historically spoken, in the diffusion of Indo-European speakers into Britain and Ireland with the arrival of the Neolithic in ~4000 B.C. Cunliffe (2001) appears to go further, describing the coalescence of the Celtic languages along the coastline of the Atlantic facade of Europe, from southern Iberia to the Shetland Islands, via maritime networks that reach back into the late Mesolithic period. The similarities in prehistoric monumental architecture and the spread of the early–Bronze Age "Beaker package," to take two examples, attest to the likely sharing of beliefs and attitudes through social networks that extended from one end of the Atlantic zone to the other.

This view implies an uncoupling of the link, established by Lhuyd, of a necessary connection between the various aspects of what in the past 200 years has come to be thought of as a "Celtic package"—including, in particular, the peoples encountered and described as "Celts" by the classical authors, the producers of Iron Age La Tène art and their descendants, and speakers of Celtic languages. Modern Celtic speakers should, by this view, be thought of rather as "Atlantic Celts," whose putative continental Iron Age ancestry is open to question (James 1999; Cunliffe 2001). At the same time, many archaeologists and a seeming majority of historians retain the traditional view with some vigor (Megaw and Megaw 1996, 1998).

Genetic evidence has recently lent some support to the suggestion of a shared ancestral heritage among the human populations of Atlantic Europe. Y-chromosome analysis has highlighted similarities between the Pyrenean populations of northern Spain and western population samples from the British Isles (Hill et al. 2000; Wilson et al. 2001). More specifically, a modal haplotype defined by SNP and STR markers (the "Atlantic modal haplotype" in haplogroup R1b [Y Chromosome Consortium 2002]) is present at an unusually high frequency in each population. This has been interpreted as a common Paleolithic genetic legacy that was relatively undisturbed at the edge of the European peninsula by subsequent dispersals from the east, such as those suggested to have taken place during the spread of the Neolithic (Wilson et al. 2001). Some classical marker systems also hint at Atlantic affinities: for example, alleles of the ABO and Rhesus blood groups display frequency peaks in Atlantic Europe (Cavalli-Sforza et al. 1994).

By contrast, studies of human mtDNA in Europe suggested a lack of structure within the continent, leading to debate about the extent to which inferences on demographic history could be justifiably drawn (Richards

We observed a total of 155 haplotypes among the 300 Irish individuals studied (including 100 from previous studies), with all but one sample falling into the main western Eurasian haplogroups: U, HV, JT, I, W, and X (Richards et al. 1998). Full results and additional supplementary information are available from the authors' Web site. A ^{2} test of mtDNA haplogroup frequencies in samples from eastern ($n = 127$) and western ($n = 128$) Ireland showed no significant differences (the remaining 45 samples did not fall into the eastern or western region). In addition, the genetic distance ($_{ST}$ value) between the two regions, on the basis of HVS-I, is small and not significantly greater than zero. This contrasts with the Y-chromosome pattern in Ireland, where eastern and western complements have been shown to be substantially different. This difference between eastern and western Irish Y chromosomes has been attributed to the preferential settlement of subsequent migrants to the accessible east coast after initial colonization (Hill et al. 2000).

Founder analysis (Richards et al. 2000) dated the entry of different mtDNA lineages into Europe by examining the levels of nucleotide diversity accumulated around haplotypes that have matches in the Near East. Roughly 20% of Europeans, principally those belonging to haplogroups J, T1, and U3, are proposed to descend from Neolithic settlers, with the remainder attributed to earlier Late Paleolithic/Mesolithic inhabitants. About 13% of Irish mtDNAs belong to putative Neolithic clusters, a value that is toward the lower end of the range found in Europe and similar to areas such as Scandinavia and the western Mediterranean (Iberia). This observation is consistent with the progressive dilution of the genetic impact of these migrants toward the north and west of Europe. Furthermore, there is an even distribution of putatively Neolithic haplogroups around the island, suggesting that females who arrived after the initial settlement were not restricted to east-facing regions. There are two potential explanations for this: either they were more mobile after arrival in the east or other regions of the island were in direct contact with the continental source populations. By contrast, however, Y-chromosome lineages of putative Near Eastern Neolithic origin (Semino et al. 2000) appear to be virtually absent from the west of Ireland (Hill et al. 2000).

We first examined broad affinities at the population level. Control-region sequences from 8,733 individuals were assembled from the current and previous studies and were grouped into 45 geographically defined population samples. Each of these was checked for quality, as recommended by Bandelt et al. (2002) (results available on the authors' Web site). Samples from some small and/or isolated populations were excluded from our analysis because of the possibility of unusually strong genetic drift that might confound any broader phylogeographical patterns. These included the Western Isles of Scotland, Orkney, and Skye (Helgason et al. 2001).

We estimated genetic distances between all populations as linearized $_{ST}$ statistics (Slatkin 1995) by use of ARLEQUIN, version 2.000 (Schneider et al. 2000). The $_{ST}$ values were based on pairwise sequence differences between positions 16090 and 16365 to allow maximum comparability between all populations.

To account for mutation-rate heterogeneity in the mtDNA control region, site rates were modeled as independently and identically distributed (i.i.d.) gamma with $= 0.26$ (Meyer et al. 1999). The resulting matrix of interpopulation $_{ST}$ values was summarized in two dimensions by use of multidimensional scaling (MDS) implemented by the ALSCAL program included in the SPSS package, version 11.0. The results are shown in figure 1. A broadly east-west—or southeast-northwest—trend is evident in the first dimension, with the Jordanian and Basque population samples occupying the respective poles. This echoes the trend observed in a PCA of haplogroup frequencies of European regions (Richards et al. 2002). Spatial autocorrelation analysis confirms that dimension 1 values are consistent with a clinal pattern across Europe (not shown).

We visualized the geographical variation of each dimension by interpolating observed values to produce a synthetic surface map of Europe by use of the Spatial Analyst extension of ArcView, version 3.2. We employed the inverse distance–weighted method, using the 12 nearest neighbors, to calculate interpolated map values. The resulting values were then divided into 12 equal classes, or contours. Again, the roughly southeast-to-northwest gradient of the first dimension is clear (fig. 2*A*). Atlantic European samples, including those from Ireland, Wales, Scotland, and Galicia, as well as Iceland and Norway, occupy positions on the edge of the European range, toward the Basque pole. The Iberian Peninsula is notable as an area of steep north-south gradient, with the north more similar to central and western Europe and the south more similar to Mediterranean Eu-

Figure 1 MDS plot of interpopulation $_{ST}$ values calculated from mtDNA control-region sequence data. The matrix has been condensed to two dimensions, which account for 82% of the original variation. Population labels are as follows: AL = Albania; AR = Armenia; AU = Austria; AZ = Azerbaijan; BA = Basque Country; BE = Belgium; BR = Brittany; BU = Bulgaria; CZ = Czech Republic; CO = Cornwall; DE = Denmark; EN = England; ES = Estonia; FI = Finland; FR = France; GA = Galicia; GE = Germany; GR = Greece; HU = Hungary; IC = Iceland; IQ = Iraq; IR = Ireland; IT = Italy; JO = Jordan; KA = Karelia; KU = Kurdistan; NO = Northern Ossetia; NY = Norway; PA = Palestine; PC = Portugal Central; PN = Portugal North; PO = Poland; PS = Portugal South; RO = Romania; RU = Russia; SA = Sardinia; SC = Scotland; SE = Sweden; SI = Sicily; SN = Spain North; SS = Spain South Central; SW = Switzerland; SY = Syria; TU = Turkey; and WA = Wales.

as a synthetic map (fig. 2A), shows a pattern that
broadly similar

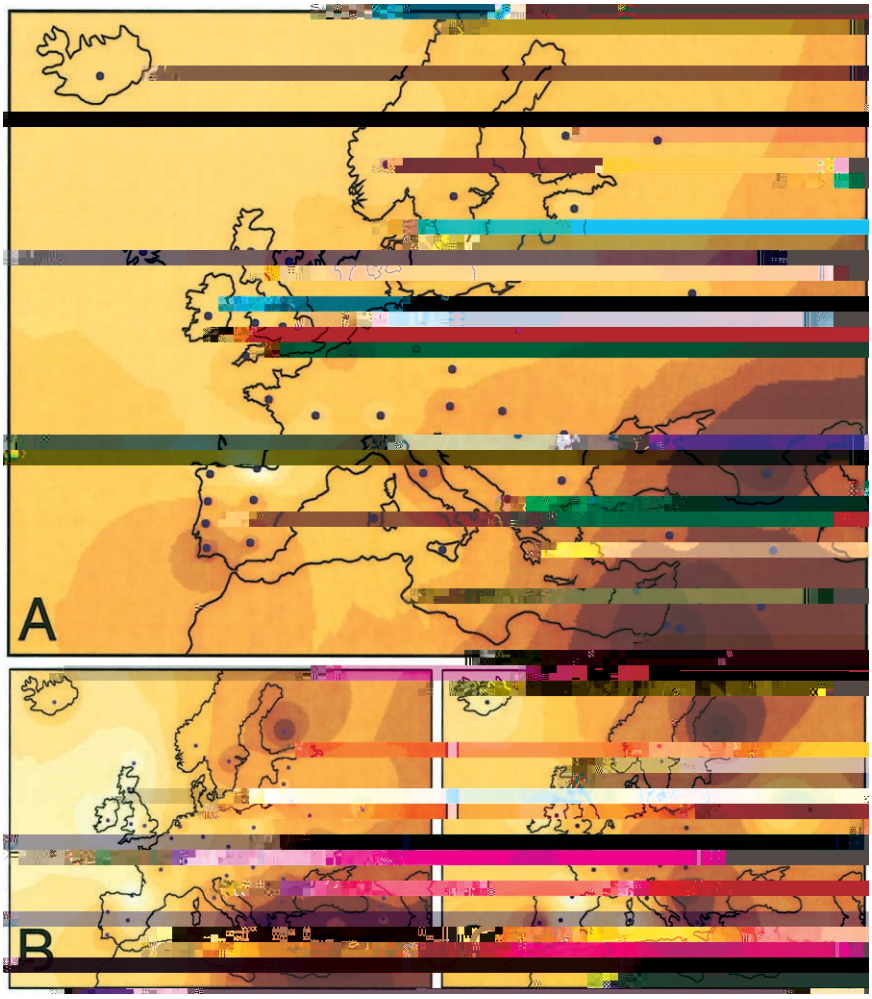

Figure 2 Synthetic maps of Europe displaying the three significantly correlated dimensions of genetic variation. These are as follows: the first dimension of mtDNA variation (*A*), the first dimension of Y-chromosome diversity (*B*), and the second dimension derived from classical gene frequencies (*C*). Points indicate sample locations.

with the predominant mtDNA trend ($r = 0.528$; $P = .043$), whereas dimension 1 is not ($r = 0.141$; $P = .86$).

Focusing on the relationships between Ireland and its neighbors, we investigated the geographical provenance of matches to Irish mtDNA haplotypes. This was implemented by comparing each haplotype found in Ireland (positions 16093–16362) with a world database of mtDNA HVS-I sequences assembled from previous studies (Röhl et al. 2001). By use of the geographical information system "mtradius" (Forster et al. 2002), which uses information on the location and frequency of the closest matching haplotypes, we calculated a center of gravity (or center of distribution), with an SD in kilometers (km) as an indication of the dispersal range of the haplotypes. Higher SDs tend to occur with common ancestral haplotypes that have widespread distributions, which are phylogeographically rather uninformative.

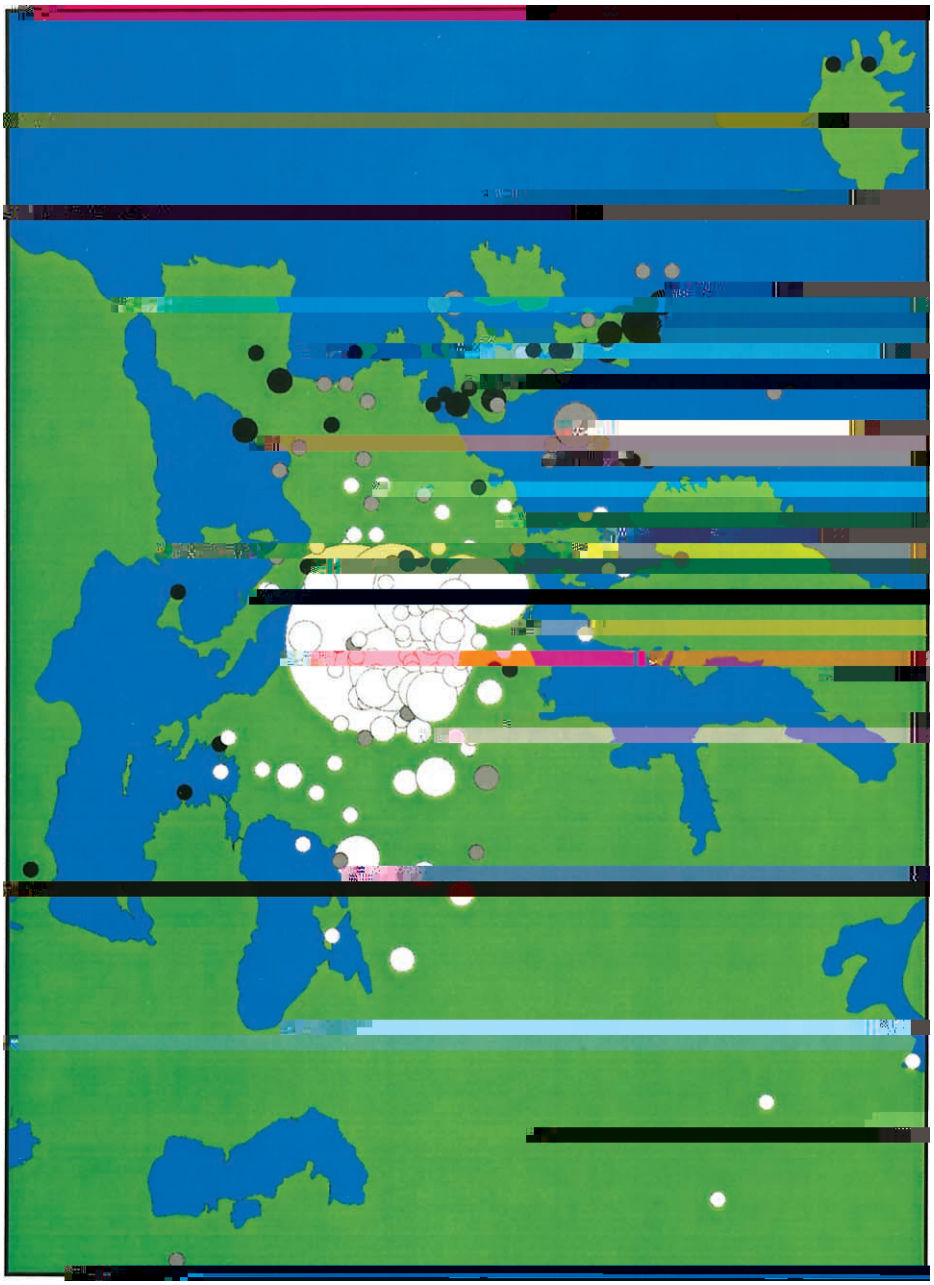

Figure 3 Estimated "dispersal points" (centers of gravity) for the 146 mtDNA haplotypes (positions 16093–16362) found in Ireland. Each circle represents a distinct haplotype. Circle size indicates the frequency of that type in Ireland, with the largest representing the CRS (n = 56) and the smallest indicating a frequency of 1; intermediate frequencies are proportional to circle area. SDs are indicated as follows: black = <500 km, gray = 500–1,000 km, and white = >1,000 km. Eleven centers (ten in Asia and one in Africa) are outside the range of this map.

Scotland. These are widely distributed throughout Ireland and are not concentrated in particular areas. A lesser degree of sharing is also apparent between Ireland and Pyrenean Spain. It is also noteworthy that particular mtDNAs that are characteristic of central Europe, such as J1a (Richards et al. 1998), are virtually absent from

means of demonstrating that geographical patterns are the result of demographic history and not (for example) of selection. These results strongly suggest—for the first time, to our knowledge—that the demographic histories of Europe, in general, and Ireland, in particular, are similarly recorded in loci with different inheritance patterns. The use of a very large data set that was checked for quality, analyzed at the level of individual lineages, and subdivided into fine population units appears to have been a key factor in the identification of the hitherto-undetected mtDNA patterns seen here.

Previous studies indicated particular affinities within the Atlantic zone of Europe on the basis of the distribution of both the Y-chromosome haplogroup R1b (which reaches frequencies approaching 100% in some parts of western Europe) and the mtDNA haplogroup V (which, however, amounts to <5% of European mtDNAs) (Torroni et al. 1998, 2001; Hill et al. 2000; Semino et al. 2000; Wilson et al. 2001). During the last glaciation, human habitation is thought to have been largely restricted to refugial areas in southern Europe; one of the most important of these is likely to have been in southwestern France and the Iberian Peninsula (Dolukhanov 1993; Housley et al. 1997; Gamble et al. 2004). The recolonization of western Europe from an Iberian refugium after the retreat of the ice sheets ~15,000 years ago could explain the common genetic legacy in the area. An alter-

data, these results point toward a distinctive Atlantic genetic heritage with roots in the processes at the end of the last Ice Age.

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Electronic-Database Information

The URL for data presented herein is as follows:

Authors' Web site, http://www.gen.tcd.ie/molpopgen/data.htm (for full Irish results, as well as the mtDNA HVS-I sequence data set used in this study)

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