

The History and Geography of the Y Chromosome SNPs in Europe: an update

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The knowledge of the evolution of the human genome is strictly dependent on the availability of appropriate genetic markers and their relative coverage of genetic variation which refine the phylogenetic reconstruction. While autosomal markers are particularly valuable for recognizing correspondence between genetic and geographic distances, markers on mitochondrial DNA (mtDNA) or Non Recombining Portion of Y Chromosome (NRY), because of their unilinear transmission, can effectively trace diachronical patterns of the human peopling.

The maximum extent of polymorphism coverage has already been reached for the very small mitochondrial genome (about 16,5 Kbp), whereas the first studies based on RFLPs (Restriction Fragment Length Polymorphisms) (Cann *et al.*, 1987) and on sequencing of the hypervariable regions (Vigliant *et al.*, 1991), were then combined to get higher resolution (Torroni *et al.*, 1996), and finally the complete genome sequencing is now routinely performed (Achilli *et al.*, 2004, Pala *et al.*, 2009), in order to detect the whole mtDNA variation. A similar approach cannot be used yet at population level for the by far larger nuclear genome. However, advances in genotyping technology have dramatically enhanced the resolution of the analysis at genome-wide level, and recent papers significantly improved the knowledge of the relationships among European populations, using 300 to 500 K SNPs (Single Nucleotide Polymorphisms) on microarrays chips (Tian *et al.*, 2008; Novembre *et al.*, 2008). As to the NRY, most of the studies before the year 2000 were performed using *Alu* insertion (Hammer, 1995) or STRs

(Short Tandem Repeats) (De Knijff *et al.*, 1997; Pritchard *et al.*, 1999) with the known limitations due to recurrence and reversion of this kind of polymorphisms. Using D-HPLC (Denaturing High Performance Liquid Chromatography) technology, Underhill and coworkers (1997) discovered 22 new SNP biallelic markers, rapidly raising in number to 167 (Underhill *et al.*, 2000), 242 (YCC, 2002), about 600 (Karafet *et al.*, 2008), up to more than 725 presently listed in the Y-DNA SNP Index 2009, (www.isogg.org), and the knowledge of Y chromosome phylogeny and of the spread worldwide of human populations raised proportionally. The next goal of the research on Y chromosome will be the use of specific microarrays that can genotype a much higher number of SNPs than nowadays routinely performed, and, ultimately, the complete Y chromosome sequencing. Waiting for future developments, this short note reports the state of the art of the phylogenetic (“history”) and phylogeographic (“geography”) research on Y chromosome SNP analyses in Europe, updating the review published in this Journal by Francalacci & Sanna at the beginning of 2008.

History

Just a few papers of this biennium deal with the deepening of the phylogenetic tree of European Y chromosomes, and involve haplogroups (hg) E, R, J and G, mostly with the aim of associate derivate alleles with small geographical areas in order to use this information in the forensic field.

The paper of Caratti *et al.* (2009) reported the molecular dissection of hg E-M78 (E1b1b1a), for applying the subhaplogrouping to detect the different frequencies in small geographical areas, to be used in forensic cases. Nine downstream population-informative SNPs (M148, M224, V12, V13, V19, V22, V27, V32, V65) were analyzed in an Italian sample. The subclades of hg R1b, defined by the marker M343, were investigated by Niederstatter *et al.* (2009), using 3 newly discovered SNPs in a population from Tyrol, Austria. Onofri *et al.* (2008) analyzed 900 individuals belonging to the common south European hg J2-M172 in order to increase its resolution using a multiplex approach with 7 downstream SNPs. The hg G, characterized by M201, is rather homogeneous in all European populations, since most of the samples belong to sub-hg G2a, defined by P15, and many of the previously described markers are very rare. Sims *et al.* (2009) uncovered 15 new SNPs, 11 of which were phylogenetically equivalent to M201 or P15, and 4 of them were able to define new separate sub-hgs.

The higher resolution of some specific clades was also used for drawing inferences in phylogeographic problems. The branch of hg J defined by 29 populations, namely J1-M267, was dissected using 20 STRs and 6 downstream SNPs by Tofanelli *et al.* (2009), to investigate its possible correlation with the demographic expansion of Islam since Middle Ages. This hg and its subclades showed to be not useful as Arabic or Jewish markers, rather indicating prehistoric climate-driven demographic dynamics. The widespread Eurasian hg R1a-M17 (now R1a1) has been commonly associated with the Indo-European linguistic family. Underhill *et al.* (2009) used some newly discovered SNP markers to distinguish between European and Asian R1a Y chromosome, in order to outline phylogeographic relationships. Among these markers, M434 has a low frequency and a late origin in West Asia, in agreement with a recent gene flow over the Arabian Sea. On the other hand, M458 has a significant frequency in Europe, and its virtual absence outside Europe is not in

agreement with the hypothesized link between Europe and India. The Paleolithic origin of the commonest European Y chromosomal lineage, R1b1b2-M269, decreasing clinally from western to eastern Europe was challenged by Balaesque *et al.* (2010), which considered its STR diversity better explained by spread from a single source in the Near East via Anatolia during the Neolithic period, in striking contrast with previous studies. This research is based on a single haplotype (R1b1b2-M269) and 9 different microsatellites on a large sample of about 2,500 European Y chromosomes. It is expected that further studies, increasing the number of STR used and extended to other haplotypes or, better, dissecting the haplotype with new downstream markers, will provide an ultimate answer to the debated question about the relative contribution to modern European populations of Paleolithic hunter-gatherers versus Neolithic farmers.

Geography

Most of the recent papers are aimed to elucidate the migration patterns in ancient and historical time, while some other studies are devoted to the description of the Y chromosome variability in local geographical areas to be used in the forensic field. The results confirmed the general aspects of the human peopling of the studied regions (with the significant exception of the above mentioned paper of Balaesque *et al.*, 2010), adding interesting insights in some specific question.

The remarkable ancient pre-Neolithic substrate in the Pyrenean mountains was pointed out by Lopez Parra *et al.* (2009), who discovered a high proportion of R1b1b2-M269 and I2a2-M26 coming from the Franco-Cantabrian glacial refuge, with some level of structuring between western and eastern Pyrenees. The paper of Adams *et al.* (2008) was focused on recent historical process of admixture in the Iberian Peninsula among people with different geographical origin and religious background, such as North African Muslims and Sephardic

Jews. The observed degree of integration was related to high level of religious conversion, due to social and religious intolerance, while the presence of North African variability nowadays does not reflect the medieval colonization and withdrawal but it is the result from later movements. The population relationship between Iberia and Northern Africa was also investigated by Alvarez *et al.* (2009) who studied a Berber settlement in Andalusia, where the low levels of the “Berber” marker E3b1b-M81 (now E1b1b1b) rejects the hypothesis of a gradual genetic assimilation of Berber settlers during the Islamic period. The former nomadic population of Roma (Gypsies) now settled in Portugal was analyzed by Gusmão *et al.* (2008). The Y chromosome detected in this sample showed traces of their migration routes, from their homeland (with the Indian haplotype H1a-M82) to the permanence in the Balkans (J2a1b-M67 now J2a2, J2a1b1-M92 now J2a2a, I-M170 and Q-M242), with traces of contacts with European populations preceding the entrance in the Iberian Peninsula (R1b1c-M269 now R1b1b2 and J2b1a-M241 now J2b2) and a high proportion of admixture with the non-Gypsy population from Iberia. A forensic study on central Portugal was carried out by Carvalho *et al.* (2008). No significant differences were found comparing this population with other samples from Portugal.

The genetic variation of Y chromosome in Russia and neighboring populations are investigated by some recent papers. The first study (Balanowsky *et al.*, 2008) recognized a general north-south clinal pattern, predating the linguistic split between west and east Slavonic-speaking people, with a relevant influence in the north from the Finno-Ugric population, as showed by the high frequencies of hg N3-Tat (now N1c). Intraethnic variation signals did not cross interethnic borders, except between Poles, Ukrainians, and central-southern Russians, thereby revealing their overwhelmingly shared patrilineal ancestry. The second paper (Malyarchuk *et al.*, 2008) followed the linguistic affiliation in the region, with the absence of statistically significant structure between Slavic populations (Russians

and Poles) and remarkable differentiation with Germans. A third study, Mirabal *et al.* (2009), increased the resolution of three sub-hgs (N1b, N1c1 and R1a1) using 15 microsatellite loci to point out the lack of correlation with linguistic or geographical proximity in population from northwestern Russia and the Uralic mountains. Finally, a couple of papers by scholar of forensic science outlined the Y chromosome variation in Hungary (Völgyi *et al.*, 2008) and in three town areas from Germany, Poland and eastern Russia (Lessig *et al.*, 2008).

Finnish researchers (Lappalainen *et al.*, 2008) investigated the genetic relationships in the Baltic Sea, finding a general homogeneity in the area, while the genetic drift played an important role especially in the underpopulated regions of the far North. The same research group (Lappalainen *et al.*, 2009) focused the study on different regions of Sweden, finding a mostly clinal population structure. Moreover, the recent immigration waves of the 20th century are visible in hg frequencies, increasing diversity in the major towns.

The historical influences of ancient Greeks and North African populations were detected in the Mediterranean island of Sicily by Di Gaetano *et al.* (2009), who estimated the genetic contribution of Greek Y chromosomes to the Sicilian gene pool to be about 37%, with a TMRCA (Time of the Most Recent Common Ancestor) in agreement with the historical data, and the contribution of North African populations in about 6%. NRY variation was also studied for forensic purposes in the central Italian region of Marche and in the northern town of Modena, by Onofri *et al.* (2007) and Ferri *et al.* (2009) respectively.

The Balkan Peninsula is of crucial importance to understand the modality of the spread of agriculture in Europe, in particular the opposing roles of population movement and cultural diffusion, together with the presence of maritime or inland diffusion pathways. The work of Battaglia *et al.* (2008) addressed the first question, tracing three Y chromosome clades, I-M423, E-V13 and J-M241, informative in distinguishing between Mesolithic hunter-gatherers and Neolithic farmers. Balkan Mesolithic populations were the earliest to adopt

agriculture maintaining their genetic background and thus indicating a case of cultural diffusion. The Adriatic sea-route was also hypothesized by the authors. A similar topic was studied by King *et al.* (2008), comparing Greek samples, with a marked affinity with Balkan populations, and samples from Crete, closer to central Mediterranean Anatolia. The results, in agreement with archaeobotanical data, suggested two possible expansion routes of farming, one toward continental Europe through the Peloponnesus, and one maritime from Anatolia to Crete and southern Italy.

The area of Levant has a great importance for showing the effects of both ancient and historical population waves. A microdifferentiation coastal-inland was detected by El-Sibai *et al.* (2009), while Zalloua *et al.* (2008b) investigated the differential impact of the newcomers from the Arabic Peninsula and from western Europe in Lebanon, studying the present day Lebanese Muslims and Christians. The predominance of hg J*(xJ2) in the former group, and haplogroup R1b in the latter, indicates the importance of the source populations in the two distinct broad ethnic and religious groups in the genetic differentiation of Lebanon, which is more strongly structured by religious affiliation than by geography. The historical diffusion of Phoenicians, who were the dominant traders in the Mediterranean Sea in the first millennium BC, was studied by the same research group (Zalloua *et al.*, 2008a). Comparing Y chromosomes from samples drawn in their Lebanese homeland and in former Phoenician colonies all over the Mediterranean, the authors identified hg J2, in general, and six Y STR haplotypes, in particular, that accounted for about 6% to the modern Phoenician-influenced populations examined. Finally, a forensic study (Robino *et al.*, 2008) provided frequency data on SNP and STR Y chromosome haplotypes in a population sample from Algeria, North Africa.

Principal Component Analysis

Population data from the recently published papers have been used for updating the dataset

reported in Francalacci & Sanna (2008) (see supplementary materials). The Principal Component Analysis (PCA) has been carried out using the XLStat (version 7.5.2) package, and the first three principal components (accounting for 35,8% of the total variance) have been tridimensionally represented in Figure 1 using the program XLStat 3DPlot (version 4.2). The main discriminant contribution is given in the first component, by the hg J2-M172 in respect to I-M170, while in the second and third component by E3b1b1-M35 and R1-M173 in respect to R1a1-M17. The peripheral populations (Anatolia, the Caucasus, the Levant and North Africa) are clearly separated from the more homogeneous proper European ones. The isolated Iberian population lying within the Anatolian group is actually represented by Sephardic Jews analyzed by Adams *et al.* (2008). Along the third component axis can be observed a population sample continuity towards Scandinavia from Iberia through the British Isles and Central Europe, and, separately, from the Balkans through Eastern Europe, following the two main Mesolithic re peopling routes from the glacial refugia, traced by R1b1b2-M269 and I-M170 respectively. Italian samples mostly lie in the intermediate position between the north-south (Scandinavia - Levant) and west-east (Iberia - Balkan) clines.

This paper is dedicated to the memory of our colleague and friend Loredana Castrì.

Info on the web

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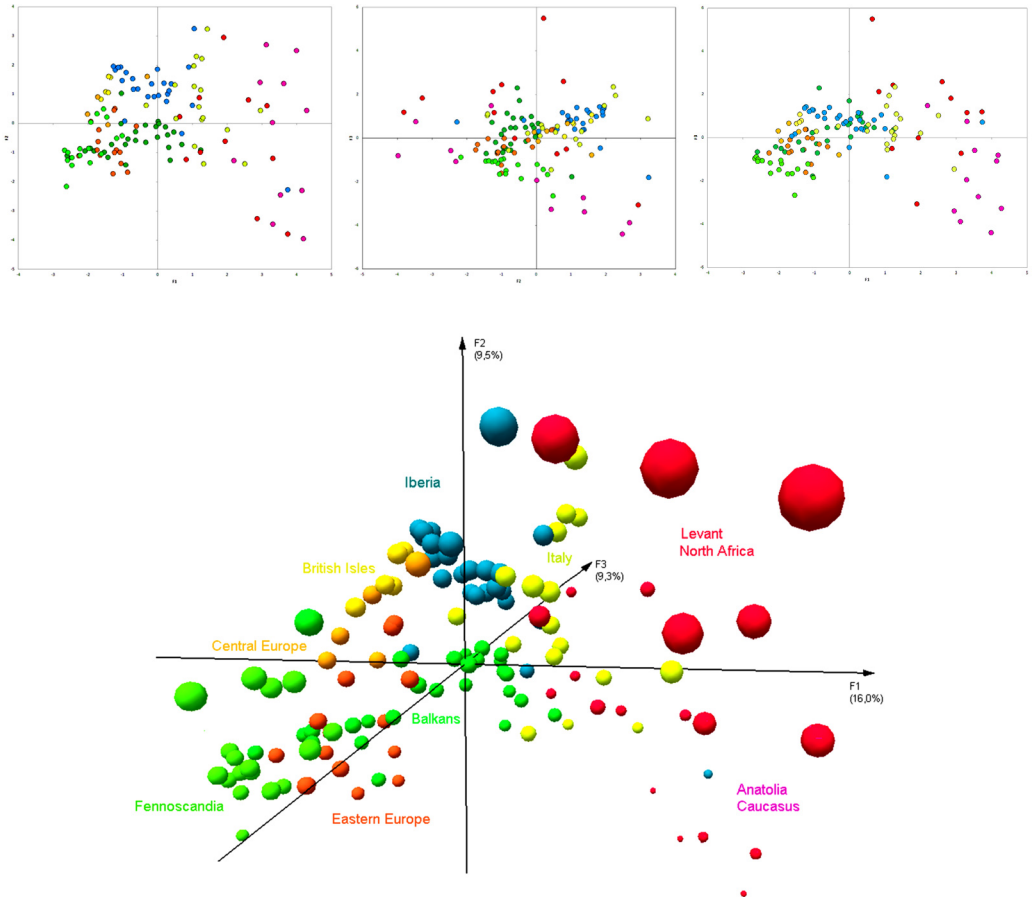


Fig.1 - Plots of the three principal components of the Euro-Mediterranean NRY variability. Above: 2D plots (F1x F2; F1x F3; F2x F3). Below: 3D plot. The colors in the 2D plots refer to the population listed on the 3D plot. The dataset used for analysis and the detailed 2D plots are available in the supplementary material.

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Editor, Cristian Capelli