## CLASSIFICATION

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- 2 BIOLOGICAL SCIENCES: Population Biology
- 3 TITLE (112; 135 CHARACTERS MAX.)
- 4 Ancient genomes from North Africa evidence prehistoric migrations to the Maghreb from
- 5 both the Levant and Europe
- 6 SHORT TITLE (48; 50 CHARACTERS MAX.)
- 7 Paleogenomics of Moroccan Neolithic populations
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ABSTRACT (249; 250 WORDS MAX.) The extent to which prehistoric migrations of farmers influenced the genetic pool of western North Africans remains unclear. Archaeological evidence suggests the Neolithization process may have happened through the adoption of innovations by local Epipaleolithic communities, or by demic diffusion from the Eastern Mediterranean shores or Iberia. Here, we present the first analysis of individuals' genome sequences from early and late Neolithic sites in Morocco, as well as Early Neolithic individuals from southern Iberia. We show that Early Neolithic Moroccans are distinct from any other reported ancient individuals and possess an endemic element retained in present-day Maghrebi populations, confirming a long-term genetic continuity in the region. Among ancient populations, Early Neolithic Moroccans are distantly related to Levantine Natufian hunter-gatherers (~9,000 BCE) and Pre-Pottery Neolithic farmers (~6,500 BCE). Although an expansion in Early Neolithic times is also plausible, the high divergence observed in Early Neolithic Moroccans suggests a long-term isolation and an early arrival in North Africa for this population. This scenario is consistent with early Neolithic traditions in North Africa deriving from Epipaleolithic communities who adopted certain innovations from neighbouring populations. Late Neolithic (~3,000 BCE) Moroccans, in contrast, share an Iberian component, supporting theories of trans-Gibraltar gene flow. Finally, the southern Iberian Early Neolithic samples share the same genetic composition as the Cardial Mediterranean Neolithic culture that reached Iberia ~5,500 BCE. The cultural and genetic similarities of the Iberian Neolithic cultures with that of North African Neolithic sites further reinforce the model of an Iberian migration into the Maghreb. SIGNIFICANCE STATEMENT (119; 120 WORDS MAX.) The acquisition of agricultural techniques during the so-called Neolithic revolution has been one of the major steps forward in human history. Using next-generation sequencing and ancient DNA techniques, we directly test if Neolithization in North Africa occurred through the transmission of ideas or by demic diffusion. We show that Early Neolithic Moroccans are

composed of an endemic Maghrebi element still retained in present-day North African populations and distantly related to Epipaleolithic communities from the Levant. However, late Neolithic individuals from North Africa are admixed, with a North African and a European component. Our results support the idea that the Neolithization of North Africa might have involved both the development of Epipaleolithic communities and the migration of people from Europe.

INTRODUCTION

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One of the greatest transitions in human history was the transition from hunter-gatherer to farming lifestyle. How farming traditions expanded from their birthplace in the Fertile Crescent has been a matter of contention. Two models were proposed: one involving the movement of people and the other based on the transmission of ideas. Over the last decade, paleogenomics has been instrumental in settling long-disputed archaeological questions<sup>1</sup>, including those surrounding the Neolithic revolution<sup>2</sup>. Compared to the extensive genetic work done on Europe and the Near East, the Neolithic transition in North Africa, including the Maghreb, remains largely uncharacterized. Archaeological evidence suggests that some of the major innovations associated with the Neolithic, such as farming and pottery production, could have been introduced into northern Morocco through sea voyaging by people from Iberia or the central Mediterranean as early as ca. 5400 BCE<sup>3,4</sup>. In fact, some of the Neolithic pottery recorded in North Africa strongly resembles that of European cultures like the Cardial Early Neolithic, the Mediterranean early farmer culture located in Iberia<sup>5</sup>. However, other innovations such as some pottery traditions and bone and lithic technical customs could be the result of *in situ* development from Epipaleolithic communities, indicating a strong continuity in the local population since the Late Pleistocene<sup>6-10</sup>. Genetic data from present-day populations 11-13 suggests that North African ancestry has contributions from four main sources: 1) an autochthonous Maghrebi component related to a back migration to Africa ~12,000 years ago from Eurasia; 2) a Middle Eastern component probably associated with the Arab conquest; 3) a sub-Saharan component derived from trans-Saharan migrations; and 4) a European component that has been linked to recent historic movements. Paleogenomic studies have begun to provide insights into North African Prehistory<sup>14-16</sup>; however, no research to date has tested whether the Neolithic transition in the Maghreb was driven by local populations who adopted cultural and technological innovations or the migration of people. Here, we perform genome-wide analysis of remains from the Early Neolithic site of Ifri n'Amr or Moussa (IAM; ~5,200 BCE, n=7) and the Late Neolithic site of Kelif el Boroud (KEB; ~3,000 BCE; n=8) (Supplementary Note 1). To test possible migrations through the Strait of Gibraltar, we also analyse human remains from the

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southern Iberian Early Neolithic site of El Toro (TOR; ~5,000 BCE; n=12) (Figure 1). This Iberian Early Neolithic culture bears similarities with early Maghrebi pottery decoration, as well as bone and lithic tool production traditions which suggest an African influence<sup>17</sup> (Supplementary Note 1). Including these southern Iberian samples in our analysis enables a direct test of this hypothesis. [Figure 1 here] RESULTS AND DISCUSSION We sequenced 38 Illumina pair-end libraries from 27 individuals, and selected the bestconserved libraries for subsequent analyses. Endogenous DNA content was generally low (2.88% on average) (Supplementary Note 2). Depth of coverage was consistently improved when enriching using baits targeting specific sites for the Multiethnic Genotyping Array (MEGA) ( $\sim$ 100X), compared to whole-genome capture ( $\sim$ 15X) (Supplementary Note 2). Following enrichment, we generated thirteen low-coverage genomes (five from IAM, four from KEB and four from TOR), with MEGA coverage ranging from 0.04X to 1.72X depth, and genome-wide coverage ranging from 0.01X to 0.74X depth (Table 1). All samples considered in this study met the standard aDNA authentication criteria, including observation of DNA fragmentation (~46 bp average read length) and damage patterns due to cytosine deamination toward the 5' ends of molecules (Supplementary Note 3). Mitochondrial DNA and Y-chromosome haplogroups obtained for IAM (Moroccan Early Neolithic) and KEB (Moroccan Late Neolithic) suggest either a population replacement or an important genetic influx into Morocco between 5,000-3,000 BCE. IAM samples belong to the mtDNA haplogroups U6a and M1—both of which are associated with the back migration to Africa from Eurasia in Upper Palaeolithic times <sup>18,19</sup>—while KEB samples belong to haplogroups K1, T2 and X2, prominently found in Anatolian and European Neolithic samples<sup>2,20</sup> (Supplementary Note 4). Regarding the paternal lineages, IAM individuals carry Y chromosomes distantly related to the typically North African E-M81 haplogroup, while

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the Y chromosome from KEB belongs to the T-M184 haplogroup; though scarce and broadly distributed today, this haplogroup has also been observed in European Neolithic individuals<sup>16</sup> (Supplementary Note 5). Both mtDNA and Y-chromosome lineages (K1, J2 and T2 haplogroups, and G-M201 haplogroup, respectively) for samples from TOR (Iberian Early Neolithic) are similar to those observed in Europe during Neolithic times<sup>20</sup>. [Table 1 here] When projected on a Principal Components Analysis (PCA) space built using sub-Saharan African, North African, European and Middle Eastern population of the Human Genome Diversity Project (HGDP) dataset genotyped with MEGA, IAM samples are placed close to Mozabites, while Iberian Neolithic samples fall close to southern European populations (Supplementary Note 6). As suspected from the mtDNA and Y-chromosome data, KEB samples do not cluster with IAM and are placed in an intermediate position between IAM and TOR. We further explored the genetic structure of these samples using the program ADMIXTURE<sup>21</sup> (Figure 2). At K=5, we observe sub-Saharan African (red), early European Neolithic (green), North African (yellow), Middle Eastern (violet) and eastern European components (orange). Congruently with PCA results, TOR is composed of the early European component, clustering with Sardinian samples, and IAM is composed of the North African component, clustering with Mozabites. Finally, KEB is placed in an intermediate position, with ~50% of both early European Neolithic and North African ancestries. It is worth mentioning that, compared to current North African samples, IAM and KEB do not show any sub-Saharan African ancestry, suggesting that trans-Saharan migrations occurred after Neolithic times. This is in agreement with the analysis of present-day genome-wide data from Morocco, which estimated a migration of western African origin into Morocco only  $\sim 1,200$  years ago<sup>11</sup>. West Eurasian populations can be modelled as admixture of four different ancestral components<sup>2</sup>: Eastern and Western European hunter-gatherers, and Iranian and Levantine Neolithic. We explored the placement of Moroccan and Southern Iberian Neolithic samples

161 in this context, and compared their genetic affinities to ancient and present-day West 162 Eurasian and Levant populations in the Human Origins panel. Interestingly, PCA reveals that 163 IAM individuals are different from any aDNA sample studied to date (Figure 2; 164 Supplementary Note 6). When projected, IAM samples are close to modern North Africans, 165 in the Levantine corner of the PCA space (Figure 2). Southern Iberian Neolithic individuals 166 from TOR cluster with Sardinians and with other Anatolian and European Neolithic samples. 167 Moreover, KEB samples are placed halfway between the IAM and Anatolian/European farmer clusters, in close proximity to Levant aDNA samples and also to Guanche samples 16, 168 the indigenous population of the Canary Islands known to have a Berber origin<sup>22</sup>. When 169 170 compared using ADMIXTURE (See Supplementary Note 7 for details), IAM samples 171 possess ~100% of a component partially shared by aDNA samples from the Middle East and 172 Levant at low K values. At K=6, this IAM-like component is observed mainly in modern 173 North Africa, following a west-to-east cline, and in the Guanches. TOR and other Early 174 Neolithic samples from Iberia cluster together with farmers from Anatolia, the Aegean area 175 and Europe. At K=8, the Early Neolithic individuals from Iberia differentiate from the 176 Anatolian, Aegean and European Early Neolithic samples, and share their main component 177 (purple) with Middle Neolithic/Chalcolitic samples (Figure 2). Finally, at low K values, KEB 178 can be explained as having both IAM-like and European Neolithic components, suggesting 179 an admixture process between IAM-like people and early farmers. Nevertheless, at K=8, the European component in KEB is predominantly "purple," with some "green" component. 180 181 This "green" component is also present, at a low frequency, in Natufians and other ancient 182 Levantine populations. The substantially larger contribution of the "purple" component, 183 when compared with the "green", suggests a significant genetic contribution of ancient 184 Iberians in Morocco (Figure 2). The same admixture profile is observed in Guanches, but the 185 amount of IAM ancestry is consistently higher in all the samples. Given that the Guanches 186 could have had originated in a different area of the Maghreb, this result might suggest that 187 the European Neolithic impact in North Africa was heterogeneous.

[Figure 2 here]

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To compare our samples directly to the genomes of ancient and modern populations, we calculated pair-wise F<sub>ST</sub> distances, which, unlike PCA and global ancestry analyses, are insensitive to the inclusion of large numbers of individuals from modern populations. F<sub>ST</sub> values indicate that the IAM samples are as differentiated from all other populations as Yoruba are from non-Africans (Supplementary Note 9), with the sole exception of KEB and, to a lesser extent, the Guanches and modern North African populations. Given the relatively low heterozygosity and high identity-by-descent proportions observed in IAM (Supplementary Note 8), this differentiation could be driven by isolation and genetic drift. IAM is divergent from the other populations, with the exception of populations that likely received genetic influx from them. This raises the possibility that IAM was isolated in North Africa since Palaeolithic times, when a back migration from Eurasia brought mtDNA haplogroups M1 and U6 to the Maghreb<sup>18</sup>. Although IAM is clearly more similar to KEB than to any other population, the converse is not true. KEB has lower F<sub>ST</sub> distances with any Anatolian, European (excluding European hunter gatherers), Levantine and Iranian population, rather than with IAM. In the modern DNA reference panel, KEB is similar to North African, European and Middle Eastern populations. Among the ancient populations, TOR is more similar to Middle Neolithic/Chalcolithic Europeans, and, among modern populations, to populations from Spain, North Italy and Sardinia. To further investigate the genetic affinities of IAM, KEB and TOR samples, we conducted outgroup f3-statistic analysis<sup>23</sup>. Results indicate that, when KEB and Guanches are excluded, IAM shares more drift with ancient Levantine populations, such as Natufians (Epipaleolithic) and Pre-Pottery Neolithic individuals (Figure 3; Supplementary Note 10), than with any other ancient population. To explore further the connection between IAM and Levantine populations, we performed an f4-statistic analysis to test whether IAM shares more alleles with any other population in the Human Origins panel<sup>2,24</sup> than with ancient populations from the Levant (Supplementary Note 10). Consistently, and also with the exception of KEB and Guanches, all comparisons indicated higher similarity with Natufians and Levantine farmers. This suggests that most of IAM ancestry originates from an out-of-Africa source, as IAM shares more alleles with Levantines than with any sub-Saharan Africans, including the

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have a similar genetic composition to that of Cardial individuals from Iberia, evidencing a common origin, and ruling out an Andalusian Early Neolithic distinct from Cardial Culture. [Figure 3 here] Finally, although limited by low coverage, phenotypic predictions based on genetic variants of known effects agree with our estimates of global ancestry. IAM people do not possess any of the European SNPs associated with light pigmentation, and most likely had dark skin and eyes. IAM samples present ancestral alleles for pigmentation-associated variants present in SLC24A5 (rs1426654), SLC45A2 (rs16891982) and OCA2 (rs1800401 and 12913832) genes. On the other hand, KEB individuals exhibit some European- derived alleles that predispose individuals to lighter skin and eye colour, including those on genes SLC24A5 (rs1426654) and OCA2 (rs1800401) (Supplementary Note 11). **CONCLUSION** Genetic analyses have revealed that the population history of modern North Africans is quite complex<sup>11</sup>. Based on our aDNA analysis, we identify an Early Neolithic Moroccan component that is restricted to North Africa in present-day populations<sup>11</sup>, and that is the sole ancestry in IAM samples. We hypothesize that this component represents the autochthonous Maghrebi ancestry associated with Berber populations. This Maghrebi component is different from those of any ancient samples studied so far and is distantly related to that of Epipaleolithic people from the Levant. Our data suggests that the IAM population was isolated in the Maghreb since the Upper Palaeolithic back migration, although it is impossible to be certain without paleogenomic data from North African Palaeolithic samples. An expansion in Early Neolithic times followed by strong genetic drift might also be plausible. Our hypothesis is in agreement with archaeological research pointing to the first stage of the Neolithic expansion in Morocco as the result of a local population who adopted some

technological innovations, such as pottery production or farming, from neighbouring areas.

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Human Origins panel<sup>2</sup> and the HGDP dataset genotyped with MEGA-ex (Illumina Inc.). For principal component analysis, we projected the aDNA samples on the PCA space built with the modern dataset, using smartpca<sup>37</sup> and LASER<sup>38</sup>. Admixture estimations were done using ADMIXTURE software<sup>21</sup>. F<sub>ST</sub> distances were calculated using smartpca<sup>37</sup>. Identity-bydescent proportions were estimated using PLINK<sup>39</sup>, and heterozygosity estimations using a newly developed method for low-coverage genomes (Supplementary Note 8). f-statistics estimates were calculated using admixtools software<sup>23</sup>. All plots were prepared using R software<sup>40</sup>. Detailed information about methods is included in the Supplementary Notes. Acknowledgements C.D.B and R.F. were funded by a grant from the National Science Foundation (1201234). R.F. was funded by Fundación Canaria Dr. Manuel Morales fellowship. A.E.R.S. was funded by Ciencia sem Fronteiras fellowship - CAPES, Brazil. B.S. and J.K. were funded by a grant from the Gordon and Betty Moore Foundation (GBMF-3804). Author Contributions R.F. and C.D.B conceived the idea for the study, D.M.S, M.D.C.M, J.S., J.M, Y.B., F.J.R.S., A.M. and A.T.M assembled skeletal material and provided archaeological background for the samples, R.F., A.E.R.S., J.K. and A.S. performed work in the wet laboratory, F.M. developed methods for data analysis, M.R. developed methods for DNA capture, R.F., F.M., M.A.A, P.A.U, G.W., analysed data, C.D.B and B.S. supervised the study, R.F., F.M. and C.D.B. wrote the manuscript and supplements with input from all coauthors. **Author Information** Sequence data are available through the European Nucleotide Archive (PRJEB22699). Consensus mtDNA sequences are available at the National Center of Biotechnology Information (Accession Numbers MF991431-MF991448). The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to R.F. (e-mail: rfregel@stanford.edu).

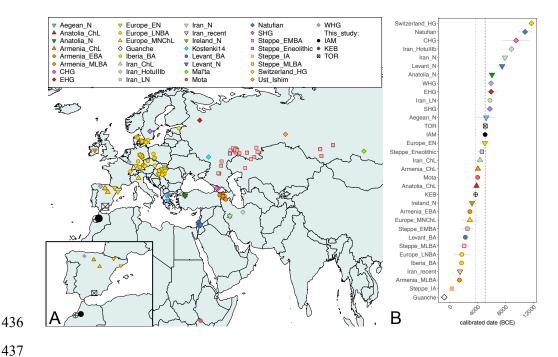
doi:https://doi.org/10.1016/j.quaint.2015.08.082 (2016).

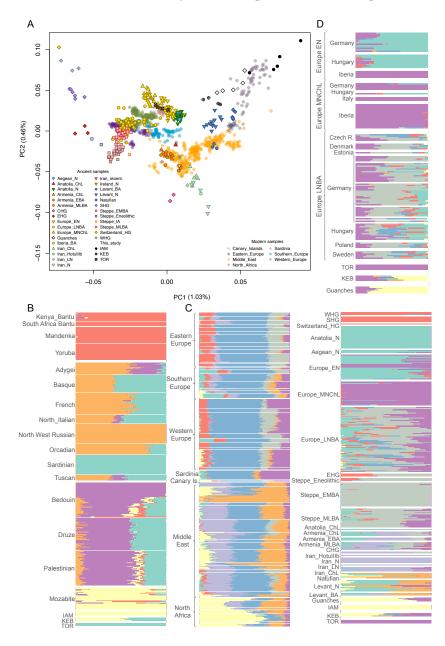
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## **FIGURES**

Figure 1. Geographical location (A) and calibrated radiocarbon date (B) of the samples included in this study, as well as other ancient DNA samples from the literature.





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## 446 f3-statistic for KEB (D).

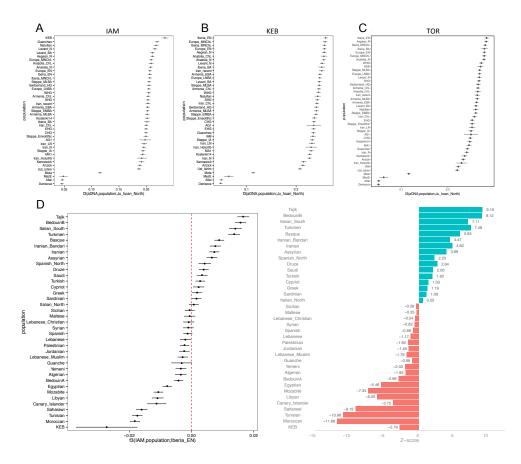


Table 1 - Summary statistics for North African and Iberian samples.

Sample	Origin	2 sigma calibrated radiocarbon date (BCE)	MtDNA coverage	MtDNA haplogroup	Contamination estimation	Molecular sex	Y-chromosome haplogroup	SNPs in MEGA dataset	SNPs in Human Origins dataset	MEGA coverage	Genome- wide coverage
IAM.3	Ifri n'Amr or Moussa	5325 - 5210	5X	M1b1	6.42% (21.49% - 1.90%)	XX	•	26,798	5,353	0.04X	0.01X
IAM.4	Ifri n'Amr or Moussa	5215 - 5005	52X	U6a1b	4.66% (6.64% - 3.26%)	XY	E-L19*	62,729	17,093	0.12X	0.02X
IAM.5	Ifri n'Amr or Moussa	5199 - 5176 5066 - 4942	82X	U6a1b	3.68% (5.26% - 2.62%)	XX	E-L19*	408,744	208,661	1.72X	0.74X
IAM.6	Ifri n'Amr or Moussa	5290 - 5265 5230 - 5195 5180 - 5060	21X	U6a7b2	5.28% (8.48% - 3.02%)	XX	1	90,226	18,285	0.17X	0.02X
IAM.7	Ifri n'Amr or Moussa	5000 - 4840	129X	U6a3	2.35% (3.39% - 1.67%)	XY		177,041	45,134	0.38X	0.06X
KEB.1	Kelif el Boroud		18X	X2b	3.03% (6.31% - 1.23%)	XX		96,946	39,312	0.16X	0.08X
KEB.3	Kelif el Boroud		20X	Klalbl	3.16% (5.73% - 1.72%)	-	-			1	
KEB.4	Kelif el Boroud		135X	Klalbl	2.49% (3.27% - 1.89%)	XX		304,607	77,964	0.64X	0.12X
KEB.6	Kelif el Boroud	3/80 - 3650	14X	Kla4al	3.77% (6.72% - 1.98%)	XY	T-M184	95,152	52,694	0.16X	0.14X
KEB.7	Kelif el Boroud		12X	T2b3	1.44% (4.31% - 0.31%)	XY					
KEB.8	Kelif el Boroud		23X	X2b	3.03% (6.23% - 1.27%)	XX		34,385	18,974	0.06X	0.05X
TOR.1	El Toro	5280 - 4780	170X	T2c1d	1.42% (2.07% - 0.98%)	-				ı	
TOR.5	El Toro	5040 - 4850	18X	J2b1a	4.47% (8.76% - 1.96%)	XY	G-M201				
TOR.6	El Toro		53X	T2b3	4.15% (5.89% - 2.94%)	XX		318,110	101,698	0.67X	0.17X
TOR.7	El Toro		126X	T2b3	7.06% (8.36% - 5.88%)	XX		115,652	24,719	0.18X	0.03X
TOR.8	El Toro	5280 - 4780	234X	Klal	3.95% (4.80% - 3.26%)	XX		212,370	46,364	0.38X	0.06X
TOR.11	El Toro		124X	K1a2a	3.88% (5.00% - 2.98%)	XX		80,687	17,306	0.15X	0.03X
TOR.12	El Toro		174X	J2b1a	1.50% (2.30% - 0.93%)	XY				ı	