

the Caucasus, and the Near East (Table 1) and combined them with published data (Finnilä et al. 2001; Herrnstadt et al. 2002). A phylogenetic network for the variation scored in the 894 haplogroup H mtDNAs is shown in Figure 1. In addition to the seven major clades defined previously, we identified a further minor sub-haplogroup defined by A4745G (recently labeled as H13 by Achilli et al. 2004). The two most frequent sub-haplogroups, H1 and H3, each show a rather star-like phylogeny. We refer to the paraphyletic collection of H mtDNAs outside these eight main sub-clades as H*.

The frequencies of haplogroup H as a whole, and its sub-haplogroups, are reported in Table 1 for the 22 populations analyzed here, with age estimates in Table 2. The majority of the European populations have an overall haplogroup H frequency of 40%–50%. Frequencies decrease in the southeast of the continent, reaching ~20% in the Near East and Caucasus, and <10% in the Gulf (Fig. 2A). Thus, haplogroup H as a whole displays a broadly southeast-northwest frequency pattern, reminiscent of the first principal component of classical marker frequencies (Cavalli-Sforza et al. 1994). However, genealogical dissection into sub-clades reveals a quite different sub-structure, showing that this overall pattern is something of a chimera.

The distribution of H1, the largest sub-clade, displays two peaks, one in Iberia and another in Scandinavia (Fig. 2B). However, the Norwegian sample size is low ($n = 18$) and haplogroup H is overrepresented (~70%, while larger data sets for Norway point to a frequency of ~50%: Richards et al. 2000). When we removed the Norwegian sample, the Scandinavian peak disappeared, and the picture showed only the decreasing frequency of sub-haplogroup H1 from the southwest to the north and east. H1 is almost exclusively European, with its only incursion into the Near East being a few Palestinian individuals bearing the most common haplotype. This absence of derived lineages in the Near

East sample suggests that the H1 sub-clade had its origin in Europe. H1 has an age of ~14,000 years (SE 4000) using coding-

into Europe. Its age based on HVS-I variation is 11,500 (SE 2700) years, and its ancestor was identified as a putative late-glacial founder type by Richards et al. (2000). However, the HVS-I database indicates that it is common (>4%) not only in Iberia but also in central, eastern, and southeast Europe, and rather less frequent in northwest Europe.

In contrast, H2 and H6 are both common in eastern Europe and the Caucasus, although there are hints that they may have

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and dispersed rapidly to the southwest of the continent. Although this was at the peak of the last Ice Age, a passage into Europe at this time is not implausible from an archaeological perspective, since there is evidence for extensive contacts between people of the Badegoulian culture of east-central Europe and those of southwest Europe. Indeed, it now seems likely that the west European Magdalenian culture had its roots in the Badegoulian, and not in the local Solutrean of the western glacial refugium. It is the Magdalenian culture that is seen to expand dramatically from the Iberian refugium from ~15,000 years ago in the radiocarbon record for western Europe, although Europe was probably never completely depopulated during the LGM (Housley et al. 1997; Terberger and Street 2002; Gamble et al. 2004).

Haplogroup V was identified, on the basis of control-region sequences, as a likely marker of a human dispersal in Late Pleistocene Europe (Torroni et al. 1998). Higher phylogenetic resolution of the lineages concerned clarified the geographic pattern by distinguishing the more derived haplogroup V from its ancestor, pre-V, which could now be seen to display a quite distinct phylogeographic pattern (Torroni et al. 2001). Haplogroup pre-V appeared to have entered Europe from the east sometime around 20,000–25,000 years ago, at the time of the LGM. However, the diversity and frequency of the derived haplogroup V suggested that it had evolved from pre-V in western Europe, with its age suggesting an expansion from a glacial refuge in Iberia ~15,000 years ago, accompanying the Magdalenian expansion.

It is clear that the phylogeographic patterns displayed by sub-haplogroups H1 and H3 both closely resemble that of haplogroup V. The star-like phylogenies, geographic distribution, and estimated ages of all three clades suggest that they all took part in a major expansion from southwest to northeast Europe ~12,000–14,000 years ago. Between them H1 and H3 amount to around half of the haplogroup H samples in our coding-region database. They comprise ~65% of haplogroup H lineages in Iberia, ~46% in the northwest, ~27% in central and eastern Europeans, and ~5%–15% in the Near East/Caucasus, falling to zero in the Gulf. It is notable that the diversity does not fall within H1 moving from west to east, unlike the situation with haplogroup V (Torroni et al. 2001), but a rapid expansion within the time-frame of the Magdalenian would in fact not be expected to result

cia, Tecnologia e Inovação (POCTI), Quadro Comunitário de Apoio III. This study is included in the Project POCTI/ANT/45139/2002 financed by Fundação para a Ciência e a Tecnologia (Eixo 2, Medida 2.3 do POCTI, QCA III).

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