



Anthropology/Anthropologie

Immunoglobulin genes in Andalusia (Spain). Genetic diversity in the Mediterranean space

Les gènes des immunoglobulines en Andalousie (Espagne). Diversité génétique dans l'espace méditerranéen

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ABSTRACT

Andalusia is the most densely populated region of Spain since ancient times, and has a rich history of contacts across the Mediterranean. Earlier studies have underlined the relatively high frequency of the Sub-Saharan $GM\ 1,17\ 5^*$ haplotype in western Andalusia (Huelva province, $n = 252$) and neighbouring Atlantic regions. Here, we provide novel data on GM/KM markers in eastern Andalusians ($n = 195$) from Granada province, where African $GM^*1,17\ 5^*$ frequency is relatively high (0.044). The most frequent GM haplotypes in Andalusia parallel the most common in Europe. Altogether, these data allow us to gain insight into the genetic diversity of southern Iberia. Additionally, we assess population structure by comparing our Iberian samples with 41 Mediterranean populations. GM haplotype variation across the Mediterranean reflects intense and complex interactions between North Africans and South Europeans along human history, highlighting that African influence over the Iberian Peninsula does not follow an isotropic pattern.

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L'Andalousie est, depuis l'Antiquité, la région d'Espagne la plus peuplée ; elle a une riche histoire de contacts dans la Méditerranée. Les premières études ont souligné la relative haute fréquence de l'haplotype sub-saharien $GM^*1,17\ 5^*$ dans l'Andalousie occidentale (province de Huelva, $n = 252$) et les régions atlantiques voisines. Dans ce travail, nous apportons de nouvelles données sur les marqueurs GM/KM en Andalousie orientale ($n = 195$), province de Grenade, où l'haplotype africain $GM^*1,17\ 5^*$ a une fréquence relativement élevée (0,044). Les haplotypes GM les plus fréquents en Andalousie sont aussi les plus communs en Europe. Ces données dans leur ensemble constituent un nouvel apport à la diversité génétique de la partie sud de la péninsule Ibérique. De plus, nous comparons la structure de nos populations ibériques avec celle de 41 populations méditerranéennes. La variation des haplotypes GM en Méditerranée reflète d'intenses et

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complexes interactions entre les populations nord-africaines et sud-européennes, soulignant, en outre, que l'influence africaine dans la péninsule Ibérique n'est pas homogène.

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1. Introduction

Human immunoglobulin (Ig) allotypic polymorphism has permitted to describe several groups of genetic markers. Currently, we know 26 antigenic determinants (allotypes), expressed in both light and heavy immunoglobulin chains. *GM* allotypes are located in immunoglobulin constant heavy G chain (IGHG) chromosome 14q32.3, and have been the most extensively studied, due to their remarkable polymorphism and linkage disequilibrium. On the other hand, *KM* locus (2p11.2) has only three allotypes [*KM*(1), *KM*(2) and *KM*(3)] encoded by alleles *KM**1, *KM**2, and *KM**3, respectively [1].

Prior to genomic DNA markers discovery and development, the *GM* system proved to be an essential complement for those anthropological studies aimed at the reconstruction of population history [2–5]. Some *GM* haplotypes show particular geographical variation patterns, especially in human populations characterized by a deeply rooted ethnicity [6–12], and this has made the *GM* system appropriate to detect admixture and gene flow scenarios [13,14].

The Mediterranean basin – where Europe, Asia, and Africa meet – represents a unique space to study recent human history. The Iberian Peninsula is included in such a geographic frame. Its strategic location (at the extreme southwest of Europe and close to Africa), its role as a refuge during the Last Glacial Maximum (LGM) [15,16], and its complex orography and population history related to demographic episodes of isolation, constriction–expansion and gene flow [17] have configured its decisive role in Europe peopling. Within the Iberian Peninsula (598,000 km²), Andalusia (87,598 km²) acquires a special relevance, since it is the most densely inhabited region of Spain from ancient times onwards.

Andalusia has been a human crossroad, a gateway open to many and varied human populations and cultures from all around the Mediterranean basin. Such ancient and long history of human contacts and admixture makes its current autochthonous population a special target for anthropological and genetic studies. One of the most remarkable historical events taking place in the Iberian Peninsula (and especially in Andalusia) was the Islamic rule – lasting in Granada region from AD 711 to 1492 – which implied substantial social, cultural and political changes [18,19].

A number of genetic studies have been published on Andalusian population based on blood group system polymorphisms [20], erythrocyte enzymes [21], leucocyte polymorphisms (HLA class II) [22,23], and DNA autosomal and uniparental markers [24–30]. These surveys show heterogeneous results on the genetic affinity between Andalusia and North Africa – neighbouring western

populations specifically. In other words, the Strait of Gibraltar's role in terms of gene flow still remains an unresolved question.

The current growing interest in the Andalusian genetic diversity focuses on the search for population substructure. Recent results obtained by our group on the composition and mtDNA variation in Andalusia [31] reveal high internal complexity and a distinctive influence of U6 and L haplogroups in both eastern and western side of region. Investigating Y-chromosome variability in the same sample sets, we also observe interpopulation genetic differentiation, though in a lesser extent ([32,33], Calderón et al. manuscript in preparation). Both selected territories – Granada and Huelva – are differentiated by their different, complex histories.

Within Europe, French [34] and Iberian populations have been the most widely studied ones in terms of *GM* and *KM* immunoglobulin allotypes. Calderón et al. [35,36] highlighted the relatively high frequency of the African *GM* 1,17 5* haplotype in western Andalusia and neighbouring Atlantic regions. These findings made worthwhile the investigation of whether that African interaction should be also expected in other southern Spanish populations. Therefore, this is one of the principal goals of the present work. Here, we provide the first *GM*/*KM* data in eastern Andalusians from Granada, and we compare these data with the existing information from the eastern side of the region (Huelva province). We also evaluate the Andalusian population's substructure and the genetic differentiation between northern and southern Iberian populations (a distance of over 1000 km). The results generated on *GM* haplotype patterns in Andalusia are then compared with other genetic information emerging from the same sample sets. *GM* haplotype data permit to take a look at the spatial patterns of this autosomal marker across the Mediterranean, and to evaluate the extent of relationships among Iberian and other Mediterranean populations from Europe, North Africa, and Near/Middle East. Gene flow and genetic affinities in the Mediterranean space are analysed and discussed.

2. Materials and methods

2.1. Samples and genetic characterization

The analysed sample consisted of 195 unrelated individuals of both sexes, randomly selected from the total sample stock ($n=470$). These individuals are autochthonous, which means maternal and paternal origins (up to the third generation) in Granada province.

Sampling of people with close genetic kinship may give rise to spurious population structure signals. This deserved special attention from our team during the collection of

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