

Differential Y-chromosome Anatolian Influences on the Greek and Cretan Neolithic

R. J. King¹, S. S. Özcan², T. Carter³, E. Kalfoğlu², S. Atasoy², C. Triantaphyllidis⁴, A. Kouvatsi⁴, A. A. Lin⁵, C-E. T. Chow⁵, L. A. Zhivotovsky⁶, M. Michalodimitrakis⁷ and P. A. Underhill^{5,*}

¹Department of Psychiatry and Behavioral Sciences, 401 Quarry Road, Stanford University, Stanford, CA 94305-5722

²Institute of Forensic Sciences, Istanbul University, Istanbul, Turkey

³Department of Anthropology, McMaster University, Chester New Hall 524, 1280 Main Street West Hamilton, L8S 4L9, Ontario, Canada

⁴Department of Genetics, Development and Molecular Biology, School of Biology, Aristotle University, Thessaloniki, 54124 Thessaloniki, Greece

⁵Department of Genetics, Stanford University School of Medicine, 300 Pasteur Drive, Stanford, CA 94305-5120

⁶N. I. Vavilov Institute of General Genetics, Russian Academy of Sciences, 3 Gubkin Street, Moscow, 119991, Russia

⁷Department of Forensic Science, University of Crete, Heraklion, Greece

Summary

The earliest Neolithic sites of Europe are located in Crete and mainland Greece. A debate persists concerning whether these farmers originated in neighboring Anatolia and the role of maritime colonization. To address these issues 171 samples were collected from areas near three known early Neolithic settlements in Greece together with 193 samples from Crete. An analysis of Y-chromosome haplogroups determined that the samples from the Greek Neolithic sites showed strong affinity to Balkan data, while Crete shows affinity with central/Mediterranean Anatolia. Haplogroup J2b-M12 was frequent in Thessaly and Greek Macedonia while haplogroup J2a-M410 was scarce. Alternatively, Crete, like Anatolia showed a high frequency of J2a-M410 and a low frequency of J2b-M12. This dichotomy parallels archaeobotanical evidence, specifically that while bread wheat (*Triticum aestivum*) is known from Neolithic Anatolia, Crete and southern Italy; it is absent from earliest Neolithic Greece. The expansion time of YSTR variation for haplogroup E3b1a2-V13, in the Peloponnese was consistent with an indigenous Mesolithic presence. In turn, two distinctive haplogroups, J2a1h-M319 and J2a1b1-M92, have demographic properties consistent with Bronze Age expansions in Crete, arguably from NW/W Anatolia and Syro-Palestine, while a later mainland (Mycenaean) contribution to Crete is indicated by relative frequencies of V13.

Keywords: Y-chromosome diversity, Neolithic Greece, Crete, bread wheat, maritime migration, Bronze Age

Introduction

The earliest archaeological evidence for Neolithic economies in SE Europe dates to c. 7000 cal BC, with the founding of a fully-fledged farming community at Knossos on the island of Crete, followed slightly later in the NW Peloponnese of mainland Greece (Efstratiou 2005; Perlès 2001: pp84–95; Runnels 2003). Concerning the origins of

agriculture in these Aegean contexts, it is an uncontested fact that both plant and animal husbandry first emerged at an earlier date in regions to the east, namely Anatolia, Cyprus and the Levant (Colledge et al., 2004; Rowley-Conwy 2003). The question thus becomes one of how Neolithic farming economies came to be introduced into SE Europe and from which external region(s) did the impetus originate? The argument is often polarized between two distinct models, namely: demic expansion of agropastoralists versus the cultural transmission of ideas (Pinhasi et al., 2005; though see Kotsakis 2003; Tringham 2000), the debate drawing upon a wide range of evidence, including archaeology, genetics and linguistics (Bellwood 2001).

* Corresponding author: Peter A. Underhill, Department of Genetics, 300 Pasteur Drive, Stanford University School of Medicine, Stanford, CA 94305-5120, Fax: 650 725 1534. phone: 650 723-5805. E-mail: under@stanford.edu

In Crete, the process of 'neolithisation' appears to be relatively straightforward. With the island seemingly uninhabited prior to its colonization by Neolithic farmers (whose associated domestic animals and plants were foreign to Crete), research has thus focused largely on these peoples' overseas origins and the routes by which they traveled (Broodbank & Strasser 1991; Efstratiou 2005: pp146–148). The situation on mainland Greece (henceforth 'Greece') is more complex, as here we do have evidence for a Mesolithic heritage (Galanidou & Perlès 2003; Runnels 2001), with a potential for contact between natives and migrants in the NW Peloponnese (Runnels 2003: pp126–127).

While patterns of genetic diversity in SE Europe and the eastern Mediterranean often display gradients (Cavalli-Sforza et al., 1994; Semino et al., 2000), distinguishing those that might have related specifically to the spread of farming remains challenging. That said, data from the haploid Y-chromosome does seem to support the movement of Anatolian/Levantine agro-pastoralists from their SW Asian origins towards SE Europe (Semino et al., 2000). More specifically haplogroups E and J have been proposed as possible signatures of this dispersal (Semino et al., 2004), with a significant correlation between haplogroups E3b and J2 and the distribution of certain distinctive types of Neolithic material culture, from the Levant, via SE Europe, to parts of the east and central Mediterranean (King & Underhill 2002).

Turning to the Aegean specifically, while this region has experienced post-Neolithic gene flows (Renfrew 1996: pp15–16), we emphasize the fact that the impact of founder effect is often maximal in situations when migrants settle previously unoccupied territory, as with Crete (Edmonds et al., 2004; Klopstein et al., 2006). With demographic population expansions following initial colonization, it is possible that these genetic variants will persist and be detectable. Similarly, many of the localities in Greece that were first settled by Initial Neolithic [IN] agriculturalists appear to have been unoccupied for some time prior to the establishment of settled farming communities (Perlès 2001, 2003, Runnels 2003, Kotsakis 2003), a situation that could also lead to the retention of genetic varieties introduced by these early migrant agriculturalists.

Patterns of Y-chromosome diversification also offer the possibility to dissect other prehistoric events subsequent to the arrival of Neolithic pioneers (Novelletto 2007). Recent Y-chromosome surveys concerning Greece (DiGiacomo et al., 2003) and Crete (Malaspina et al., 2001; Martinez et al., 2007) discuss Neolithic migrations in the Mediterranean. In addition, other studies have supported the notion of one or more subsequent migrations into SE Europe (Cavalli-Sforza et al., 1994; DiGiacomo et al., 2004; Semino et al., 2004), poten-

tially supporting earlier archaeological claims that population movements played a role in the emergence of the Aegean's great Bronze Age cultures of the 3rd and 2nd millennia BC: the so-called Minoans of Crete and the mainland Mycenaeans (Caskey 1960: pp301–302; Coleman 2000; Hood 1990; Renfrew 1987, 1996).

As a means of understanding the complexities of the neolithisation process in SE Europe and the Aegean, and the role of alleged population expansions at the start of the Neolithic, we investigate the components of the Y-chromosome phylogenies of Crete and Greece. The results of the study are then contrasted with data from a larger Mediterranean, SW Asian and Arabian context. This report investigates the local, micro-geographic variation of Y chromosome haplotypes, data that suggests strongly that the demic diffusion model has merit, whereby in the discussion section we address the following issues: 1) What is the degree of affinity between the pioneer Neolithic agriculturalists of Greece and Crete? 2) By extent, what does the combined genetic and archaeological data inform us with regard to the regional source(s) of these early farmers? 3) What do the genetic data tell us with regard to post-Neolithic migrations to Crete and the role of demographic change in the emergence of the Bronze Age 'Minoan' culture?

Methods

Sampling Rationale and Details

Using an informed consent process, 193 healthy adult males from the four main prefectures of Crete were sampled for DNA, a not entirely dissimilar strategy to that proposed by Renfrew for a study of the island's molecular genetic history over a decade ago (Renfrew 1996: p16). These samples from Crete are independent from those reported in Martinez et al. (2007). A further 171 males were sampled from three areas in Greece in villages near known Initial Neolithic [IN] and Early Neolithic [EN] sites (Figure 1). These comprised Central Macedonia near the site of Nea Nikomedeia ($n = 57$); Thessaly within the southeast Larissa basin ($n = 30$) and near Sesklo/Dimini ($n = 27$); and in the NW Peloponnese, near the Franchthi Cave ($n = 21$) and Lerna ($n = 36$). Only individuals whose paternal grandfather was from the designated areas were sampled.

Y-chromosome Polymorphisms

Binary polymorphisms were genotyped either by DHPLC, RFLP or direct sequencing methodology following the hierarchy of the Y-chromosome phylogeny. The majority of the binary markers have been previously described (Cinnioğlu et al., 2004; Cruciani et al., 2006; Sengupta et al., 2006; Shen et al., 2004; Underhill et al., 2001). We report for the first time a new

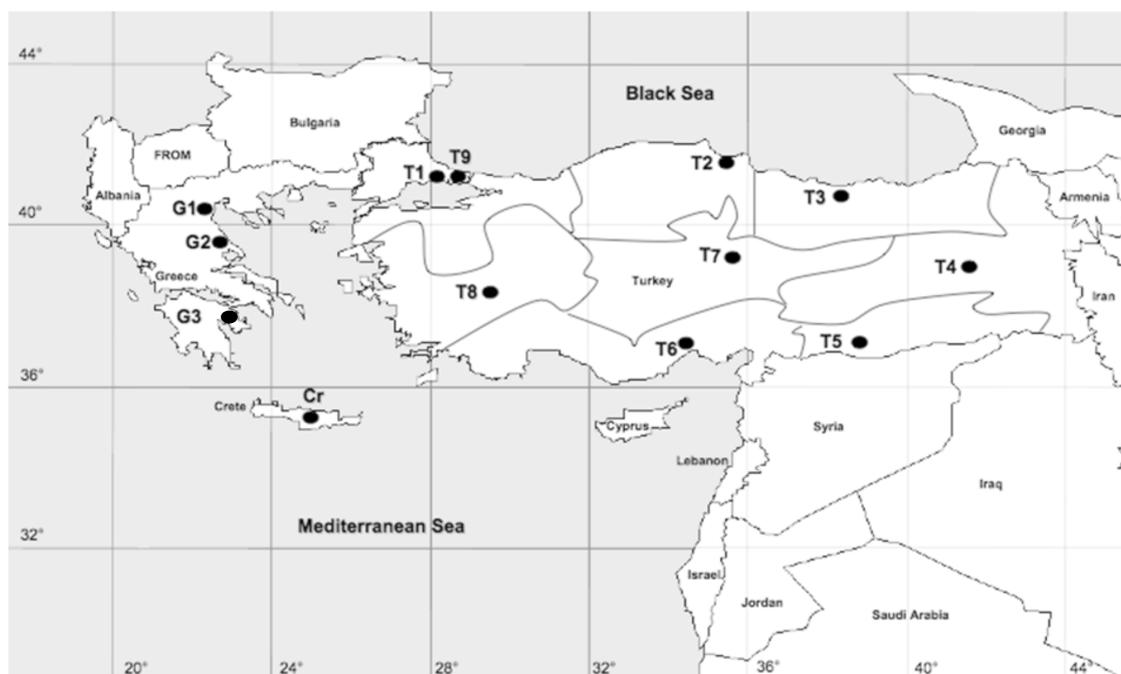


Figure 1 Map of sample locations. The T1-T9 data points indicate the nine geographic regions in Turkey (Cinnioğlu et al., 2004). Data point correspondences: Cr (Crete); G1 (Nea Nikomedeia); G2 (Sesklo and Dimini); G3 (Lerna and Franchthi Cave).

T to G transversion substitution that defines an informative G2 sub-clade. The M406 site occurs at position 81 within a 370 nucleotide amplicon defined by the following PCR primers: F: 5'-CCCCAAAAGCTATTCTGTAA-3' and R: 5'-GAAGCACTTTAGAGCAGGG-3'. All of the samples were also genotyped at 10 Y microsatellite loci previously described (Cinnioğlu et al., 2004) to compute mean haplotype variance within specific haplogroups defined by the binary markers. In addition, both the dinucleotide DYS413 and DYS445 tetranucleotide microsatellite loci were also analyzed in all hgHG J2a-M410 related lineages.

Statistical Analysis

Analysis of molecular variance (AMOVA [Excoffier et al., 1992]) with pairwise F_{st} analysis of the haplogroup frequencies comparing Crete and the three Greek areas was performed using the Arlequin 2000 program (Schneider et al., 2000). To locate our data within a broader SW Asian and Mediterranean context a PC analysis was performed using published haplogroup frequencies from 16 Middle East and SE European regions, nine regions from Anatolia, together with the Crete and Greek samples.

Ten YSTR loci DYS19, DYS388, DYS389I(CD), DYS389II(AB), DYS390, DYS391, DYS392, DYS393, DYS439 and DYS461(A7.2) were genotyped on haplogroup J2a-M410, J2b-M12, E3b1a2-V13 backgrounds. To ascertain the STR affinities between the three Greek regions, Crete and Anatolia, a PC analysis was performed on the 10 STR repeat scores on all M410 (xM319) backgrounds using the Rst covari-

ance distance metric (Slatkin 1995). The M319 chromosomes were excluded because of their outlier microsatellite pattern on Crete (Malaspina et al., 2001, Martinez et al., 2007). See Electronic Supplementary Material as Table S1 in the online edition for YSTR haplotypes.

Expansion times on selected M410 terminal backgrounds (M92 and M319) in Crete, and M12 and V13 backgrounds in Greece, were calculated using the method and evolutionary mutation rate of Zhivotovsky (2001, 2004). See Electronic Supplementary Material as Table S2 in the online edition for YSTR haplotypes.

Results

A total of 32 binary polymorphisms were typed to define 24 informative haplogroups. Figure 2 illustrates the Y-chromosome haplogroup phylogenetic relationships and frequencies for the observed haplogroups in the three Greek regions and Crete. In the Greek data overall, the most frequent haplogroups include E3b1a2-V13 (28%), R1b3-M269 (13%), R1a1-M17 (11%), I2a-P37 (9.0%), J2b-M12 (6%). In Crete, the most frequent haplogroups are R1b3-M269 (17%), G2-P15 (11%), J2a1-DYS413* (9.0%) and J2a1h-M319 (9.0%).

The F_{st} analysis of the haplogroup frequencies demonstrates that Crete is significantly different from each of the three sampled Greek locations ($p < 0.001$). In turn, the

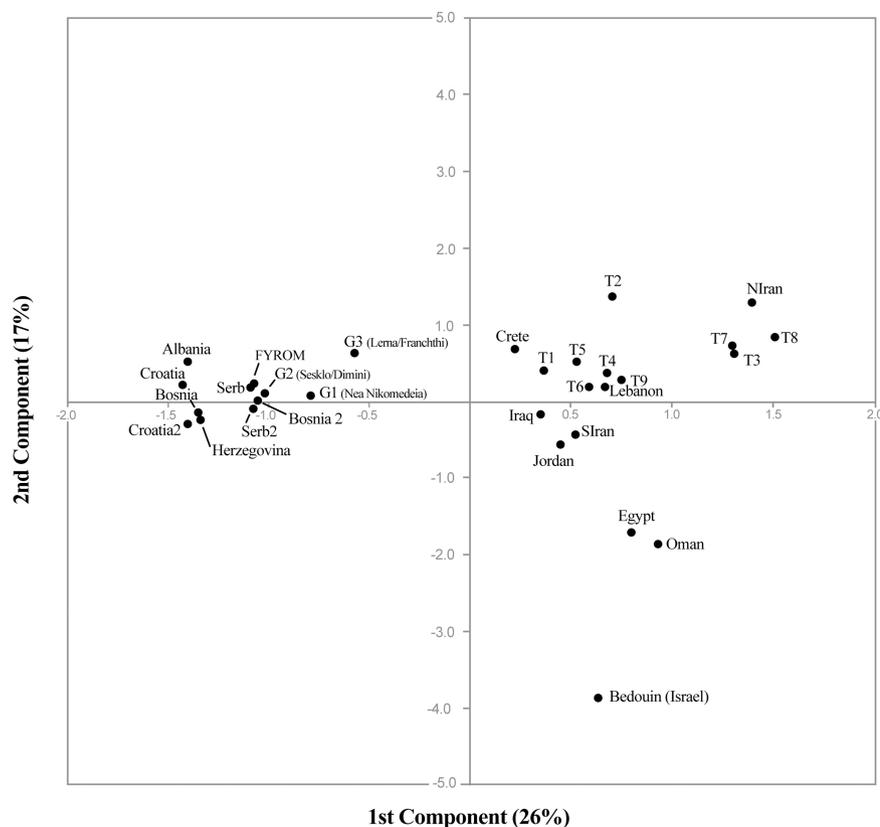


Figure 3 Principal Component Factor Analysis of Middle Eastern and South East European population affinities from the gene pool of Y-chromosome haplogroup frequencies. Albania, Bosnia, Croatia, FRYOM (Former Republic of Macedonia), Herzegovina, Serb (Serbia) Peričić et al. 2005; Bosnia2, Croatia2, Serb2 (Marjanovic et al., 2005); NIran, SIran (Reguerio et al., 2006); Egypt, Oman (Luis et al., 2004); Jordan from Amman (Flores et al., 2005); Iraq (Al-Zahery et al., 2003, Semino et al., 2004); Lebanon (Semino et al., 2000, Semino et al., 2004); Bedouin (Israel), unpublished. The T1-T9 data points indicate the nine geographic regions in Turkey (Cinnioğlu et al., 2004). G1, G2 and G3 labels are the same as given Figure 1.

samples from the Negev tend to form an isolated cluster, distinct from the Greek and Cretan data. Vector analysis (not shown) demonstrates that the Balkan cluster is most associated with haplogroups J2b-M12, E3b1a-M78, I-M170 and R1a1-M17. The Crete and Anatolian cluster was most influenced by J2b-M410 while the Arabian Peninsula and north Egypt cluster by J1-M267.

Since haplogroup J2a-M410 is hypothesized to be associated, at least in part, with the spread of agriculture (Sengupta et al., 2006), a PC analysis of YSTR haplotypes was conducted to investigate the Anatolian contribution to Greece and Crete. Figure 4 shows a plot of the PC factor scores for the three Greek regions, Crete, and the nine Anatolian regions for the M410 (xM319) haplotype data. The plot demonstrates an affinity between both Crete and Lerna/Franchthi Cave and central and Mediterranean

Anatolia (T7/T6), with the two other Greek sample-sites (Nea Nikomedeia and Sesklo/Dimini) forming outliers in the plot. The M319 defined sub-clade was excluded from the PC analysis since its frequency is informative only in Crete.

Estimates of the expansion time should be considered preliminary because of the small sample sizes and inherent uncertainties in the calibration of the YSTR molecular clock. These estimates for J2b-M12 and E3b1a2-V13 from Greece and J2a1h-M319 and J2a1b1-M92 from Crete are given in Table 2. The mean expansion time for J2b-M12 in Greece is consistent with a late Neolithic population expansion (Halstead 1994: p200), while V13 expands in the Peloponnese earlier than the IN presence there indicating that it may reflect a Mesolithic expansion. On the other hand M319 and M92 in Crete both have significantly

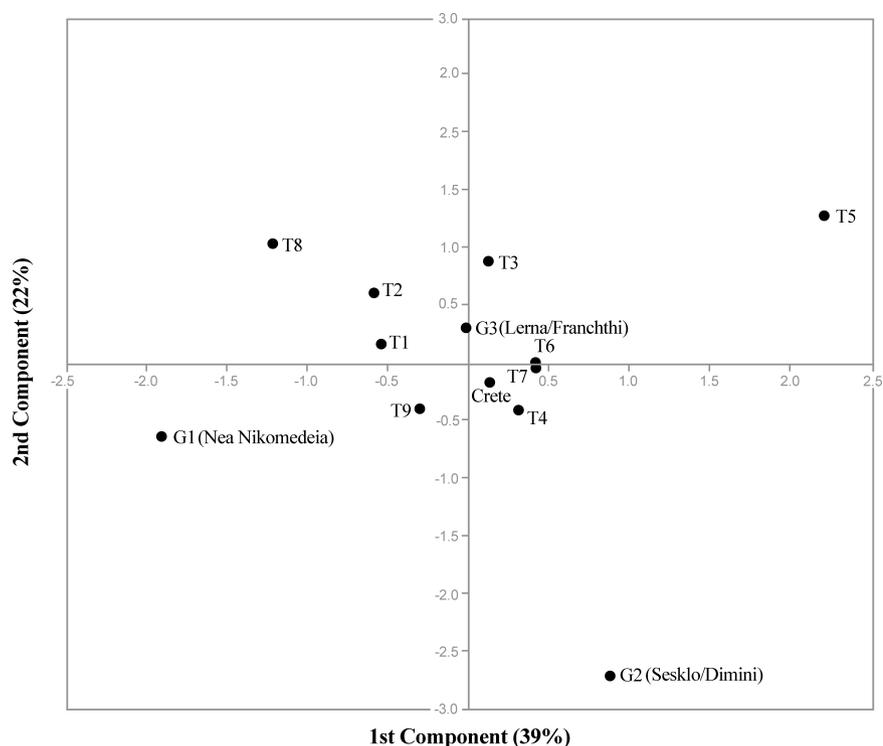


Figure 4 Principal Component Factor Analysis of the affinities of haplogroup J2a-M410 chromosomes (i.e. lineages), without the M319 representatives, from Turkey, Crete and mainland Greece, based upon 10 Y-STR loci. The T1–T9 data points indicate the nine geographic regions in Turkey (Cinnioglu et al., 2004). G1, G2 and G3 labels are the same as given Figure 1.

Table 2 Haplogroup expansion times

Mainland Greece	Sample size	Age (kya)
J2b-M12	10	6.7+/- 3.1
Nea Nikomedeia		
E3b2-V13	6	8.6+/- 4.0
Sesklo/Dimini		
E3b2-V13	20	4.3+/- 1.8
Lerna/Franchthi		
E3b2-V13	20	9.2+/- 4.3
Crete		
J2a1b1-M92	5	5.1+/- 1.5
Crete		
J2a1h-M319	17	5.1+/- 2.2
Crete		
J2b-M12	5	0.9 +/- 0.9
Crete		
E3b2-V13	13	3.1+/- 1.5

later expansion times, dating to the end of the Neolithic / beginning of the Early Bronze Age [EBA]. Haplogroup E3b1a2-V13 has an expansion time in Crete dating to the end of late Bronze Age (1100 BCE) arguably reflecting the presence of a mainland Mycenaean population in Crete.

Discussion

The results of our Y-chromosome survey provide a means to compare and contrast the role of migration in the establishment of the first Neolithic farming economies in Greece and Crete. Archaeological links had previously been drawn between the first settlers of Knossos and their central Anatolian predecessors/contemporaries, based on their common use of mud-brick technology and shared suites of domesticates, with particular reference made to bread wheat (*Triticum aestivum*). This is the predominant cereal from the earliest levels at Knossos (Evans 1994: p5), well attested in Anatolia, yet rare, if not completely absent from the archaeobotanical record of most Balkan and Greek IN sites (Perlès 2001: p62, p155). Moreover, a recent survey of archaeobotanical data has demonstrated that the suite of plants (including invasive weeds) recovered from the earliest levels of Knossos are known not only from earlier sites in central and Mediterranean Anatolia, but also Cyprus and the Levant (Colledge et al., 2004: pp42–44, Figs. 6–7). Our Y-chromosome data allows us to explore the issue of possible parallelisms with the botanical patterns. For example, haplogroup J2a-M410 is frequent in central and

Mediterranean Turkey (Cinnioğlu et al., 2004) and Crete but rare in the northern Greek Neolithic sites (Figure 2). Furthermore the J2a1k-DYS445 sub-clade (Schrack et al., 2006) is present on Crete (Heraklion prefecture, 3.8%) and also occurs at high frequencies (7.3%) in regions T6 and T7. On the other hand, in Greece, the most frequent J2 haplogroup is J2b-M12 that is however rare (1.7%) in Anatolia (Cinnioğlu et al., 2004). In general when all Y-chromosome data are considered, Crete clusters with near Eastern populations whereas mainland Greece groups with Balkan populations (Figure 3). Within mainland Greece there is differentiation among the three sampling sites. Most notable is Lerna/Franchthi Cave, in the Peloponnese region, which displays affinity to Crete with the exception of haplogroup E3b1a2-V13. This could reflect regional interaction between Crete, Peloponnese and Anatolia.

The presence of haplogroups I and R1b in Crete are similar to levels reported by Martinez et al. 2007. The variety of haplogroup I in Crete is I2-M438* rather than I2a-P37 which predominates in the Balkans. Interestingly, haplogroup R1b YSTR haplotypes showed affinity to those of Italy rather than the Balkans (Martinez et al., 2007). Moreover, the PC plot (Figure 4) of J2a(xM319) linked YSTR haplotypes shows a close genetic relationship between Crete and central / Mediterranean Anatolia (T6 & T7). The genetic data thus appears to support the long-held theory that the island's colonists came from Anatolia (Evans 1921: p14), specifically those in those areas where the well-known Neolithic sites of Aşıklı Höyük, Çatalhöyük and Hacilar (region T7), Mersin/Yumuktepe and Tarsus (region T6) were located. Within mainland Greece, only the data from the NW Peloponnese (Lerna/Franchthi Cave) exhibit a high frequency of J2a(xM319) lineages comparable to those in central and Mediterranean Anatolia (Crete to a large degree and Lerna/Franchthi Cave to a lesser degree). The Y-chromosome distinction between the Greek sites is significant as it mirrors other differences between the first farmers of north and south Greece. While Franchthi dates to the beginning of the 7th millennium BC, the IN of Thessaly is nearer the middle of the 7th millennium (Kotsakis 2003: p218; Perlès 2001: pp84–93). The implications are that distinct populations may have in part underwritten the regional differences witnessed in the establishment of farming economies. A much-debated topic is whether the earliest farmers to Greece arrived via terrestrial or maritime colonization routes (Perlès 2005). The absence of J2b-M12 in regions T1 and T8 (Cinnioğlu et al., 2004), i.e. those next to the land bridge from Anatolia to Greece, suggests that the first farmers of Greece and the Balkans are less likely to have come overland.

The Thessalian and Greek Macedonian samples exhibit a high frequency (7–9%) of J2b-M12 with an approximate

expansion time dating to the Neolithic era of c. 5000BC (Table 2). Previous work on the Balkans (Peričić et al., 2005; Marjanovic et al., 2005) regarding the frequency of J2b-M12 is consistent with our observations in Greece. The geographic origin of J2b-M12 remains unknown; however, Cinnioğlu et al., (2004) report its occurrence in SE Anatolia near the Euphrates River (T5) at 4.7%, i.e. the region with some of the first Neolithic communities to have been established beyond the original Levantine core, such as Çayönü, Göbekli Tepe and Hallan Çemi (Cauvin 2000: pp78–91). While the source of J2b-M12 chromosomes in Greece/Balkans remains unclear, it is likely to reside in those regions with an early Neolithic domestic economy based upon unleavened wheat such as present day Syria and the Levant.

The calculated expansion time of haplogroup E3b1a2-V13 in mainland Greece is 8,600 y BP at Nea Nikomedeia and 9,200 y BP at Lerna/Franchthi Cave and is consistent with the late Mesolithic/initial Neolithic horizon. These dates exceed those reported previously for Europe (Cruciani et al., 2007) that date to the Bronze Age. This discrepancy arises mainly because of differences in the choice of mutation rate used. Our choice of the evolutionary mutation rate is based upon its concordance with other episodes of rapid demographic growth (e.g. the Bantu Iron Age expansion in Africa and the colonization of New Zealand by Polynesians (Zhitovtovsky et al., 2004). The expansion of E3b1a2-V13 in Crete provides a consistent internal control our choice of mutation rate. Namely the Late Bronze Age expansion date of 1100 BC coincides with the alleged arrival of mainland Mycenaean Greeks that is well documented in the archaeological and epigraphic record.

The calculation of expansion times of terminal binary mutations from linked YSTR variance yields insight into post-Initial Neolithic demographic events in our study area. In Crete, the binary mutation M319 defines a unique J2a-M410 sub-haplogroup that is rarely observed elsewhere (Martinez et al., 2007). This category of chromosomes was first recognized because of an unusual DYS413 YSTR allelic pattern (Malaspina et al., 2000). The J2a1h-M319 haplogroup confirms this association. A reanalysis of the Anatolian data (Cinnioğlu et al., 2004) shows there were only two such chromosomes in this gene pool. Previously, mutation M319 was also reported in Iraqi and Moroccan Jews at 5% and 10% respectively (Shen et al., 2004). The J2a1h-M319 expansion time in Crete dates to 3100 BC, while haplogroup J2a1b1-M92 also has an expansion time dating to approximately 3100 BC (Table 2). The latter is found at relatively high frequencies in western Anatolia (T1 and T8) (Cinnioğlu et al., 2004; Semino et al., 2004). Our data are consistent with the proposal that haplogroup

J2a1b1-M92 is a signature of Bronze Age expansions in Europe (Di Giacomo et al., 2004).

The archaeological implications of these data are tantalizing. A date of 3100 BC is a highly significant one for Aegean prehistorians, as it marks approximately the boundary between the Neolithic and Bronze Age on Crete (Manning 1995), a period associated with a series of major changes in settlement patterns, demography, material culture, technology, iconography and burial practices. Many scholars have suggested that new influxes of population were responsible for triggering these changes, a sociocultural impetus from which emerged the island's famed Minoan culture. The new features associated with EBA Crete have been linked variously with Egypt/Libya, Syro-Palestine, the East Aegean/NW Anatolia and the Cyclades (Betancourt 2003; Branigan 1988: pp199–200; Evans 1924: px, pxiii; Hood 2000: p21; Nowicki 2002; Warren 1973, 1984). Regarding the purported link to Egypt/Libya, the majority of E3b1-M78 chromosomes are derived at V13, both in Crete and Greece, whereas all samples from northern Egypt lack the V13 SNP (Luis et al., 2004). This suggests that there has not been a recent genetic affinity between Egypt and Crete or Greece. Conversely, the Y-chromosome results do provide data that support population movements from both western and north-western Anatolia (regions T1 and T8) and Syro-Palestine. One can point to another post-colonization population influx into Crete (1100 BC) this time from Greece, as represented by V13 which occurs at ca. 35% frequency in both Thessaly and the Peloponnese while its frequency on Crete is only 7%, indicating a mainland contribution to the Cretan Y chromosome inventory, albeit no more than 20%. Once again, the genetic data resonates with a major debate in Aegean prehistory; that of the processes involved in the 'Mycenaeanisation' of Cretan society towards the end of the Bronze Age. Sometime around the mid 15th century BC, Crete witnessed another series of major sociocultural changes, as evidenced by the adoption of the mainland proto-Greek Linear B script/language, burial practices, iconography and material culture. These cultural transformations have been interpreted by many as indicative of Crete's invasion by its mainland Mycenaean neighbors (Popham 1994; Warren 1973: p45). The Y chromosome data can be taken as further evidence that some of these later Bronze Age changes in Crete were indeed underwritten by an incursion of mainland populace.

One final field of research that our data affects is that of the archaeology of languages. While correlations between genes and languages must be interpreted cautiously, their co-analysis may provide useful insights. The differential phylogenetic pattern of J2a-M410 and J2b-M12 lineages to Crete and southern European respectively are broadly consistent with the model of Renfrew (1998), and with the

linguistic analysis of Gray & Atkinson (2003), that claim an early split of the Anatolian languages from the rest of Indo-European languages around 7000BC. In this model the J2a-M410 speakers in Anatolia and Crete may have been speaking Anatolian related languages that may be reflected in the un-deciphered scripts of the 2nd millennium BC: Cretan hieroglyphic and Linear A (Finkelberg 1997, 2001). Alternatively, the J2a-M410 populations may have been speaking a non-Indo-European language with affinities to the Hattic language of central Anatolia (Nichols 2007).

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References

- Al-Zahery, N., Semino, O., Benuzzi, G., Magri, C., Passarino, G., Torrioni, A. & Santachiara-Benerecetti, A. S. (2003) Y-chromosome and mtDNA polymorphisms in Iraq, a crossroad of the early human dispersal and of post-Neolithic migrations. *Mol Phylogenet Evol.* **28**, 458–72.
- Bellwood, P. (2001) Early agriculturalist population diasporas? Farming, languages and genes. *Annual Review of Anthropology* **30**, 181–207.
- Betancourt, P. (2003) The impact of Cycladic settlers on Early Minoan Crete. *Mediterranean Archaeology and Archaeometry* **3**, 3–12.
- Branigan, K. (1988) *The Foundations of Palatial Crete. A Survey of Crete in the Early Bronze Age*. Amsterdam: Adolf M. Hakkert.
- Broodbank, C. & Strasser, T. (1991) Migrant farmers and the Neolithic colonisation of Crete. *Antiquity* **65**, 233–45.
- Caskey, J. L. (1960) The Early Helladic period in the Argolid. *Hesperia* **XXIX**, 285–303.
- Cauvin, J. (2000) *The Birth of the Gods and the Origin of Agriculture*. Cambridge: Cambridge University Press.
- Cavalli-Sforza L. L., Menozzi P & Piazza A (1994) *The History and Geography of Human Genes*. Princeton: Princeton University Press.
- Cinnioğlu, C., King, R., Kivisild, T., Kalfoglu, E., Atasoy, S., Cavalleri, G. L., Lillie, A. S., Roseman, C. C., Lin, A. A., Prince, K., Oefner, P. J., Shen, P., Semino, O., Cavalli-Sforza, L. L. & Underhill, P. A. (2004) Excavating Y-chromosome haplotype strata in Anatolia. *Hum Genet* **114**: 127–148.
- Coleman, J. E. (2000) An archaeological scenario for the 'Coming of the Greeks' ca. 3200 B.C. *J Indo-European Studies* **28**, 101–153.
- Colledge, S. Conolly, J. & Shennan, S. (2004) Archaeobotanical evidence for the spread of farming in the Eastern Mediterranean. *Curr Anthropol* **45**, 35–58.
- Cruciani, F., La Fratta, R., Torrioni, A., Underhill, P. A. & Scozzari, R. (2006) Molecular dissection of the Y chromosome haplogroup E-M78 (E3b1a): a posteriori evaluation of a microsatellite-network-based approach through six new biallelic markers. *MIB#916 Hum Mutation* **27**, 831–841.
- Cruciani, F., La Fratta, R., Trombetta, B., Santolamazza, P., Sellitto, D., Colomb, E. B., Dugoujon, J. M., Crivellaro, F., Benincasa, T., Pascone, R., Moral, P., Watson, E., Melegh, B., Barbujani, G., Fuselli, S., Vona, G., Zagradsnik, B., Assum, G., Brdiczka, R., Kozlov, A. I., Efremov, G. D., Coppa, A., Novelletto, A. & Scozzari R. (2007) Tracing past human male movements in

- northern/eastern Africa and western Eurasia: new clues from Y-chromosomal haplogroups E-M78 and J-M12. *Mol Biol Evol* **24**, 1300–1311.
- Di Giacomo, F., Luca, F., Anagnou, N., Ciavarella, G., Corbo, R. M., Cresta, M., Cucci, F., Di Stasi, L., Agostiano, V., Giparaki, M., Loutradis, A., Mammi', C., Michalodimitrakis, E. N., Papola, F., Pedicini, G., Plata, E., Terrenato, L., Tofanelli, S., Malaspina, P. & Novelletto, A. (2003) Clinal patterns of human Y chromosomal diversity in continental Italy and Greece are dominated by drift and founder effects. *Mol Phylogenet Evol* **28**, 387–395.
- Di Giacomo, F., Luca, F., Popa, L. O., Akar, N., Anagnou, N., Banyko, J., Brdicka, R., Barbujani, G., Papola, F., Ciavarella, G., Cucci, F., Di Stasi, L., Gavrilu, L., Kerimova, M. G., Kovatchev, D., Kozlov, A. I., Loutradis, A., Mandarino, V., Mammi', C., Michalodimitrakis, E. N., Paoli, G., Pappa, K. I., Pedicini, G., Terrenato, L., Tofanelli, S., Malaspina, P. & Novelletto, A. (2004) Y chromosomal haplogroup J as a signature of the post-Neolithic colonization of Europe. *Hum Genet* **115**, 357–371.
- Edmonds, C. A., Lillie, A. S. & Cavalli-Sforza, L. L. (2004) Mutations arising in the wave front of an expanding population. *Proc Natl Acad Sci U S A* **101**, 975–9.
- Efstratiou, N. (2005) Tracing the story of the first farmers in Greece – A long and winding road. In: *How Did Farming Reach Europe?* (ed. C. Lichter), pp. 143–153. Istanbul: BYAZ 2, Eye Yayinlari.
- Evans, A. J. (1921) *The Palace of Minos at Knossos. Volume I*. London: Macmillan.
- Evans, A. J. (1924) 'Preface', to S. Xanthoudides, *The Vaulted Tombs of Mesara*. London: Hodder and Staughton, University Press of Liverpool, pp. v–xiii.
- Evans, J. D. (1994) The early millennia: continuity and change in a farming settlement. In: *Knossos a Labyrinth of History: Papers Presented in Honour of Sinclair Hood*. (eds. D. Evely, H. Hughes-Brock and N. Momigliano), pp. 1–20. London: British School at Athens, Oxford.
- Excoffier, L., Smouse, P. E. & Quattro, J. M. (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* **131**, 479–91.
- Finkelberg, M. (1997) Anatolian Languages and Indo-European Migrations to Greece. *Classical World* **91**, 3–20.
- Finkelberg, M. (2001) The Language of Linear A: Greek, Semitic, or Anatolian?, In R. Drews (ed.), *Greater Anatolia and Indo-European Language Family. Papers presented at a Colloquium Hosted by the University of Richmond, March 18–19, 2000 Journal of Indo-European Studies*. Monograph Series 38 (Washington) 81–105.
- Flores, C., Maca-Meyer, N., Larruga, J. M., Cabrera, V. M., Karadshah, N. & Gonzalez, A. M. (2005) Isolates in a corridor of migrations: a high-resolution analysis of Y-chromosome variation in Jordan. *J Hum Genet* **50**, 435–41.
- Galanidou, N. & Perlès, C. (2003) *The Greek Mesolithic: Problems and Perspectives*. British School at Athens Studies 10, London.
- Gray, R. D. & Atkinson, Q. D. (2003) Language-tree divergence times support the Anatolian theory of Indo-European origin. *Nature* **426**, 435–439.
- Halstead, P. (1994) The North-South divide: regional paths to complexity in Prehistoric Greece. In: *Development and Decline in the Mediterranean Bronze Age*. (eds. C. Mathers & S. Stoddart), pp. 195–219. Sheffield: Sheffield Archaeological Monographs 8.
- Hood, M. S. (1990) Settlers in Crete c.3000 B.C. *Cretan Studies*: **2**, 151–158.
- Hood, M. S. (2000) Crete, Syria and Egypt. In: *Krith-Aigyptos. Politismikoi Desmoi Trion Chilition*. (ed. A. Karetsou), pp. 21–23. Athens.
- King, R. & Underhill, P. A. (2002) Congruent distributions of Neolithic painted pottery and ceramic figurines with Y-chromosome lineages. *Antiquity* **76**, 707–14.
- Klopfstein, S., Currat, M. & Excoffier, L. (2006) The fate of mutations surfing on the wave of a range expansion. *Mol Biol Evol* **23**, 482–90.
- Kotsakis, K. (2003) From the Neolithic side: The Mesolithic/Neolithic interface in Greece, In: *The Greek Mesolithic: Problems and Perspectives*. (eds. N. Galanidou & C. Perlès) pp. 217–221. London: British School at Athens Studies 10.
- Luis, J. R., Rowold, D. W., Regueiro, M., Caeiro, B., Cinnioglu, C., Roseman, C., Underhill, P. A., Cavalli-Sforza, L. L. & Herrera, R. J. (2004) The Levantine versus the Horn of Africa: evidence for bi-directional corridors of human migrations. *Am J of Hum Genet* **74**, 532–544.
- Malaspina, P., Cruciani, F., Santolamazza, P., Torroni, A., Pangrazio, A., Akar, N., Bakalli, V., Brdicka, J., Jaruzelska, J., Kozlov, A., Malyarchuk, B., Mehdi, S. Q., Michalodimitrakis E, Varesi L., Memmi M. M., Vona G., VILLEMS R., Parik, J., Romano, V., Stefan, M., Stenico, M., Terrenato, L., Novelletto, A., & Scozzari, R. (2000) Patterns of male-specific inter-population divergence in Europe, West Asia and North Africa. *Ann Hum Genet* **64**, 395–412.
- Malaspina, P., Tsopanomalou, M., Duman, T., Stefan, M., Silvestri, A., Rinaldi, B., Garcia, O., Giparaki, M., Plata, E., Kozlov, A. I., Barbujani, G., Vernesi, C., Papola, F., Ciavarella, G., Kovatchev, D., Kerimova, M. G., Anagnou, N., Gavrilu, L., Veneziano, L., Akar, N., Loutradis, A., Michalodimitrakis, E. N., Terrenato, L. & Novelletto, A. (2001) A multistep process for the dispersal of a Y chromosomal lineage in the Mediterranean area. *Ann Hum Genet* **65**, 339–349.
- Manning, S. W. (1995) *The Absolute Chronology of the Aegean Early Bronze Age*. Monographs in Mediterranean Archaeology 1, Sheffield Academic Press, Sheffield.
- Marjanovic, D., Fornarino, S., Montagna, S., Primorac, D., Hadzisehimovic, R., Vidovic, S., Pojskic, N., Battaglia, V., Achilli, A., Drobic, K., Andjelinovic, S., Torroni, A., Santachiara-Benerecetti, A. S., Semino, O. (2005) The peopling of modern Bosnia-Herzegovina: Y-chromosome haplogroups in the three main ethnic groups. *Ann Hum Genet*. **69**, 757–63.
- Martinez, L., Underhill, P. A., Zhivotovsky, L. A., Gayden, T., Moschonas, N. K., Chow, C-E.T., Conti, S., Mamolini, E., Cavalli-Sforza, L. L., Herrera, R. J. (2007) Paleolithic Y-haplogroup heritage predominates in a Cretan highland plateau. *Eur. J. Hum. Genet.* **15**, 485–493.
- Nichols, J. (2007) Language dispersal from the Black Sea region. In: *The Black Sea Flood Question: Changes in coastline, climate and human settlement*. (eds. V. Yanko-Hombach, A. S. Gilbert, N. Panin, P. M. Dolukhanov), pp. 775–796. Springer.
- Novelletto, A. (2007) Y chromosome variation in Europe: Continental and local processes in the formation of the extant gene pool. *Ann. Hum Biol.* **34**, 139–172.
- Nowicki, K. (2002) The end of the Neolithic in Crete. *Aegean Archaeology* **6**, 7–72.
- Peričić, M., Barać Lauc, L., Martinović Klarić, I., Rootsi, S., Janičević, B., Rudan, I., Terzić, R., Čolak, I., Kvesić, A., Popović, D., Sijački, A., Behluli, I., Dordević, D., Efreimovska, L., Bajec, D. D., Stefanović, B. D., Villems, R. & Rudan, P. (2005) High-resolution phylogenetic analysis of southeastern Europe traces major episodes of paternal gene flow among Slavic populations. *Mol Biol Evol* **22**, 1964–1975.
- Perlès, C. (2001) *The Early Neolithic in Greece*. Cambridge. Cambridge University Press.

- Perlès, C. (2005) From the Near East to Greece: Let's reverse the focus. Cultural elements that didn't transfer. In: *How Did Farming Reach Europe?* (ed. C. Lichter): pp. 275–290. Istanbul: BYAZ 2, Eye Yayınları.
- Pinhasi, R., Fort, J. & Ammerman, A. J. (2005) Tracing the origin and spread of agriculture in Europe. *PLoS Biology* **3**, 2220–2228.
- Popham, M. R. (1994) Late Minoan II to the end of the Bronze Age. In: *Knossos a Labyrinth of History: Papers Presented in Honour of Sinclair Hood*. (eds D. Evely, H. Hughes-Brock and N. Momigliano), pp. 89–102. London: British School at Athens, Oxford.
- Regueiro, M., Cadenas, A. M., Gayden, T., Underhill, P. A. & Herrera, R. J. (2006) Iran: Tricontinental Nexus for Y-Chromosome Driven Migration. *Hum Hered* **61**, 132–143.
- Renfrew, C. (1987) *Archaeology and Language: The Puzzle of Indo-European Origins*. Methuen, London.
- Renfrew, C. (1996) Who were the Minoans? Towards a population history of Crete. *Cretan Studies* **5**, 1–27.
- Renfrew, C. (1998) Word of Minoan: the Minoan contribution to Mycenaean Greek and the linguistic geography of the Bronze Age Aegean. *Cambridge Archaeological J.* **8**, 239–64.
- Rowley-Conwy, P. (2003) Early domestic animals in Europe: Imported or locally domesticated? In: *The Widening Harvest* (eds A. J. Ammerman & P. Biagi), pp. 99–117. Boston: Archaeological Institute of America.
- Runnels, C. (2001) The stone age of Greece from the Palaeolithic to the advent of the Neolithic. In: *Aegean Prehistory. A Review*. (ed. T. Cullen), pp. 225–258. Boston: American Journal of Archaeology Supplement 1, Archaeological Institute of America.
- Runnels, C. (2003) The origins of the Greek Neolithic: A personal view. In: *The Widening Harvest*. (eds A. J. Ammerman & P. Biagi), pp. 121–133. Boston: Archaeological Institute of America.
- Schneider, S., Roessli, D. & Excoffier, L. (2000) Arlequin v 2000: a software for population genetics data analysis. Genetics and Biometry Laboratory, University of Geneva, Switzerland.
- Schrack, B. E., Athey, T. W. & Wilson, J. F. (2006) Cluster analysis of extended Y-STR haplotypes leads to discovery of a large and widespread sub-clade of Y Haplogroup J2 pathway [abstract 994]. Presented at the annual meeting of The American Society of Human Genetics, October, 2006, New Orleans, Louisiana.
- Semino, O., Passarino, G., Oefner, P., Lin, A. A., Arbuzova, S., Beckman, L. E., De Benedictis, G., Francalacci, P., Kouvatsi, A., Limborska, S., Marcikja, M., Mika, A., Mika, B., Primorac, D., Santachiara-Benerecetti, A. S., Cavalli-Sforza L. L., & Underhill, P. A., (2000) The genetic legacy of Palaeolithic Homo sapiens sapiens in extant Europeans: a Y-chromosome perspective. *Science* **290**, 1155–1159.
- Semino, O., Magri, C., Benuzzi, G., Lin, A. A., Al-Zahery, N., Battaglia, V., Maccioni, L., Triantaphyllidis, C., Shen, P., Oefner, P. J., Zhivotovsky, L. A., King, R., Torroni, A. L., Cavalli-Sforza, L. L., Underhill, P. A. & Santachiara-Benerecetti, A. S. (2004) Origin, diffusion and differentiation of Y-chromosome haplogroups E and J: inferences on the Neolithization of Europe and later migratory events in the Mediterranean area. *Am J Hum Genet* **74**, 1023–1034.
- Sengupta, S., Zhivotovsky, L. A., King, R., Mehdi, S. Q., Edmonds, C. A., Chow, C.-E. T., Lin, A. A., Mitra, M., Sil, S. K., Ramesh, A., Rani, M. V. U., Thakur, C. M., Cavalli-Sforza, L. L., Majumder, P. P. & Underhill, P. A. (2006) Polarity and temporality of high resolution Y-chromosome distributions in India identify both indigenous and exogenous expansions and reveal minor genetic influence of Central Asian pastoralists. *Am J Hum Genet* **78**, 202–221.
- Shen, P., Lavi, T., Kivisild, T., Chou, V., Sengun, D., Gefel, D., Shpirer, I., Woolf, E., Hillel, J., Feldman, M. W. & Oefner, P. J. (2004) Reconstruction of patrilineages and matrilineages of Samaritans and other Israeli populations from Y-chromosome and mitochondrial DNA sequence variation. *Hum Mutat* **24**, 248–260.
- Slatkin, M. (1995) A measure of population subdivision based on microsatellite allele frequencies. *Genetics* **139**, 457–462.
- Tringham, R. (2000) Southeastern Europe in the transition to agriculture in Europe: bridge, buffer or mosaic, in T.D. Price (ed.), *Europe's First Farmers*. Cambridge University Press, Cambridge: 19–56.
- Underhill, P. A., Passarino, G., Lin, A. A., Shen, P., Foley, R. A., Mirazón Lahr, M., Oefner, P. J. & Cavalli-Sforza, L. L. (2001) The phylogeography of Y chromosome binary haplotypes and the origins of modern human populations. *Ann Hum Genet* **65**, 43–62.
- Underhill, P. A., Myres, N. M., Rootsi, S., Chow, C.-E. T., Lin, A. A., Ollilar, R. P., King, R., Zhivotovsky, L. A., Balanovsky, O., Pshenichnov, A., Ritchie, K. H., Cavalli-Sforza, L. L., Kivisild, T., Villems, R. & Woodward, S. R. (2007) Chapter 3. New phylogenetic relationships for Y-chromosome haplogroup I: Reappraising its phylogeography and prehistory. in *Rethinking the Human Revolution*, eds P. Mellars, K. Boyle, O. Bar-Yosef & C. Stringer (McDonald Institute Monographs.) Cambridge: McDonald Institute for Archaeological Research, 33–42.
- Warren, P. (1973) Crete, 3000–1400 B.C.: Immigration and the archaeological evidence. In: *Bronze Age Migrations in the Aegean*. (eds R.A. Crossland & A. Birchall), pp. 41–47. Archaeological and Linguistic Problems in Greek Prehistory. London: Duckworth.
- Warren, P. (1984) Early Cycladic – Early Minoan chronological correlations. In: *The Prehistoric Cyclades*. (eds J. A. MacGillivray and R.L.N. Barber), pp. 55–62. Edinburgh.
- Zhivotovsky, L. A. (2001) Estimating divergence time with the use of microsatellite genetic distances: impacts of population growth and gene flow. *Mol Biol Evol* **18**, 700–709.
- Zhivotovsky, L. A., Underhill, P. A., Cinnioglu, C., Kayser, M., Morar, B., Kivisild, T., Scozzari, R., Cruciani, F., Destro-Bisoli, G., Spedini, G., Chambers, G. K., Herrera, R. J., Yong, K. K., Gresham, D., Tournev, I., Feldman, M. W. & Kalaydjieva, L. (2004) On the effective mutation rate at Y-chromosome STRs with application to human population divergence time. *Am J Hum Genet* **74**, 50–61.

Supplementary Materials

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Table S1.

Table S2.

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