. 1994), Great Britain (Richards, Hedges 1999; Schulting, Richards 2002; Richards et al. 2003), and the Danube Gorges (Nehlich et al. 2010). All of the cited studies have reached the same conclusion, stating that there was a large input of marine and riverine food in the human diets of the Mesolithic period, while with the onset of the Neolithic, humans started consuming primarily terrestrial food (see Milner et al. 2004; Richards, Schulting 2006 for further discussion). The scholars mainly explain this pattern either by agricultural colonisation by new people, whose diet was based on domesticates, or by the rapid adoption of Neolithic culture and domesticates by the indigenous people.

In contrast, it is worth mentioning that a stable isotope analysis cannot distinguish between wild and domesticated resources, consequently the shift from marine and freshwater resources may not indicate that they were replaced by domesticates, but it is possible that this pattern is connected with subsistence diversity as well. Cereals could not be used as staples in the Neolithic, but in a range of different ways such as special-purpose food or alongside wild foods (Thomas 2003; 2007). Julian Thomas (2003, 69–70) further argues that Neolithic people had access to a rich source of food in the form of fishing and that the shift in dietary preferences can be explained by a cultural prohibition on marine food, a new relationship between humans and the sea, a certain kind of cultural identification, or the marker of taking on a new identity – “being Neolithic”.

2.3 Lithic studies
The potential of the lithic studies for the question of the Mesolithic studies of the Mesolithic-Neolithic transition in Central Europe has been emphasised by an entire range of authors (recently Gronenborn 1999; Mateiuciucová 2003; 2004; 2008), since analysis of chipped stone artefacts is one of the few sources to be used by both the Mesolithic hunter-gatherers, as well as by the early farmers. Inna Mateiuciucová (2003; 2004; 2008), whose studies build on the work of S. Vencl (1960) and D. Gronenborn (1997), has concentrated her study on the following features of the chipped stone industry: the technology of blade production, the distribution of raw stone sources, and the occurrence of so-called “culturally specific” tool types (trapezes, borers, and retouched blades) in order to answer questions concerning LBK origin and dispersals into a vast area of Central Europe with an emphasis on the local Mesolithic background.

On the basis of the identification of different techniques of regular blade production at Mesolithic and Neolithic sites, Mateiuciucová suggests that the process of Neolithisation in Central Europe was not unified. Furthermore, indigenous Mesolithic populations played an important part in certain regions, and were gradually acculturated. Moreover, the Balkan cultural complex (including the Starčevo and Körös culture) most likely participated in the Neolithisation of Central Europe through mediation, the transfer of information via contacts in the exchange of raw materials, products, and partners. Consequently, the participation of the indigenous Mesolithic population in the formation of the Körös and possibly also the Starčevo culture is indicated by the Danubian tradition of blade production which originated in the late Mesolithic period as a local response to technological changes in the Mediterranean, which Mateiuciucová calls “a variation on the Mediterranean tradition” (Mateiuciucová 2004, 91–96; 2008, 57–110; 165–166).

The second focus of her study has been placed on the issue of the distribution of stone raw materials with special attention to the raw materials that may have played an important role in the Neolithisation process in Central Europe (Szentigáld radiolarite, Carpathian obsidian, Krakow Jurassic silicites). Mateiuciucová suggests that the earliest LBK may have spread through pre-existing networks in Central Europe, since the distribution of raw materials indicates that a network of contacts already existed in certain areas of Central Europe at the end of the Early Mesolithic. These networks, connecting areas of Central Europe with areas in the Balkans, enabled the flow of information and formed an ideal basis for the later rise of the Neolithic. In addition, certain features of distribution typical for the Mesolithic period also continued to appear in the Early Neolithic period. Attention should be especially drawn to the network of Transdanubian radiolarites, the dispersion of which corresponds with the west and north-west spread of the earliest phase of the LBK culture (Mateiuciucová 2004, 96–98; 2008, 111–155; 165–167).
On the basis of the information noted above, Mateiiciucová concludes that the LBK culture developed autochthonously from the local Mesolithic substrate in the region of Transdanubia and immediately adjacent areas, but under the influence of contacts and partial mixing with the Starčevo culture communities (Mateiiciucová 2004, 99–101; 2008, 165–167). Her hypotheses also emphasise the psychological implications of the Neolithisation process by suggesting that initially, there was a Neolithisation of the hunter-gatherers’ soul or psyche, followed by the Neolithisation at the material level (Mateiiciucová 2004, 99–100).

2.4 Demographic aspects of the Neolithic transition
Although many different disciplines have been involved in explaining the mechanism of Neolithic dispersal, surprisingly little attention has been paid to the demographic aspects of the agricultural transition (Galeta, Brůžek 2009). Given the fact that the crucial prerequisite of colonisation would have been a high rate of population growth, LBK farmers would have had to reproduce at a rate approaching the theoretical maximum for human population (Brůžek 2003; Galeta, Brůžek 2009).

A population growth rate from 2.0% to 3.5% per year has been established as the input value in the models of Ammerman for human population (Brůžek 2003; Galeta, Brůžek 2009, 2010). In a subsequent study, Galeta and Brůžek (2009, 141) have, in contrast, argued that these estimates do not account for the uncertainty connected with adopting input parameters from archaeological sources. Instead, they have developed their demographic model of the Neolithic transition in Central Europe.

In their study, Galeta and Brůžek (2009) estimated the level of fertility (around 6–13 children per woman) and growth rate (0.64–1.96% per year) of the LBK population via demographic modelling in order to assess whether such a level of fertility and population growth rate would be high enough to allow the LBK farmers to spread across Central Europe within less than 200 years without any admixture with indigenous hunter-gatherers. On the basis of this and other data from human demography, archaeology, and human ecology, they constructed a stochastic demographic model of changes in farming population size and concluded that the establishment of farming communities in Central Europe without an admixture with foragers may be rejected in 92% of the simulations. Their study thus provides a strong argument against the colonization hypothesis and supports the integrationist view of the Neolithic transition in Central Europe.

3. Vedrovice: a case study in South Moravia
The site Vedrovice is located in South Moravia in the Czech Republic, within the drainage basin of the rivers Jihlava and Svratka (figure 1). Sections of the site were excavated between 1961 and 2001, and have yielded a settlement, three enclosures as well as two cemeteries: the early LBK cemetery “Široká u lesa” and that called “U Vinklerovy cibulny” (Ondruš 2002). The conditions on site provided excellent preservation. Therefore the site of Vedrovice encompasses a significant range of material culture including ceramic vessels, figurine fragments, housing structures, construction pits, ovens, ceramic weights, flaked and polished stone tools, grinding stones, faunal remains as well as bones and bone tools and last but not least human skeletal remains (Podborský, ed. 2002).

Recently, there has been a comprehensive international collaborative research programme focused on the human skeletal remains recovered from the cemetery “Široká u lesa” with an emphasis on two key goals: first, to establish comprehensive holistic bioarchaeological research, and secondly, to generate new knowledge about the emergence of the LBK culture and the transition to farming in Central Europe in the broader context of European Neolithisation. To do so, multiple bioarchaeological approaches have been applied including AMS radiocarbon dating, palaeopathology studies, dental microwear studies, material culture studies, and also ancient DNA analysis as well as chemical trace analyses (Lukes et al. 2008).

3.1 The origins and ancestry of the Vedrovice community: isotopic and ancient DNA analyses
Although the Vedrovice samples are not among the genetically best preserved ones, Bramanti (2008) has successfully sequenced ancient mitochondrial DNA polymorphism from three male and three female individuals. She observed a prevalence of T2 (2 individuals) and K (2 individuals) sequences, whose founders are proposed to have been introduced into Europe during the Lower Upper Palaeolithic. These have also been observed in another LBK sample from north-central Europe (Haak et al. 2005). The remaining two individuals belong to the haplogroup H, also deriving from the European Upper Palaeolithic, and haplogroup J1c, which might be associated with the spread of the Neolithic (Richards et al. 2000; Zvelebil, Pettitt 2008). It is also worth noting that Bramanti (2008) has thus supported the results of a recent study by Kračmarová et al. (2006), who have claimed that modern Czech male ancestry shows about a 80% predominance of the Palaeolithic genetic markers as indicated by Y-chromosome polymorphisms.

To reconstruct human mobility, strontium and sulphur isotope analyses of skeletal remains have also been undertaken. The results indicate that most of the humans buried at Vedrovice spent their childhood, as indicated by the strontium isotope values, and adulthood, indicated by the sulphur isotope value, at or near Vedrovice. In contrast, there are eight individuals with different isotopic values, which means, that they spent their childhood or adulthood elsewhere, so they are likely to have been immigrants to the site. These results thus suggest that a small percentage of the Vedrovice community were allochthonous and derived from
areas at all points of the compass (Richards et al. 2008). As observed by Zvelebil and Pettitt (2008, 199), these migrants may have derived from or interacted with hunter-gatherers from the upland areas. This is a pattern that has been observed elsewhere, for instance by Price et al. (2001).

It can be seen quite clearly that ancient DNA and isotopic analyses have contributed to our understanding of the transition to agriculture in Central Europe. Additionally, the results of bioarchaeological research at Vedrovice have provided information about the health condition, palaeodemography and nutrition of Vedrovice inhabitants, their social status, and the transmission of cultural traditions (Zvelebil, Pettitt 2008). On the basis of all these results, Zvelebil and Pettitt (2008, 213–214) have concluded that Vedrovice was likely a Neolithic “gateway community”, both receiving individuals from afar and maintaining long-distance contacts, and also serving as a founder community for other early LBK settlements. They propose that Vedrovice was founded by a small community of incomers, who probably originated in western Hungary, since links with western Hungary are evident in the material culture. Soon after Vedrovice was founded (at some point prior to 5300 BC), it attracted people from hunting-gathering communities within the region of the Bohemian-Moravian Uplands and north-east Bohemia. Zvelebil and Pettitt go on to suggest that Vedrovice also served as the focal point of a far-flung contact network that facilitated the exchange of goods and information. The evidence for these connections is apparent from the material culture, such as the Spondylus ornaments, flints from southern Poland, Hungarian radiolarite, or schist/amphibolite from northern Bohemia. They even go on to reconstruct the life biographies of selected individuals from the Vedrovice community in order to reconstruct the personal diversity and variability of the Vedrovice community and to emphasise that we can, within the bioarchaeological approach, reconstruct the life histories of people who died long ago (Zvelebil, Pettitt 2008).

4. Certain concluding remarks

The current research into the Neolithisation process in Central Europe can be summarised as follows:
1. Although much attention has been paid to the agricultural transition, archaeological attitudes towards the transition to farming have been influenced by a variety of reasons such as the political and academic climate (Zvelebil 1995a; Pluciennik 1998). Therefore, prehistorians placed a great emphasis on the Neolithic, whereas the study of Mesolithic hunter-gatherers has remained one of the neglected issues in European prehistory. This has been particularly true in the case of Czech prehistory (Beneš 2004).
2. It is believed that the first farmers of Central Europe originated in the Transdanubia, and spread rapidly across a broad area extending from the western Ukraine to the Rhine River in Germany (Lukes, Zvelebil, eds. 2004; Gronenborn 2007). These first farmers appeared in Central Europe around 5500 BC (Pavlů 2005). Recently, it has become clear that the spread of agriculture involved a variety of mechanisms and cannot be merely explained by a simple model of migration or acculturation (Zvelebil 2004; Robb, Miracle 2007). According to the integrationist model, local Mesolithic groups played an important role in this process and, at present, the majority of researchers concerned with Early Neolithic archaeology prefer this intermediate scenario (Gronenborn 2007).
3. The integrationist model finds strong support in a number of disciplines. Genetic studies of classical markers, mtDNA, and the Y-chromosome have indicated the major contribution of Mesolithic foragers to the gene pool of modern Europeans. The contribution of Near Eastern lineages to the European gene pool has been indicated at around a quarter or less (Richards 2003). Similarly, ancient DNA supports gene admixture on a regional scale (Haak et al. 2005).
4. In addition, strontium isotope analyses of LBK skeletons from Germany have revealed a high incidence of nonlocals, which may indicate that people from hunting-gathering groups had joined agriculturalist communities (Price et al. 2001).
5. The admixture view has also been supported by recent lithic studies, which suggest continuity in stone tool production and the distribution of stone raw materials from the Mesolithic to the Early LBK (Gronenborn 2007; Mateciucová 2008).
6. The integrationist view of the Neolithic transition in Central Europe is supported by a demographic model, which has indicated that LBK fertility was not high enough to allow farmers to spread over Central Europe without an admixture with the local Mesolithic population (Galeta, Brůžek 2009).
7. Imported LBK finds within the late Mesolithic context of Central Europe may demonstrate contacts between Mesolithic foragers and LBK farmers, which also supports the integrationist view of the agricultural transition (Zvelebil 2004; Gronenborn 2007).
8. With regard to LBK homogeneity, traditionally considered as evidence of the rapid colonisation of Central Europe by farming groups, currently, a number of scholars regard this uniformity as an actively chosen phenomenon for social reasons (Robb, Miracle 2007). Since current research has reached the conclusion that the LBK culture has numerous origins (an admixture of intrusive Near Eastern farmers and indigenous Mesolithic populations) (Zvelebil 2004, 199), the LBK culture had to be symbolically standard and uniform. In other words, people from various communities joined the LBK and accepted a new way of life and new identity. This strategy, consequently, enabled rapid and successful spread of the LBK to all of Central Europe (Zvelebil 2009). On a continental scale, the sharp shift in subsistence practice with the onset of the Neolithic
might also have been bound up with the assumption of a new cultural identification (“being Neolithic”) (Thomas 2003).

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