Congruent distribution of Neolithic painted pottery and ceramic figurines with Y-chromosome lineages

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The authors propose a correlation between certain elements of Neolithic material culture — painted pottery and anthropomorphic figurines — and Y-chromosome haplotypes, suggesting a shared history of dispersal of human populations and cultural ideas.

Key-words: Y-chromosome haplotypes, genetic contours, Neolithic painted pottery, ceramic figurines

Introduction

Painted pottery and anthropomorphic figurines frequently occur in the Neolithic and Chalcolithic in a broad region of the Levant, Anatolia, southeastern Europe and areas of the central and eastern Mediterranean. Painted pottery is often associated with similar material culture, such as clay sealing stamps and ceramic figurines, and settlements, such as tells (Whittle 1996). The interpretation of figurines associated with early agricultural Near Eastern communities of the Pre-Pottery Neolithic B (~7500 BC) is a topic of debate (Gimbutas 1974; Ucko 1968; Voigt 2000; Hodder 1990; Tringham 1991; Chapman 2000; Bailey 2001). Cauvin (2000) and Garfinkel (1998) have proposed that a series of ideologies originating from the Levant and Anatolia in the Pre-Pottery Neolithic B (PPNB) may have been carried to Greece, the Balkans, the Danube basin and the coastal Mediterranean. These novel cultural activities included not only anthropomorphic figurines but also other symbols such as dance motifs in the visual depictions of social and ritual events.

Here we examine the geographic correlations between the occurrence of Neolithic/Chalcolithic painted pottery and ceramic figurines and the frequencies of various Y-chromosomal haplotypes that evolved over time without recombination. A haplotype is an arrangement of two or more specific alleles on a single chromosome. An allele is any one of multiple DNA sequence character states possible, typically a nucleotide substitution, insertion or deletion. The genetic markers used to define haplotypes are considered representative of unique mutational events. These haplotypes have been proposed as genetic signatures of putative Neolithic migrations of transitional agriculturists from Anatolia and the Levant into Europe during the process of Neolithization (Semino *et al.* 1996; 2000; Hammer *et al.* 1998). Implicit is the fact that demic expansion is a manifestation of population growth and migration. This Neolithic migration hypothesis in its original forms (Ammerman & Cavalli-Sforza 1971; 1984; Renfrew 1987) never stated that demic expansion and cultural diffusion were mutually exclusive. Nonetheless, it has been criticized from both the archaeological and the population genetic communities (Zvelebil & Dolukhanov 1991; Richards *et al.* 1996) for being overly global as well as underestimating the contribution of local indigenous Mesolithic foragers in the adoption of agricultural techniques. However, recent mitochondrial and Y-chromosomal DNA studies concur that the average contribution of individuals whose lineages originated from the ancient Near East to the European population is of the order of 20–25% (Richards *et al.* 2000; Semino *et al.* 2000). This frequency is, moreover, clinal in distribution with its highest values in Greece and in the Balkans, decreasing to near-0% frequencies in northwestern Europe where indigenous Mesolithic cultures are most likely to have adopted agro-pastoral techniques. Likewise, the distribution of painted pottery and anthropomorphic clay figurines declines

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as one traverses Europe from the southeast to the northwest, suggesting that indigenous Mesolithic populations, while adopting technical agricultural methods, chose not to adopt the symbolic/ideological/stylistic processes of pre-fired painted ceramics and figurines during the Neolithic period.

The archaeological model of demic expansion in southeastern Europe (van Andel & Runnels 1995) proposes that Neolithic migrations from the Konya plain of south-central Anatolia (Hacilar, Can Hasan, Çatal Höyük) first settled on the riverine regions of Thessaly around 7000 BC. The concentration of early Neolithic sites in Greece is densest on the Thessalian floodplains, while indigenous Mesolithic sites are more frequent in the coastal areas of southern and eastern Greece. In addition, Perlès (2001) underscores the evidence that there may have been multiple events from a variety of locations in the Near East contributing to agro-pastoralism in southeastern Europe. Moreover, with Early Neolithic Greece, there is much regional variation in the distribution of figurines and in the styles of painted pottery (Andreou *et al.* 1996). This suggests that local processes, not yet resolvable at the current haplotype level, have been important in the development of Neolithic material culture.

Thus three basic approaches can be used to explain the presence of Neolithic pottery and figurines in southeastern Europe:

1 independent development without contact with Anatolia and the Near East;
2 spread of ideas and practices without a significant population movement from Anatolia and the Near East; implying a continuous presence of related peoples in southeast Europe throughout the Palaeolithic–Neolithic continuum;
3 actual migrations of populations conveying symbolic and ritual practices.

In this work we will statistically test the third hypothesis outlined above; i.e., there is an association between the frequency of Y-chromosome haplotypes in current populations linked to flows from Neolithic communities in the Levant and Anatolia and the appearance of painted pottery and anthropomorphic figurines in specific Neolithic sites. It is important to recognize that possible links between independent lines of evidence like specific Y-chromosome lineages and items of material culture does not imply there is any inherent association between a particular gene or haplotype and specific cultural or behavioural traits. Such parallelisms may only be reflective of a historical episode of specific temporal and spatial context.

Population genetic background

Considerable recent progress in determining evolutionarily stable Y-chromosome sequence variation from the non-recombining region (NRY) has now made it possible to elucidate more fully the paternal heritage of human populations (Underhill *et al.* 2000). Although patterns of Y-chromosome variation reflect just the history of a single genetic locus, and thus must be interpreted cautiously, the unequivocal sequential accumulation of DNA variation during the lineal life spans of these haplotypic molecules provides new insights into the origins, affinity and diversification of populations. This provides an alternative perspective for recovering aspects of genetic prehistory. Specifically, the particular distinctive clinal patterns of NRY haplotypes over space mark trajectories of gene flow and, by inference, the origins and movement of populations (Underhill *et al.* 2001). The combination of binary polymorphism haplotype frequency *plus* related diversity associated with more rapidly mutating microsatellite polymorphisms reveals the directionality of gene flow.

Although genetic clines can occur because of natural selection or continuous gene flow between adjacent populations with distinctive molecular signatures, these data are also consistent with repopulation events in southeast Europe since the Last Glacial Maximum. Early Y-chromosome studies of two distinctive lineages revealed a contrasting geographic frequency pattern (Semino *et al.* 1996). The distribution of the 8kb allele at the 12f2 locus ranged from 45–60% in Syria, Lebanon, Israel, and the Zagros mountain areas of Iran to 30–40% in Greece, Cyprus, Crete and Turkey, 10–30% in Italy and the Balkan countries and less than 10% in the rest of Europe. This has been confirmed by additional, independent studies (Mitchell *et al.* 1996; Rosser *et al.* 2000; Quintana-Murci *et al.* 2001) (see FIGURE 1a). Alternatively, another lineage (ht 15) affiliated with the 49a,f locus displayed an opposing distribution that was interpreted as a signature of Palaeolithic heritage. Interestingly, another Y-chromosome lineage (ht 4) with a derived approximately 300 base pair Alu insertional element is widely distributed in a circum-Mediterranean pattern (Hammer *et al.* 1997). The highest frequency occurs among the Berbers and Arabs of northwest Africa (70–80%) decreasing to 40–50% among the Algerians and Egyptians, 20–40% in Greek, Cypriot and Lebanese populations and 10–20% in Syria, Israel, Turkey and Southern European regions (Hammer *et al.* 1997; Rosser *et al.* 2000; Bosch *et al.* 2001) (see FIGURE 1a).

Since there is essentially no recombination associated with the Y-chromosome, both the 12f2 8 kb and Hammer *et al.*'s (1997) YAP defined ht 4 lineages have distinctive, independent primogenitors. The common geographic distribution of both haplotypes suggests that the original populations in the Levant and Anatolia contained descendants of both forefathers at the time(s) of dispersal. A recent study of 25 populations in Europe and the Levant (Semino *et al.* 2000) showed that 95% of the European paternal gene pool is comprised by 10 distinctive high-resolution Y-chromosomal lineages. Some of these lineages were analogous to the 12f2 8kb and YAP ht 4 lineages. Specifically, 12f2 8 kb corresponds to Eu9 (M172) and Eu10 (M89), while Eu4 (M35) corresponds to YAP ht 4. Semino *et al.* (2000) note that other genetic data (49a,f, ht 8) from the Y-chromosome indicate that Eu11 (M201) lineages and 12f2 8-kb lineages may share a common ancestor. Almost all the Eu10 samples where subsequently determined to have the 12f2 8 kb allele (unpublished results) This work showed that the four above Eu lineages demonstrated a clinal distribution in frequencies from the Near East to northwest Europe. Thus Eu9, Eu10, Eu11 and Eu4 comprise a consistent set of Y-chromosomal markers that have been postulated to trace the migration of Near Eastern Neolithic agro-pastoralists to Europe. Here we use the Semino *et al.* data to demonstrate a significant concordance between lineages with a presumed Near Eastern provenance and the occurrence of Neolithic painted pottery and figurines.

Archaeological record

Of the 25 populations in the Semino *et al.* (2000) paper, 15 were scored as containing a large collection of local Neolithic figurines, while 10 were not. The following regions and their Neolithic referent populations were scored as figurine positive: Syria, Lebanon, Turkey (PPNB); Georgia (Trans-Caucasia, Mongait 1959); Ukraine (Tripolye, Zbenovich 1996); Hungary, Macedonia, Greece, Croatia (Sesklo, Starcevo, Karanovo, Körös, Vinča and Criş); Albania (Petruso 1993); Czech Republic/Slovakia (Lengyel); Calabria (Genick 1993); Sardinia (Bonu Ighinu and Ozieri); Central-Northern Italy (Arene Candide) and France (Montjardin & Roger 1993). Conversely, areas scored as 'Neolithic figurines largely absent' were Andalusia and Catalonia, because of the argument (Renfrew 1967; Chapman 1990) that Chalcolithic 'idols' are stylistically different and arose independently from the anthropomorphic figurines of southeast Europe; French Basque and Spanish Basque; Netherlands; Germany; Poland; the Saami area of Northern Scandinavia; and the Udmurt and Mari cultures of Russia.

The distribution of painted pottery was narrower than that of Neolithic figurines. France, Sardinia, Central-Northern Italy and Czech Republic/Slovakia were excluded from the geographic regions that demonstrate the presence of Neolithic pre-fired painted pottery (see FIGURE 1b).

Statistical methods

The Y-chromosomal frequency data of Eu4, Eu9, Eu10 and Eu11 of Semino *et al.* (2000) for the 25 regions under investigation were analysed for the presence *versus* the absence of Neolithic painted pottery and figurines found in sites within each region.

T-tests were performed comparing the frequencies of the four haplogroups in the 15 figurine present (fig+) populations to the 10 figurine absent (fig–) populations and in the 11 painted pottery present (paint+) to the 14 painted pottery absent (paint–) populations. Additionally, two stepwise logistic regressions with figurines present *versus* absent and painted pottery present *versus* absent as the predicted classifications were performed using the four haplogroup frequencies as the predictor variables to be entered into the regression. All analyses were performed using the SPSS 11.0 computational statistics application.

Results

TABLES 1 & 2 show the comparison of means between the population groups (fig+ *versus* fig–) and (paint+ *versus* paint–) for the four Y-chro-

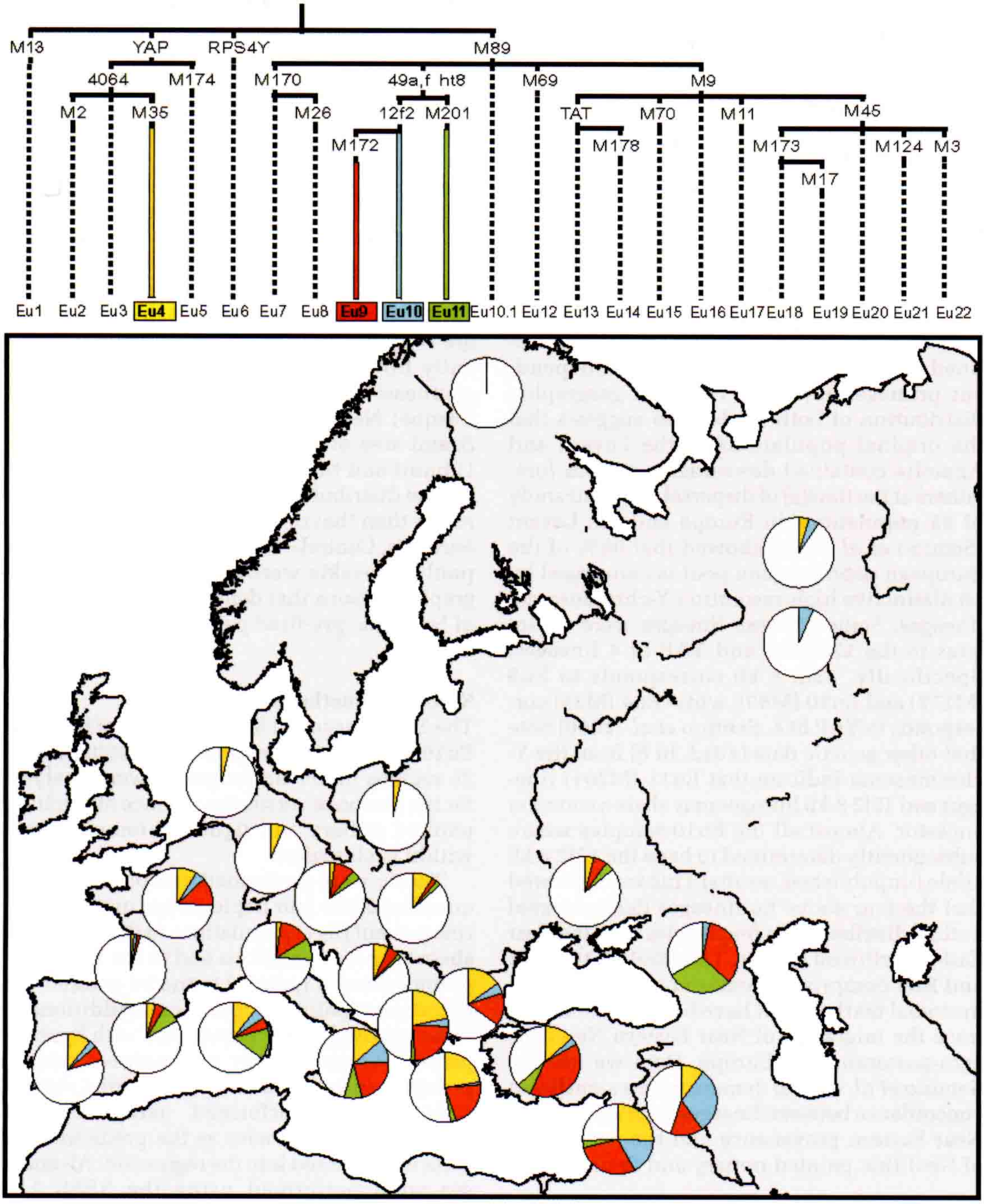

FIGURE 1a. Top: *maximum parsimony phylogeny of Middle Eastern Y chromosome lineages possibly associated with the transition to agro-pastoralism. Note that the 49a,f ht 8 node should be considered tentative, since recurrent mutation can occur in the complex 49a,f polymorphic system. However, the fact that 49a,f ht 8 and its derivatives are only observed in 12f2, 8kb and M201 defined lineages strongly suggests that they share a common ancestor.* Bottom: *Frequency distributions of relevant haplotypes reproduced from Semino* et al. *2000.*

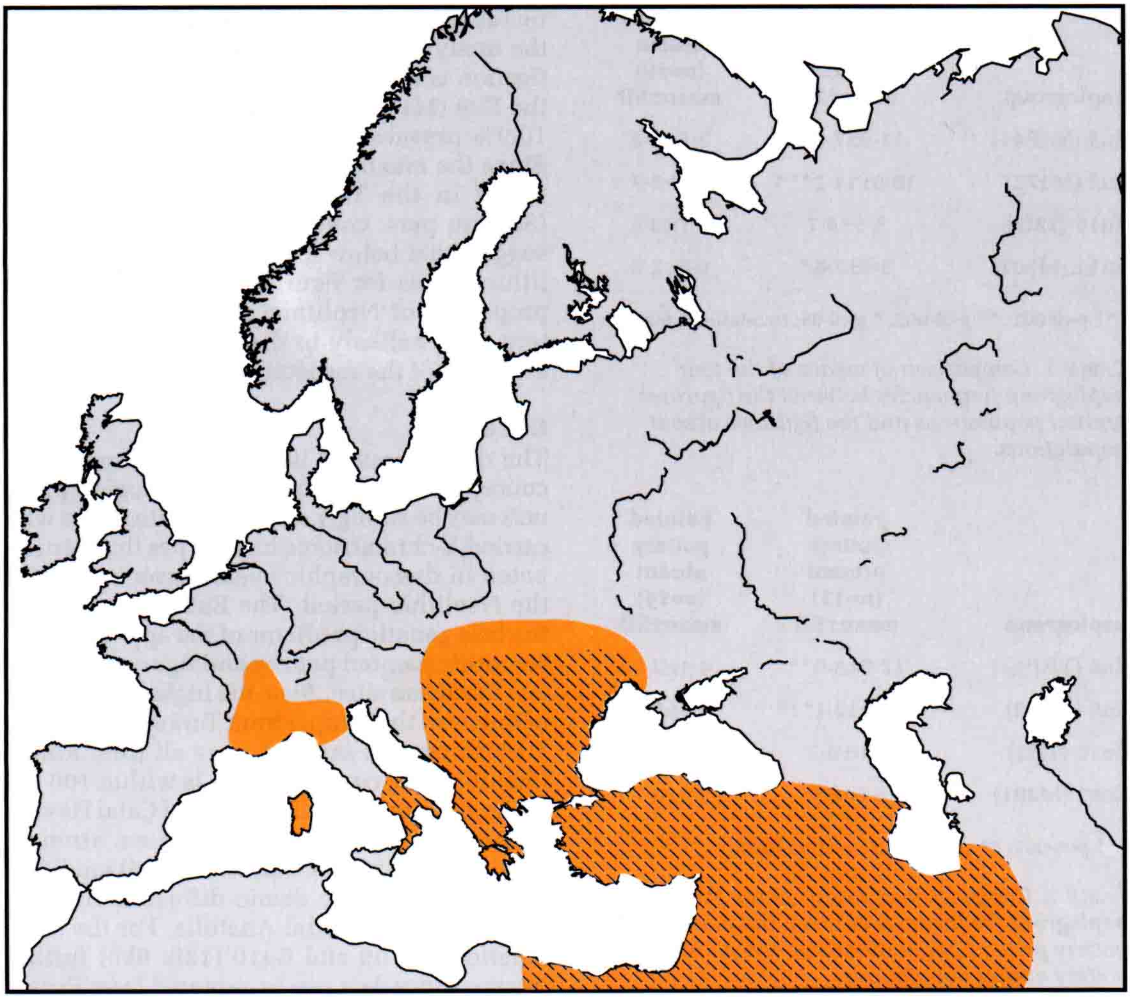

FIGURE 1b. *Approximate regional distributions of Neolithic figurines* (orange) *and Neolithic painted pottery* (hatched).

mosome haplogroup frequencies from the Semino *et al.* (2000) paper. As predicted, both the 12f2 8 kb related Eu9 (M172) and the Eu4 (YAP4+) haplogroups were significantly more common among present-day populations in regions which during the Neolithic period constructed anthropomorphic figurines and decorated pottery with pre-fired painting. In addition, the group Eu11 (M201) also significantly predicted the presence of figurines. The results for Eu10 (8 kb) were similar whether or not data from the two Urals populations was included in the analysis. The stepwise logistic regressions (TABLE 3) sequentially entered the four-haplogroup frequencies in order to predict fig+/– and paint+/– group memberships. Only the Eu9 (M172) haplogroup successfully predicted the distribution of both Neolithic figurines (88% accuracy) and painted pottery (80% accuracy). Neither Eu4 nor Eu11 added significant predictive ability to the regression after controlling for the contribution of Eu9. For the logistic regression of figurine distribution, Andalusia and the French Basque regions were predicted to contain figurines, while Hungary was predicted not to contain figurines. For painted pottery, the logistic regression predicted that France and Central-Northern Italy would contain painted pottery, while Croatia, Hungary and the Ukraine would not. The non-linear character of a logistic regression allows one to find the point of inflection where the logis-

haplogroup	figurines present (n=15) mean±SD	figurines absent (n=10) mean±SD
Eu4 (YAP4+)	11·0±7·8**	3·5±3·2
Eu9 (M172)	16·9±11·2***	1·6±2·7
Eu10 (12f2)	5·5±8·1	1·7±2·5
Eu11 (M201)	5·9±7·8*	0·8±2·5

*** p<0·001; ** p<0·005; * p<0·05; two-tailed t-test

TABLE 1. *Comparison of means of the four haplogroup frequencies between the figurines present populations and the figurines absent populations.*

haplogroup	painted pottery present (n=11) mean±SD	painted pottery absent (n=14) mean±SD
Eu4 (YAP4+)	12·9±8·0**	4·1±3·5
Eu9 (M172)	19·3±12·1***	4·1±5·0
Eu10 (12f2)	6·6±9·2	1·9±2·5
Eu11 (M201)	5·6±8·5	2·6±4·7

*** p<0·002; ** p<0·005; two-tailed t-test

TABLE 2. *Comparison of means of the four haplogroup frequencies between the painted pottery present populations and the painted pottery absent populations.*

variable	B	SE	Wald	DF	significance
1 figurines±					
Eu9 (M172)	0·531	0·246	4·66	1	0·031
constant	–2·53	1·22	4·30	1	0·038
2 painted pottery±					
Eu9 (M172)	0·208	0·082	6·50	1	0·011
constant	–2·27	0·89	6·49	1	0·011

The logistic regression for figurines entered Eu9 (M172) haplogroup frequencies at the first step: Chi-squared=20·16; DF=1; p<0·001. No other variable met criteria for entering after Eu9 was entered. Similarly for painted pottery, only Eu9 predicted membership in this category (Chi-squared=14·04; DF=1; p<0·001.

TABLE 3. *Stepwise logistic regressions predicting figurines and painted pottery present* versus *absent from the four haplogroup frequencies.*

tic function most steeply shifts from 0 to 1. For the analyses performed here the point of inflection is at the level of a 4·8% prevalence of the Eu9 (M172) haplotype for figurines and a 10·9% prevalence of Eu9 for painted pottery. Since the maximal frequency of Eu9 (40%) is found in the Turkish sample from Konya (Semino pers. comm.), the regression would suggest that below a 12% proportion of 'Neolithic' genes for figurines and below a 27% proportion of 'Neolithic' genes for painted pottery, it is unlikely to discover archaeological evidence of the respective material cultures.

Discussion

The data presented in this report support the concept that certain symbolic/ideological products may be strongly associated with males who carried Y-chromosome haplotypes that participated in demographic events associated with the Neolithic period. The Eu9 haplogroup is the best genetic predictor of the appearance of Neolithic painted pottery and figurines at various European sites. Also, the highest frequency of Eu9 is in the sample from Turkey (40%). The Turkish genetic samples were all from Konya (Semino pers. comm.) which is within 100 km of the significant Neolithic site of Çatal Höyük. The results of this paper, therefore, strongly support van Andel & Runnels' (1995) modified model of Neolithic demic diffusion originating from south central Anatolia. For the combination of Eu9 and Eu10 (12f2 8kb) further interpolatory data can be garnered from Rosser *et al.* (2000). Cyprus with a 12f2 8kb frequency of 33% and Bulgaria with 12% exhibit both relatively high proportions of the 12f2 8kb haplotype and densely settled early Neolithic sites (van Andel & Runnels 1995).

The outliers to the logistic regression raise important *caveats*. The Andalusian and French Basque regions were predicted to contain sites with Neolithic figurines, but were scored as figurines absent. The 5–10% frequency of the Eu9 (M172) haplotype in these areas may reflect the historically attested Greek and Phoenician colonization of the southern Iberian Peninsula. Likewise Hungary, Croatia and the Ukraine, which contain sites of Neolithic painted pottery, had low frequencies of the Eu9 haplotype (2–6%). Perhaps Mesolithic populations in these regions indigenous independently utilized anthropomorphic figurines and painted pottery concurrently with the transition to agro-pastoralism. It is noteworthy, on a microgeographic scale, that western Romania has a high frequency of the 12f2 8kb haplotype (17–32%) (Stefan *et al.* 2001). Thus west of the Danube bend and east of the Carpathians there is a sharp decline in 12f2 8kb frequency.

From a more global cultural perspective, the association between the Eu9 (M172) and Eu4 (YAP4+) haplotypes and Near Eastern and southeastern European populations offers supportive evidence for a migration and/or significant demographic interaction between PPNB cultures of the Near East and indigenous societies of Mediterranean and southeastern Europe. Other cultic products appear in the Near East and in southeastern Europe, along with the figurines and painted pottery, such as the building models made of clay, the burial of cultic objects, the presence of dancing scenes and zoomorphic cattle figurines (Garfinkel 1998). The population genetic data do not resolve the issue of the 'meaning' of the figurines; it is equally consistent with the variety of current interpretations (Hamilton 1996).

Although the associations found in this work support a modified Neolithic migration and subsequent interaction/exchange with indigenous Mesolithic foragers, accurate dating of the Eu9 (M172) mutation and expansion is difficult to pinpoint. Nebel *et al.* (2001) suggest a 5000 BC date of the M172 demographic event based on microsatellite data associated with this lineage, while Zhivotovsky proposes a 30000 BC date (pers. comm.). Uncertainties regarding microsatellite mutation rate estimates and population dynamics are the main explanations for the discrepancy. Fortunately, good dating is available for the archaeological material. It is probable that M172 originated in the Near East during the late Upper Palaeolithic/Epi-Palaeolithic and subsequently spread to southeast Europe. The perimeter of its spread almost precisely delimits the range of Neolithic painted pottery and clay figurine assemblages. Recovering historical events is best achieved *via* an integrative multidisciplinary approach (Brown & Pluciennek 2001; Bellwood 2001). The recent ability to define high-resolution evolutionarily stable Y-chromosome haplotypes in extant populations provides new opportunities for testing hypotheses in prehistorical studies. Further support of inferences gleaned from contemporary phylogeographic data await the refinement of ancient nuclear DNA methodology applied to Neolithic samples from key archaeological sites.

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