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Genomic and dietary transitions during the Mesolithic and Early Neolithic in Sicily

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1 Genomic and dietary transitions during the Mesolithic and 2 Early Neolithic in Sicily

3 4 Short title

5 Genomic and dietary shifts in Sicilian prehistory

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37 **Abstract**

38 Southern Italy is a key region for understanding the agricultural transition in the Mediterranean due to its
39 central position. We present a genomic transect for 19 prehistoric Sicilians that covers the Early Mesolithic
40 to Early Neolithic period. We find that the Early Mesolithic hunter-gatherers (HGs) are a highly drifted
41 sister lineage to Early Holocene western European HGs, whereas a quarter of the Late Mesolithic HGs
42 ancestry is related to HGs from eastern Europe and the Near East. This indicates substantial gene flow from
43 (south-)eastern Europe between the Early and Late Mesolithic. The Early Neolithic farmers are genetically
44 most similar to those from the Balkan and Greece, and carry only a maximum of ~7% ancestry from Sicilian
45 Mesolithic HGs. Ancestry changes match changes in dietary profile and material culture, except for two
46 individuals who may provide tentative initial evidence that HGs adopted elements of farming in Sicily.

47

48 **One-sentence summary**

49 Genome-wide and isotopic data from prehistoric Sicilians reveal a pre-farming connection to (south-)
50 eastern Europe, and tentative initial evidence that hunter-gatherers adopted some Neolithic aspects prior to
51 near-total replacement by early farmers.

52

53 **Key words**

54 Ancient DNA, isotopes, Europe, Sicily, Ice Age, Mesolithic, Neolithic, Castelnovian, farming

55 **MAIN TEXT**

56 **Introduction**

57 Southern Italy and Sicily feature some of the earliest evidence for agricultural food production in
58 the Central Mediterranean, starting as early as ~6,000 calBCE (1) or earlier (~6,200 calBCE (2)). In the
59 Mediterranean area, two Early Neolithic meta-horizons had developed in parallel by ~5,500 calBCE (3-5).
60 In the eastern and central Mediterranean, Early Neolithic farmers produced Impresa Wares with various
61 decorative impressed designs made with a wide selection of tools. In contrast, in the western Mediterranean
62 the decorative designs were preferentially made with *Cardium* seashell impressions, resulting in the typical
63 Cardial Ware pottery (6). In Sicily and southern Italy two Impresa Ware horizons appeared rapidly in a
64 timeframe of ~500 years. The very first aspect of Impresa Wares appeared 6,000-5,700 calBCE followed
65 by the Impressed Ware of the Stentinello group (Stentinello/Kronio) around 5,800-5,500 calBCE (1, 7, 8).
66 The Early Neolithic horizons in Sicily may have their origin in the early farming traditions in the Balkans
67 (9-11).

68 Grotta dell'Uzzo, in northwestern Sicily, is a key site for understanding human prehistory in the
69 Central Mediterranean, and has provided unique insights into the cultural, subsistence and dietary changes
70 that took place in the transition from hunting and gathering to agro-pastoralism (12-14). The cave
71 stratigraphy covers the late Upper Palaeolithic through the Mesolithic and up to the Middle Neolithic, with
72 traces of later occupation. Quite uniquely in the Mediterranean region, deposits at Grotta dell'Uzzo show a
73 continuous occupation during the Mesolithic (12). Zooarchaeological and isotopic investigations indicated
74 shifts in the economy and diet of the cave occupants, who subsisted by hunting and gathering for most of
75 the Mesolithic, started to exploit marine resources towards the end of the Mesolithic, and combined all the
76 previous activities with the exploitation of domesticates and increased fishing during the Early Neolithic
77 (12-14).

78 Genome-wide data has been published for six (Epi-)Gravettian HGs and one tentatively
79 Sauveterrian Mesolithic HG from peninsular Italy, and one Late Epigravettian HG from *OrienteC* in Sicily
80 (15-17). To date, no ancient genomes are available for Early Neolithic and Late Mesolithic individuals from
81 Sicily or southern Italy. The question of whether the agricultural tradition was adopted by local HGs or
82 brought to Sicily by incoming farmers, thus, remains open.

83

84 **Results**

85 Here, we investigated the biological processes underlying the transition from hunting and gathering
86 to agropastoralism in Sicily. We reconstructed the genomes for 19 individuals from Grotta dell'Uzzo dating
87 to a period from the Early Mesolithic ~8,810 calBCE to the Early Neolithic ~5,210 calBCE (Data file 1).
88 We obtained a direct accelerator mass spectrometry (AMS) radiocarbon (^{14}C) date on the skeletal elements
89 that were used for genetic analysis for 15 individuals, and determined carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$)
90 isotope values from the same bone collagen for dietary reconstruction (Data file 1).

91 We extracted DNA from bone and teeth in a dedicated clean room, built DNA libraries and enriched
92 for ~1240k single nucleotide polymorphisms (SNPs) in the nuclear genome and independently for the
93 complete mitogenome (18) using in-solution capture (19). We restricted our analyses to individuals with
94 evidence of authentic DNA, and removed ~300k SNPs on CpG islands to minimize the effects of residual
95 ancient DNA damage (20). The final data set includes 868,755 intersecting autosomal SNPs for which our
96 newly reported individuals cover 53,352-796,174 SNP positions with an average read depth per target SNP
97 of 0.09-9.39X (Data file 1). We compared our data to a global set of contemporary (21) and 377 ancient
98 individuals from Europe, Asia and Africa (15-17, 21-51).

99

100 **Genetic grouping of the ancient Sicilians**

101 First, we aimed to group the individuals for genetic analysis. For this we co-analysed one
102 Epigravettian HG (*OrienteC*) from the Grotta d’Oriente site on Favignana island in southwestern Sicily
103 (12,250-11,850 calBCE, ¹⁴C date on charcoal from the deposit (15, 17). The ancient Sicilians form three
104 genetic groups that we distinguished based on the individuals’ ¹⁴C dates (Fig. 1B, Data file 1), position in
105 Principal Component Analysis (PCA, Fig. 1C), mtDNA haplogroups (Supplementary Section S7), and
106 degree of allele sharing in outgroup-*f*₃ statistics and qpWave-based ancestry models (Supplementary
107 Section S2).

108 The first two groups consist of individuals that fall close to a cluster of western European Mesolithic
109 hunter-gatherers (‘WHG’) that includes the 14,000-year-old individual from the Villabruna site in northern
110 Italy (‘Villabruna’) (16) (Fig. 1C). The first and oldest genetic group, which we labelled Sicily Early
111 Mesolithic (Sicily EM, n=3), contains the previously published Epigravettian *OrienteC* (12,250-11,850
112 calBCE (15, 17)) and the two oldest HGs from Grotta dell’Uzzo (~8,800-8,630 calBCE). These three
113 individuals carried mitogenome lineages that fall within the U2’3’4’7’8’9 branch (Supplementary Section
114 S7, and (15, 17) for *OrienteC*). From that haplogroup node they shared nine mutations specific to their
115 lineage and were differently related to each other with regard to three additional private mutations.
116 U2’3’4’7’8’9 mitogenome lineages have already been reported for Upper Palaeolithic European HGs, such
117 as *Paglicci108* associated with the Gravettian in Italy (26,400-25,000 calBCE (52)). The second genetic
118 group, which we labelled as Sicily Late Mesolithic (Sicily LM, n=9), contains nine individuals dated to
119 ~6,750-5,850 calBCE. The mitogenome haplogroups carried by the Sicily LM HGs are U4a2f (n=1), U5b2b
120 (n=2), U5b2b1a (n=1), U5b3(d) (n=3), U5a1 (n=1), and U5a2+16294 (n=1), which are typical for European
121 Late Mesolithic WHGs (52, 53).

122 The third and most recent genetic group, which we labelled as Sicily Early Neolithic (Sicily EN,
123 n=7), contains seven individuals dated to ~5,460-5,220 calBCE. In PCA, these individuals show
124 substantially Near-Eastern-related ancestry and fall close to early farmers from the Balkans (Croatia,
125 Greece), Hungary, and Anatolia, but not Iberia (Fig. 1C) (17, 38, 39, 54). All the individuals in the Sicily

126 EN group, with sufficient coverage for genome reconstruction, carried mitogenome haplogroups
127 characteristic for European early farmers: U8b1b1 (n=2), K1a2 (n=1), N1a1a1 (n=1), J1c5 (n=1) and H
128 (n=1) (55).

129

130 **Mesolithic substructure and dynamics**

131 Previous research has shown that the genetic diversity among European HGs after the Last Glacial
132 Maximum (LGM) was shaped by various deeply diverged ancestries (16, 17, 32, 38, 50, 56). One such
133 ancestry came from a group of pre-LGM individuals dating to ~30,000 calBCE and associated with the
134 Gravettian industry (Věstonice cluster). Another one was from individuals associated with the Magdalenian
135 industry (El Mirón cluster) that appeared in Europe by ~17,000 calBCE (16). Individuals of the Villabruna
136 cluster, also referred to as western European hunter-gatherers (WHGs), appeared ~12,000 calBCE
137 throughout continental Europe, and replaced most of the ancestry of the earlier clusters in European HGs.
138 In Mesolithic HGs from eastern Europe (EHGs, ~6,000 calBCE) and the Iron Gates HGs from southeastern
139 Europe (~9,500-5,800 calBCE), ancestry related to Upper Palaeolithic Siberians (Ancient North Eurasians,
140 ANE) was found in addition to WHG ancestry.

141 To visualize the genetic differentiation among the Sicily EM and LM HGs, and their relation to
142 other West Eurasian HGs, we plotted pairwise genetic distances calculated as $f_3(\text{Mbuti}; \text{HG1}, \text{HG2})$ in a
143 Multidimensional Scaling (MDS) plot (Fig. 2A). The genetic variation among post-LGM European HGs is
144 structured along two clines: 1) a WHG-EHG-ANE cline, confirming the genetic gradient found in
145 Mesolithic HGs from western to eastern Europe and 2) a WHG-GoyetQ2 cline between WHG and Central
146 European Magdalenian-associated individuals on which Iberian HGs take an intermediate position (15-17,
147 38, 50, 56). As previously reported for *OrienteC* (15), the Sicily EM HGs *UZZ5054* and *UZZ96* fall at the
148 extreme WHG-end of both ancestry clines, slightly outside the genetic variation of the Villabruna cluster,
149 named after the site name of its oldest representative individual (~12,230-11,830 calBCE) (Fig. 2A). The

150 position of the Sicily EM HGs on the MDS plot either hints at a WHG ancestry component that is more
151 basal than that found in Villabruna cluster individuals, and/or at substantial genetic drift. Compared to the
152 Sicily EM HGs, the Sicily LM HGs fall closer to the Villabruna cluster in between Sicily EM HGs and
153 Mesolithic Iron Gates HGs (Fig. 2A).

154 First, we investigated whether the Sicily EM HGs contain substantial lineage-specific genetic drift.
155 We hence determined the nucleotide diversity (π) by calculating the average proportion of nucleotide
156 mismatches for all possible combinations of individual pairs within the Sicily EM HG group, and compared
157 that to the average of other HG groups. We indeed found significant lower nucleotide diversity for the Sicily
158 EM HGs (95% confidence interval (95CI) $\pi = 0.161-0.170$), compared to HGs from Italy from the preceding
159 Upper Palaeolithic (95CI $\pi = 0.227-0.239$), and the subsequent Sicily LM HGs (95CI $\pi = 0.217-0.223$), and
160 later farmers (Fig. 3 and fig. S3.1). In addition, the nucleotide diversity for the Sicily EM HGs is ~20%
161 lower compared to contemporaneous HG groups from Central Europe, Iberia and the Iron Gates (Fig. 3).
162 The reduced genetic diversity of Sicily EN HG hence appears to be both geographical- and temporal-
163 specific.

164 Secondly, we compared the ancestry component as found in Sicily EM and LM HGs, and their
165 respective affinities to West Eurasian HGs, using an f_4 -cladality test of the form $f_4(\text{Chimp}, X; \text{Sicily EM}$
166 $\text{HG}, \text{Sicily LM HG})$. We found a pattern that is linked with geography (Fig. 4A): Sicily EM HGs share
167 significantly more alleles with HGs from western Europe, including Villabruna cluster HGs, and Iberian
168 Upper Palaeolithic and Mesolithic HGs that carry Magdalenian-associated ancestry (16, 50). In contrast,
169 the Sicily LM HGs share significantly more alleles with Upper Palaeolithic and Mesolithic HGs from
170 (south-)eastern Europe and Russia, including *AfontovaGora3*, EHG, *Mal'tal* and Iron Gates HGs.
171 Notably, comparing the ancestry in Sicily EM HGs with that of *Villabruna* with the cladality statistic
172 $f_4(\text{Chimp}, X; \text{Sicily EM HG}, \text{Villabruna})$ results in a similar geographical pattern (fig. S4.3). Also here,
173 Sicily EM HGs share an excess of alleles with western European HGs, including the majority of Villabruna
174 cluster individuals, whereas *Villabruna* does with (south-) eastern European HGs. Fu et al. (16) already

175 showed an East Asian affinity for some individuals of the Villabruna cluster individuals compared to older
176 individuals. However, using the Sicily EM HGs as a baseline for WHG ancestry pulls out the difference in
177 genetic affinities to Magdalenian-associated and EHG/ANE-related ancestry more strongly between
178 western and eastern West Eurasian HGs (Supplementary Section S4).

179 With more explicit modelling using qpGraph (57) we further examined the phylogenetic position
180 of Sicily EM HGs. In the least complex scaffold tree Sicily EM HGs and *Villabruna* form a clade on an
181 unadmixed branch, with *GoyetQ2*, a Magdalenian-associated HG, as an outgroup to both of them (fig. S5.3).
182 However, trees that place either *Villabruna* or Sicily EM HGs on an admixed branch with an additional
183 ancestry contribution from *AfontovoGora3* and *GoyetQ2*, respectively, fit the allele frequencies
184 approximately equally well (Supplementary Section S5). Overall, the results suggest that the Sicily EM
185 HGs represent a highly drifted branch closely related to the Villabruna cluster. We can however not rule
186 out that Sicily EM HGs derived an ancestry contribution from Magdalenian-associated individuals or that
187 Sicily EM HGs descended from a more basal lineage that admixed into Iberian HGs and Villabruna cluster
188 individuals (fig. S5.5).

189 Subsequently, we characterized the ancestry profile of the Sicily LM HGs in more detail. Since the
190 position of Sicily LM HGs on the MDS and PCA plots (Fig. 1D, 2A) is closer to *Villabruna* cluster
191 individuals and EHG, we investigated whether their gene pool is the result of admixture between the
192 preceding Sicily EM HGs and a group high in EHG-ancestry, or is genetically drifted from Villabruna
193 cluster HGs.

194 First, we used the outgroup f_3 -statistic $f_3(\text{Mbuti}; \text{Sicily LM HGs}, X)$ to investigate for various West-
195 Eurasian HGs (X) which one is genetically closest to Sicily LM HGs (fig. S4.1). Sicily LM HGs shows the
196 highest degree of allele sharing with Sicily EM HGs, followed by other individuals from the Villabruna
197 cluster. Moreover, the statistic f_4 (Chimp, Sicily LM HGs; Sicily EM HGs, X) is strongly significantly
198 negative for all tested West-Eurasian HGs, including Villabruna cluster individuals (fig. S4.2). This implies
199 that the Sicily LM HGs form a clade with Sicily EM HGs to the exclusion of other West-Eurasian HGs.

200 Taken together, these statistics indicate substantial continuity in ancestry between the Sicily EM and LM
201 HGs. However, when Sicily EM HGs is used as baseline for the ancestry in Sicily LM HGs in the f_4 -statistic
202 $f_4(\text{Chimp}, X; \text{Sicily EM HGs}, \text{Sicily LM HGs})$, additional admixture signals are found for various HGs from
203 (south)-eastern Europe and Russia (Fig. 4A). Therefore, Sicily EM HGs do not represent the full gene pool
204 of the Sicily LM HGs.

205 Subsequently, using qpAdm-based admixture models (36) we aimed to more explicitly model the
206 gene pool of the Sicily LM HGs. We found that a three-way ancestry combination of $75.0 \pm 1.6\%$ Sicily EM,
207 $15.5 \pm 2.4\%$ EHG and $9.5 \pm 2.8\%$ Pınarbaşı, a $\sim 13,300$ calBCE HG from central Anatolia (25), results in a
208 good fit ($P = 0.123$, Table 1). Notably, replacing the Sicily EM ancestry with that of *Loschbour* resulted in
209 poorly fitting models ($P_{\text{Adm}} = 4.27\text{E-}09$, Table 1). The assigned ancestry components confirm both the
210 substantial continuation of the local Sicily EM ancestry, and the influx of a non-local ancestry from (south-
211)eastern Europe, in Sicily during the Mesolithic. Moreover, the Upper Palaeolithic Pınarbaşı-related
212 ancestry in the Sicily LM HGs is striking, and underlines previous indications for a pre-Neolithic genetic
213 connection between the Near East and European HGs by at least 12,000 calBCE (16, 17, 25).

214 In a last step, we characterised the ancestry profiles of the Sicily LM HGs on an individual level
215 (Fig. 2B and Fig. 5A). The Sicily LM HGs form a heterogeneous group, with some individuals containing
216 both the EHG and Near Eastern-related ancestry in addition to the preceding local Sicily EM ancestry,
217 whereas others contain solely the additional EHG-related ancestry. The summed proportion for the non-
218 local (EHG + Pınarbaşı) ancestry component in Sicily LM HGs ranges between $17 \pm 2\%$ and $33 \pm 4\%$ (Fig.
219 2B, Fig. 5A, Data file 1). Interestingly, whereas a Near Eastern-related ancestry component is discerned in
220 many of the Mesolithic HGs from the Iron Gates and other areas in the Balkan, Baltic or Scandinavia, this
221 is not the case for any of the Villabruna cluster individuals. In contrast to previous statements that the
222 Villabruna cluster individuals form a genetically homogenous group (16, 25), here the individuals show
223 rather diverse ancestry profiles with various combinations of Sicily EM, EHG and *GoyetQ2*-related
224 ancestry. Since the Sicily LM HG gene pool contains the distinct Near Eastern-related ancestry but not the

225 *GoyetQ2*-related ancestry, it is unlikely that the diversity of this group originated solely from genetic drift
226 from these Villabruna cluster individuals. We speculate that a single hitherto unsampled population, with
227 an ultimate origin perhaps in the Near East or Caucasus, might harbor the genetic diversity that fits the
228 combined EHG- and Near Eastern-related ancestry in Sicily LM HGs and additional West-Eurasian HGs
229 (e.g. related to the ~24,000 calBCE Caucasus HGs from Dzudzuana Cave (56).

230

231 **Expanding early farmers replace local HGs in Sicily**

232 Recent ancient human DNA studies have shown that the genetic variation in Early Neolithic groups
233 from central and southwestern Europe is a subset from that found in early farmers from Barcin in
234 northwestern Anatolia and Revenia in northern Greece (30, 34-37, 39). Interestingly, early farmers from
235 Diros in Peloponnese Greece might harbour an ancestry component that places them outside of the genetic
236 diversity represented by those from Anatolia Barcin (17).

237 In PCA (Fig. 1C, Data file 1) the Sicilian early farmers (Sicily EN) plot closest to Early Neolithic
238 groups from the Balkan, Serbia, Hungary, Greece and Anatolia, but not from Iberia. With the f_3 -outgroup
239 statistic $f_3(\text{Mbuti}; \text{Sicily EN}, X)$ we aimed to determine the best genetic proxies for the overall gene pool
240 related to Sicily EN. Congruent to the PCA results, the Sicilian early farmers share most genetic drift with
241 various Early Neolithic farmers from the Balkan and Central Europe (Fig. 4B). In addition, in the PCA the
242 Sicilian early farmers do not fall on a cline towards the Sicilian Mesolithic HGs. This suggests that HG
243 ancestry is either absent or low, which would imply a large population replacement in Sicily with the
244 appearance of the Early Neolithic horizons.

245 To investigate this more formally, we first tested whether Sicilian early farmers contain a distinct
246 HG ancestry component that is not found in early farmers from Anatolia EN Barcin (38). For this we used
247 the admixture f_4 -statistic $f_4(\text{Chimp}, X; \text{Anatolia EN Barcin}, \text{Sicily EN})$ that tests for an excess of shared
248 alleles between Sicilian early farmers and various West Eurasian HGs (X) when Anatolia EN Barcin is used

249 as a baseline for the early farmer ancestry (fig. S6.1). Sicily EN shows strongly significant signals for
250 admixture for the preceding local Sicily EM ($z = 4.12$) and Sicily LM HGs ($z = 4.09$).

251 To test whether the HG component in Sicily EN is genetically closer to the ancestry of the local
252 preceding Sicily LM HGs or to that of a specific non-local HG source, we performed the f_4 -admixture
253 statistic $f_4(\text{Chimp}, \text{Sicily EN}; \text{Sicily LM HG}, \text{non-local HG})$ (fig. S6.2). For HGs from central and
254 southwestern Europe this statistic is negative, indicating that none of them is genetically closer to the HG
255 ancestry in Sicily EN than Sicily LM HGs are. Contrastingly, Mesolithic HGs from southeastern Europe,
256 including Iron Gates HGs, Croatia Mesolithic and Koros EN HGs, do show an excess of shared genetic
257 drift with Sicily EN (fig. S6.2). However, southeastern European HGs and early farmers from Anatolia
258 Barcin and the Balkan share a part of their ancestry (17, 25). The excess genetic attraction for southeastern
259 European HGs might hence be driven by the farmer, rather than HG, ancestry component in Sicily EN.

260 To further investigate what combination of early farmer and HG ancestry fits the Sicily EN gene
261 pool best, and their respective admixture proportions, we used qpWave (P_{Wave}) and qpAdm-based (P_{Adm})
262 ancestry models. We required a test result to be more extreme (larger) than $P = 0.1$ in order not to reject the
263 null-hypothesis of a full ancestry fit (full rank). We found that the ancestry for approximately half of the
264 Sicilian early farmers can be fitted as entirely early farmer ancestry as found in Anatolia EN Barcin, Greece
265 EN Peloponnese, Croatia EN Cardial and Impressa, Hungary EN Koros or Germany LBK (Fig. 4, Data file
266 7). However, these early farmer sources were rejected as sole ancestry sources to the combined Sicily EN
267 gene pool (max. $P_{\text{Wave}} \leq 0.011$ for Croatia EN Cardial, Data file 7). We could improve the model fit to the
268 Sicily EN gene pool by adding ~4-9% ancestry from Sicily LM or Sicily EM HGs as a second source to
269 early farmer ancestry from either Anatolia EN Barcin ($P_{\text{Adm}} \geq 0.016$), Greece EN Peloponnese ($P_{\text{Adm}} \geq$
270 0.059), Croatia EN Cardial ($P_{\text{Adm}} \geq 0.056$) or Hungary EN Koros ($P_{\text{Adm}} \geq 0.300$) (Table 1, Data file 7).
271 Notably, three-way mixture models, in which the ancestry from Anatolia EN Barcin was combined with
272 that from early farmers from Ganj Dareh as a proxy for the early farmer ancestry, improved the fit to the
273 Sicily EN gene pool even further ($P_{\text{Adm}} \geq 0.335$, Table 1). We can therefore not exclude the possibility that

274 the early farmer ancestry in Sicily EN falls partly outside of the broader genetic diversity of the early
275 farmers from Europe and Anatolia Barcin (Supplementary Section S6).

276 Replacing the local Sicilian HG ancestry with that from Iron Gates HGs or many other Mesolithic
277 European HGs often resulted in similar fits (Table 1, Data file 7). To the limits of the genetic resolution,
278 we hence could not accurately discern whether the Sicilian early farmers derived their HG ancestry from a
279 Mesolithic local Sicilian HG source or from a geographically more distant one. However, a local
280 contribution appears to be the most plausible explanation, which is in line with the hypothesized continuity
281 in occupation at Grotta dell'Uzzo (14, 58-60).

282

283 Discussion

284 Southern Italy has long been viewed as a southern refugium (61, 62) during the LGM, ~25,000
285 years ago, from where Europe was repopulated (16, 52, 63). The earliest evidence for the presence of *Homo*
286 *sapiens* in Sicily dates to ~17,000-16,000 calBCE, following the time when a land bridge connected the
287 island to peninsular Italy (64, 65). Some Late Epigravettian sites in Sicily contain rock panels with engraved
288 animal figures, which are indistinguishable from those of the Franco-Cantabrian style typical of the
289 Magdalenian (66). Moreover, the presence of some decorated pebbles at sites in northwestern Sicily is also
290 suggestive of cultural links with the Azilian in the French Pyrenees (66). Although there are many sites in
291 peninsular Italy and Sicily with evidence of Late Upper Palaeolithic occupation, this decreases during the
292 Mesolithic (67). The Early Mesolithic HGs from Grotta dell'Uzzo analysed here produced a lithic industry
293 of Epigravettian tradition ((68), Supplementary Section S1) and, in continuity with their predecessors,
294 subsisted mainly by hunting large terrestrial game with important contributions of plant foods and limited
295 consumption of marine resources (12) (Fig. 5B). Here we showed that, compared to the ~12,000 calBCE
296 *Villabruna* individual, the Sicily EM HGs have a higher genetic affinity to Magdalenian-associated Iberian
297 HGs *El Miron* and *Balma Guilanyà*. Given the profoundly reduced genetic diversity in the Sicily EM HGs

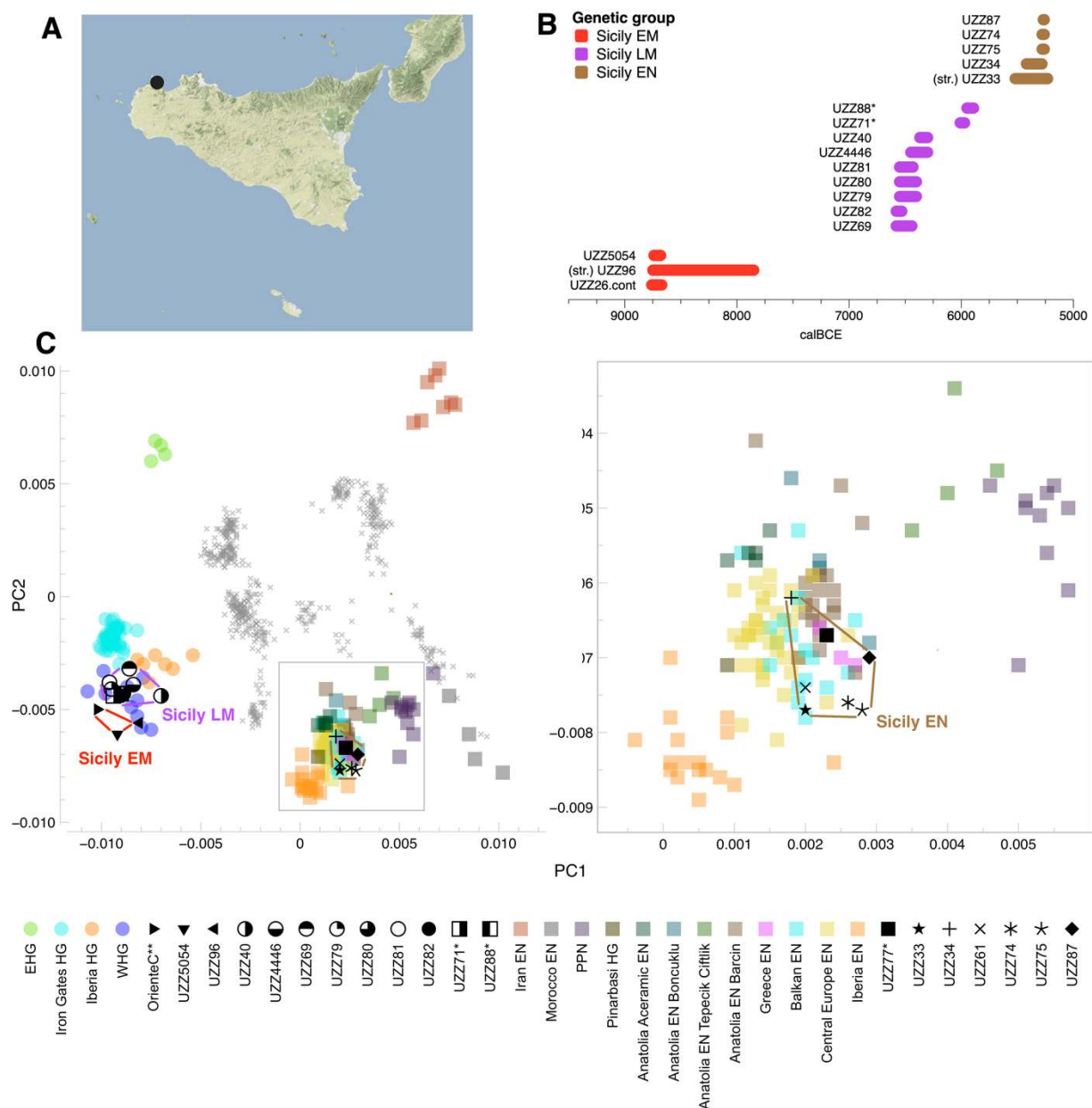
298 and their closely related non-identical mitogenomes in the U2'3'4'7'8'9 branch, we speculate that these
299 individuals are unadmixed descendants from a peri-glacial refugium population.

300 The subsequent ~6,750-5,850 calBCE Late Mesolithic HGs derive between 15-37% of their
301 ancestry from an EHG-related source with an affinity to the Near East. The substantial influx of non-local
302 ancestry indicates a large genetic turnover in Sicily during the Mesolithic, and is matched by a change in
303 diet that is characterized by a statistically significantly higher intake of marine-based protein (Fig. 5B). The
304 seven oldest individuals in this group (dated ~6,750-6,250 calBCE) are tentatively assigned to the
305 Castelnovian *sensu lato* facies (12, 14, 69) (Supplementary Section S1). The Castelnovian is part of the
306 pan-European Late Mesolithic blade and trapeze lithic complex, and appeared throughout Italy ~6,800-
307 6,500 calBCE ((70), D. Binder personal communication). These lithic industries have been argued to
308 originate from the Circum Pontic area (71, 72), with a possible ultimate origin from as far as eastern Asia
309 (73, 74), or alternatively from the Capsian culture in northwestern Africa (75, 76). The ancestry profiles of
310 the individuals associated with the Castelnovian *sensu lato* show a similarity to those of Mesolithic HGs
311 from the Iron Gates, eastern Europe and the Baltic, hence providing support for a connection to the East.

312 The Sicilian early farmers carried almost exclusively ancestry characteristic for early European
313 farmers. The preceding Late Mesolithic HGs may have contributed only a maximum of ~7% ancestry (Fig.
314 5A). Six individuals in this group are from layers that chronologically coincide with the presence of Early
315 Neolithic Stentinello Wares, and one individual (UZZ77, undated) tentatively with older aspects of Impresa
316 Ware (Supplementary Section S1). The isotope values of the Stentinello Ware associated early farmers are
317 congruent with them having a terrestrial-based farming diet (Fig. 5B). Their ancestry composition points to
318 a full-scale demographic transition during the Early Neolithic, similar to the Mesolithic-Neolithic transition
319 in other regions in Europe (30, 34, 36, 37, 53, 54, 77). Intriguingly however, two individuals UZZ71 and
320 UZZ88, dated ~6,050-5,850 calBCE, chronologically coincide with layers at the site that may contain the
321 very first aspects of Impresa Wares (12). These two individuals fall fully within the genetic diversity of
322 the Late Mesolithic HGs associated with the Castelnovian *sensu lato*, despite postdating them by ~200 years

323 (Fig. 1C, 5A, Supplementary Section S1, S2). Both these individuals show isotope values that are strikingly
324 different from both the later Sicilian Early Neolithic farmers associated with Stentinello pottery and
325 preceding Late Mesolithic HGs (Fig. 5B, Data file 1). The diet of the *UZZ71* individual included a large
326 proportion of freshwater protein, similarly to what is recorded for Mesolithic hunter-gatherers from the Iron
327 Gates on the Balkan peninsula (e.g. (78, 79)). On the other hand, *UZZ88* has an isotopic composition ($\delta^{13}\text{C}$
328 = -19.2‰ , $\delta^{15}\text{N} = 7.1\text{‰}$) that suggests a terrestrial-based farming diet with very low levels of animal protein
329 consumption and that is significantly different from the hunter-gatherers it descended from (mean $\delta^{13}\text{C} = -$
330 $16.6 \pm 1.8\text{‰}$, mean $\delta^{15}\text{N} = 13.0 \pm 1.0\text{‰}$), who relied for around half of their protein on seafood. Given the
331 distinct diets and the intermediate ^{14}C dates, these two individuals might provide tentative initial evidence
332 that HGs adopted elements of farming in Sicily, as was hypothesized by Tusa (59, 60). However, more
333 extensive research on the stratigraphy of Grotta dell'Uzzo is necessary to determine whether the Impressa
334 Ware aspects are indicative of a transitional period (80) or should be considered intrusive (81).

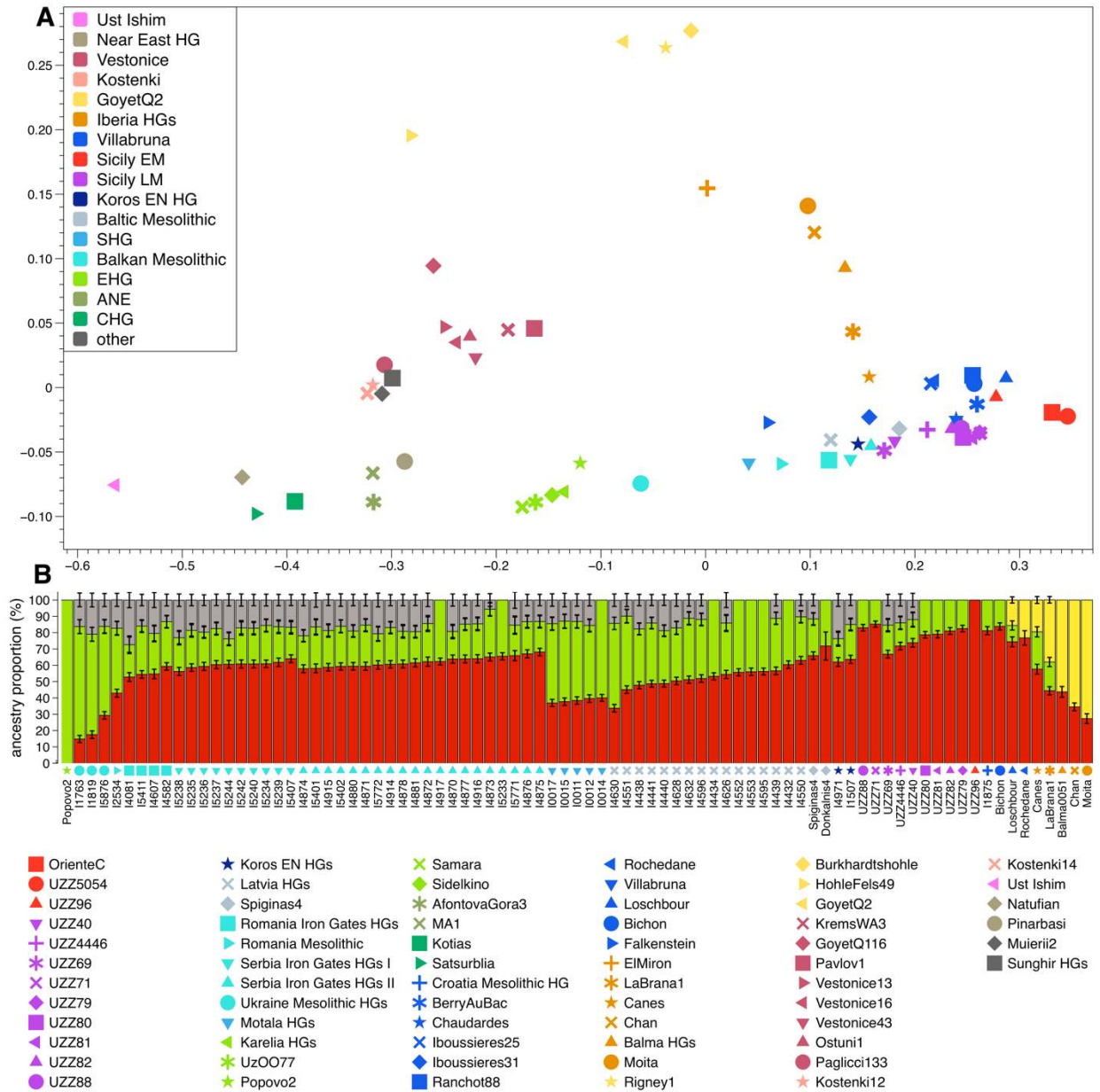
335 Although individuals that blur the Mesolithic and Neolithic dichotomy are rather rare, they have
336 been reported before (17, 29, 78). Taken together, these individuals could indicate that hunter-gatherers
337 may have met early farmers in different areas of the Mediterranean for which the frequency and exact
338 geographical interaction sphere remains to be unravelled.



339

340 **Fig. 1. Genetic structure of ancient West Eurasians.** (A) The geographical location of Grotta dell'Uzzo
 341 in Sicily. (B) Dating of the ancient Sicilians. Dates were determined from direct radiocarbon (^{14}C)
 342 measurements, and for *UZZ96* and *UZZ33* from the stratigraphy (str.) (Supplementary Section S1). Dates
 343 could not be inferred for individuals *UZZ61*, and -77. The individuals fall into three temporal groups, and
 344 are coloured according to their assigned genetic group. *UZZ71*, -88 and -77 may be contemporaneous with

345 early Impressa Ware aspects at the site (marked by *). (C) PCA plots for the genetic distances between
346 West-Euradians with principal components constructed from individuals from 43 modern Eurasian groups
347 (grey crosses). The ancient Sicilians are projected (black symbols) together with relevant previously
348 published hunter-gatherers (coloured dots) and early farmers (coloured squares). We co-analyzed an
349 Epigravettian HG from OrienteC (15) (marked by **). The genetic variation of the ancient Sicilians forms
350 three genetic groups, that we labelled Sicily EM, LM and EN. The individuals in the Sicily EM and LM
351 genetic group fall close to individuals from the Villabruna cluster that are characterized by high levels of
352 WHG ancestry. In contrast, those from the Sicily EN genetic group contain substantially more Near Eastern
353 ancestry, and fall among early farmers from the Balkan and Central Europe but not from Iberia.



354

355 **Fig. 2. Genetic profile characterization for the Sicilian HGs. (A)** MDS plot showing structure in the

356 genetic variation among West Eurasian HGs. Genetic distances are based on pairwise f_3 -outgroup statistics

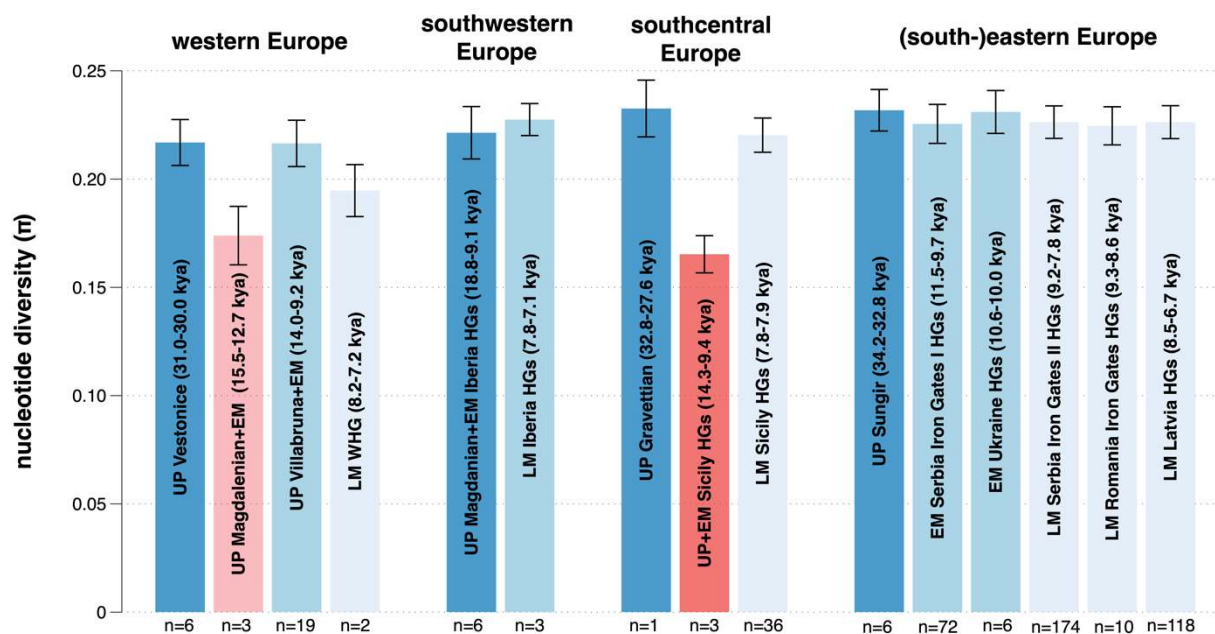
357 of the form $f_3(Mbuti; HG1, HG2)$. Colours reflect various ancestry clusters or geographical groups. The

358 genetic variation among West Eurasian HGs is structured along a WHG-EHG-ANE and WHG-GoyetQ2

359 ancestry cline. The Sicily EM HGs (red) fall at the extreme WHG end of both ancestry clines. Sicily LM

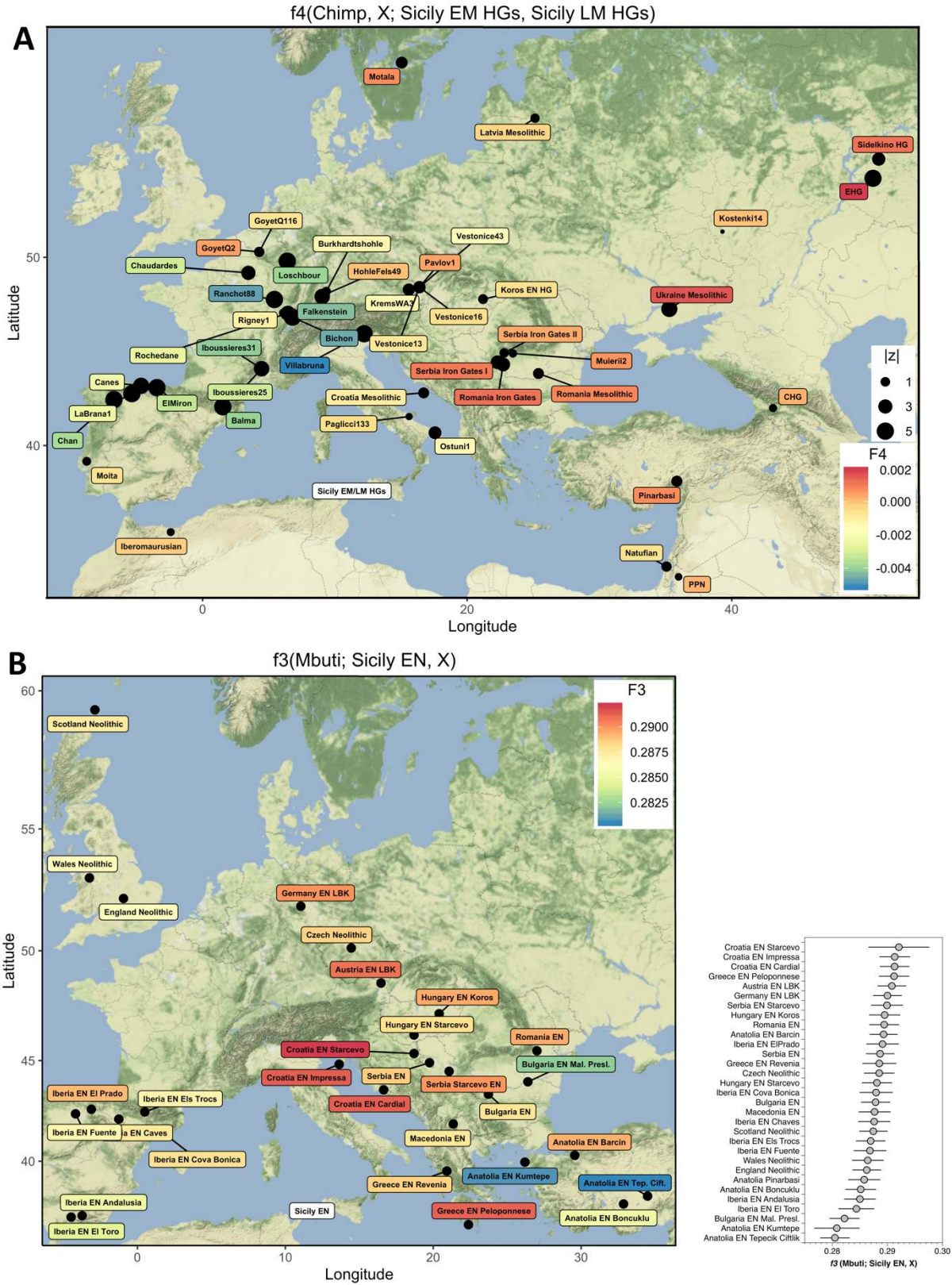
360 HGs (purple) fall among Villabruna cluster HGs (blue) in between Sicily EM HGs and Mesolithic HGs

361 from the Balkan (turquoise). **(B)** Individual ancestry profiles for Sicily LM HGs and other relevant West-
362 Eurasian HGs. Results are from qpWave- and qpAdm-based admixture models that inferred the ancestry of
363 each target HG as a one-, two- or three-way source mixture of ancestry approximated by Sicily EM (red:
364 *UZZ5054*, *OrienteC*), *GoyetQ2* (yellow), EHG (lime green: Karelia HGs, *Uz0077*, *Samara*, *Sidelkino*), and
365 *Pınarbaşı* (brown). Sicily EM, *GoyetQ2* and *Pınarbaşı* are taken as proxies for WHG-, Magdalenian- and
366 Near Eastern HG-related ancestry, respectively. Error bars reflect 1 standard error (SE). Individuals with
367 >150k SNPs covered are plotted. Sicily LM HGs, *Bichon* and the Croatia Mesolithic HG contain the highest
368 proportions of Sicily EM ancestry. The Near Eastern-related ancestry is found in some Sicily LM HGs, and
369 frequently among Mesolithic HGs from the Balkan, Baltic and Scandinavia. Congruent to their position in
370 the MDS plot, the Sicily LM HGs ancestry profiles appear intermediate to those of *Bichon* and the Croatia
371 Mesolithic HG (Villabruna cluster), and Mesolithic HGs from the Iron Gates in southeastern Europe.



372

373 **Fig. 3. The genetic diversity in Sicilian Early Mesolithic HGs is significantly reduced.** Nucleotide
 374 diversity (π) was inferred from pseudo-haploid genotypes, calculated as the average proportion of
 375 nucleotide mismatches for autosomal SNPs covered in individual pairs within a given HG group. The
 376 averages for HG groups from different time periods in different regions in Europe are plotted. UP = Upper
 377 Palaeolithic, EM = Early Mesolithic, LM = Late Mesolithic. Individuals are grouped based on their assigned
 378 genetic cluster, geographical and temporal proximity (see Data file 1). The number of individual pairs (n)
 379 that is used to determine the average for each time period is given. Error bars reflect 95% confidence
 380 intervals from 5Mb jackknifing. The nucleotide diversity for UP + EM Sicily HGs (red) is significantly
 381 lower compared to that for HGs from other time periods or regions in Europe, except for Magdalenian-
 382 associated individuals from western Europe (UP Magdalenian + EM: *Rigney1*, *Burkhardshole*, *Hohlefels49*,
 383 *GoyetQ2*).

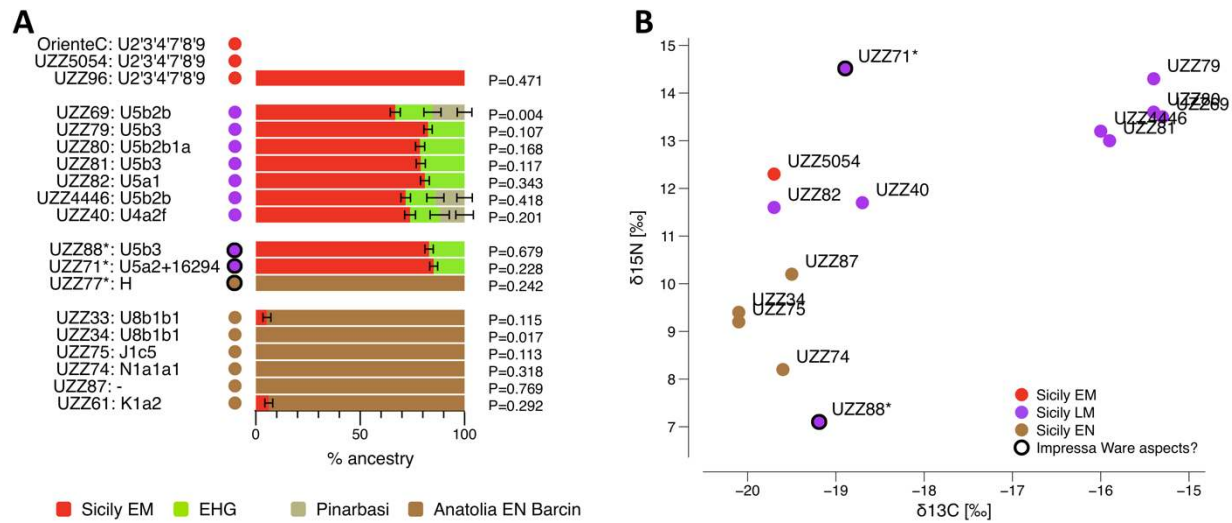


384

385

20

386 **Fig. 4. Genomic affinity of the ancient Sicilians. (A)** Comparing the ancestry in Sicily EM and LM HGs
387 to various West Eurasian HGs (X), as measured by $f_4(\text{Chimp}, X; \text{Sicily EM HGs}, \text{Sicily LM HGs})$. Cooler
388 colours indicate that X shares more genetic drift with Sicily EM HGs than with Sicily LM HGs, and warmer
389 colours indicate the opposite. Dot sizes reflect $|z|$ -scores. Not plotted: *AfontovaGora3* ($f_4 = 0.0023$, $z = 3.73$),
390 *BerryAuBac* ($f_4 = 0.0063$, $z = 5.10$). Whereas Upper Palaeolithic and Mesolithic HGs from western Europe,
391 including Villabruna cluster individuals, are genetically closer to Sicily EM HGs, those from eastern Europe
392 are closer to Sicily LM HGs. **(B)** Early Neolithic Sicilian farmers show high genetic affinity to
393 contemporaneous farmers from the Balkan (Croatia and Greece EN Peloponnese), as measured by $f_3(\text{Mbuti};$
394 *Sicily EN, X*). Warmer colours indicate higher levels of allele sharing. Error bars in the bar plot indicate 1
395 SE.



396

397 **Fig. 5. Genomic and dietary turnovers in Sicily during the Mesolithic and Early Neolithic.** The

398 coloured dots indicate the individuals' assigned genetic group with dark outlines those individuals that may

399 be contemporaneous to the earliest Impressed Ware aspects. **(A)** Individual ancestry profiles for the ancient

400 Sicilians determined from qpWave- and qpAdm-based ancestry models. The pre-Neolithic ancestry

401 proportion that is approximated by Sicily EM (*OrienteC/UZZ5054*) is in red, EHG in lime green, Pınarbaşı

402 in light brown, and the early farmer ancestry approximated by Anatolia EN Barcin in dark brown. The 5 cM

403 jackknifing standard errors are marked by horizontal bars. The mitogenomes haplogroups are given.

404 Compared to the preceding Sicily EM HGs, 15-37% of the ancestry in the Sicily LM HGs is from a non-

405 local source that is deeply related to both EHG and Near Eastern HGs, such as Pınarbaşı. The Sicilian early

406 farmers contain almost entirely early farmer ancestry, indicating an almost complete ancestry replacement

407 during the Early Neolithic. **(B)** Isotope values for diet reconstruction of the ancient Sicilians. The values

408 for the Sicilian early farmers are indicative of a predominantly terrestrial-based farming diet. The Sicily

409 LM HGs associated with the Castelnuovian *sensu lato* relied for around half of their protein on seafood.

410 *UZZ71* and *UZZ88*, two individuals that are tentatively contemporaneous to Impressed Ware aspects, show

411 dietary profiles that are strikingly different from the preceding Late Mesolithic Castelnuovian HGs and later

412 Early Neolithic Stentinello farmers. *UZZ71* consumed a much higher proportion of freshwater protein,

413 similarly to what is recorded for Mesolithic HGs from the Iron Gates. *UZZ88* consumed more terrestrial
414 plants and less animal protein than the Sicilian early farmers.

Target	Source1	Source2	Source3	P _{wave} (Sources)	P _{Adm} (Target + Sources)	Source1 (%)	Source2 (%)	Source3 (%)	SE1 (%)	SE2 (%)	SE3 (%)	Note
Sicily EM	Sicily LM	NA	NA	7.60E-34*	NA	NA	NA	NA	NA	NA	NA	A
Sicily LM	Sicily EM	EHG	Pınarbaşı	5.70E-113	0.12	75	15.5	9.5	1.6	2.4	2.8	B
Sicily LM	Sicily EM	EHG	Natufian	3.16E-172	0.17	75.2	17.3	7.5	1.6	1.9	2.1	
Sicily LM	Sicily EM	EHG	Iran EN Ganj Dareh	2.57E-135	0.09	78	15	7.1	1.4	2.7	2.2	
Sicily LM	Sicily EM	EHG	PPN	3.67E-218	0.15	76.1	16.5	7.4	1.5	2.1	2.1	
Sicily LM	Sicily EM	EHG	NA	2.19E-299	5.56E-03	78	22	NA	1.5	NA	NA	C
Sicily LM	Sicily EM	Pınarbaşı	NA	1.42E-224	4.72E-08	76.5	23.5	NA	1.7	NA	NA	
Sicily LM	Sicily EM	Natufian	NA	1.32E-310	2.03E-14	80.6	19.4	NA	1.9	NA	NA	
Sicily LM	Sicily EM	Iran EN Ganj Dareh	NA	0	4.68E-06	82.8	17.2	NA	1.3	NA	NA	
Sicily LM	Sicily EM	PPN	NA	0	9.44E-11	81.4	18.6	NA	1.5	NA	NA	
Sicily LM	Sicily EM	Serbia Iron Gates HG I	NA	7.17E-68	0.02	37.3	62.7	NA	2.9	NA	NA	D
Sicily LM	Sicily EM	Serbia Iron Gates HG II	NA	4.28E-68	0.05	35.4	64.6	NA	2.8	NA	NA	
Sicily LM	Sicily EM	Romania Iron Gates HG	NA	1.61E-69	4.56E-03	44.6	55.4	NA	2.9	NA	NA	
Sicily LM	Loschbour	EHG	NA	7.98E-255	2.90E-09	89.8	10.2	NA	1.8	NA	NA	E
Sicily LM	Loschbour	EHG	Pınarbaşı	3.07E-110	4.27E-09	88.1	7.4	4.6	2	2.6	3	
Sicily LM	Loschbour	EHG	Natufian	1.95E-194	1.60E-07	86.9	6.5	6.6	1.9	2.1	2	
Sicily LM	Loschbour	EHG	Iran EN Ganj Dareh	4.32E-125	1.59E-07	89.6	3.7	6.7	1.8	2.8	2.1	
Sicily LM	Loschbour	EHG	PPN	1.20E-213	4.15E-08	88	6.5	5.6	1.8	2.2	2	
Sicily EN	Anatolia EN Barcin	Sicily EM	NA	0	0.02	95.7	4.3	NA	1	NA	NA	F
Sicily EN	Anatolia EN Barcin	Sicily LM	NA	0	0.02	94.6	5.4	NA	1.2	NA	NA	
Sicily EN	Anatolia EN Barcin	Loschbour	NA	0	7.74E-03	95	5	NA	1.2	NA	NA	
Sicily EN	Anatolia EN Barcin	Serbia Iron Gates HG I	NA	0	0.01	93.8	6.2	NA	1.4	NA	NA	
Sicily EN	Anatolia EN Barcin	Serbia Iron Gates HG II	NA	0	0.01	93.9	6.1	NA	1.4	NA	NA	
Sicily EN	Anatolia EN Barcin	Romania Iron Gates HG	NA	0	0.03	92.6	7.4	NA	1.6	NA	NA	
Sicily EN	Anatolia EN Barcin	Iran EN Ganj Dareh	Sicily EM	1.02E-20	0.47	69.6	21.2	9.2	7.6	6.2	1.7	G
Sicily EN	Anatolia EN Barcin	Iran EN Ganj Dareh	Sicily LM	1.15E-24	0.34	71	18.6	10.5	7.3	5.7	1.9	
Sicily EN	Anatolia EN Barcin	Iran EN Ganj Dareh	Loschbour	7.39E-16	0.4	63	24.8	12.2	9.1	7	2.4	H
Sicily EN	Anatolia EN Barcin	Iran EN Ganj Dareh	Serbia Iron Gates HG I	7.47E-27	0.09	73.5	15.5	11	7.6	5.7	2.3	
Sicily EN	Anatolia EN Barcin	Iran EN Ganj Dareh	Serbia Iron Gates HG II	1.46E-26	0.15	72.8	16.2	11	7.6	5.7	2.2	
Sicily EN	Anatolia EN Barcin	Iran EN Ganj Dareh	Romania Iron Gates HG	4.01E-30	0.15	75	13.3	11.7	7.1	5.2	2.3	

416 **Table 1. Overview of key qpWave- and qpAdm-based ancestry models for Sicily EM HGs, Sicily LM HGs and Sicily EN farmers referred**
417 **to in the main text.** For a more comprehensive overview, see Data file 7. For all qpAdm-based admixture models, the P_{Wave} -value for the *Sources*
418 is small, indicating that that our used *Outgroups* can distinguish the ancestries between the *Sources*. Note A: The allele frequencies of the Sicily EM
419 and LM HG gene pools do not fully overlap, and hence could not be fitted via one ancestry stream (P_{Wave} -value marked by * indicates a model for
420 *Target* and *Source1*). B: A three-way mixture of Sicily EM, EHG and one of various Near Eastern sources results in a full ancestry fit to the Sicily
421 LM HG gene pool. C: Modeling Sicily LM HGs either as a two-way mixture of Sicily EM and EHG or Near Eastern-related ancestry is rejected as
422 a full model fit. D: Replacing the ancestry from EHG with that of Mesolithic Iron Gates HGs marginally improves the model fit. The proportion of
423 assigned Sicily EM ancestry is lower compared to the model that uses EHG as a second ancestry source, due to the substantial amount of WHG
424 ancestry in Iron Gates HGs ((17) and see Fig. 2B). E: Replacing the ancestry of Sicily EM with that of *Loschbour* in two or three-way mixtures are
425 strongly rejected as full ancestry fits to the Sicily LM gene pool. F: A two-way mixture of the early farmer ancestry in Anatolia EN Barcin and a
426 West-Eurasian HG source does not adequately fit the Sicily EN gene pool. G: Modelling the early farmer ancestry as a combination of Anatolia EN
427 Barcin and an additional basal ancestry, approximated here by Iran EN Ganj Dareh, and the local preceding Sicilian Mesolithic HGs does result in
428 a full fit to the Sicilian early farmer gene pool. H: The Sicily EN ancestry can also be adequately modelled using a non-local HG ancestry source in
429 addition to early farmer ancestry as approximated by a combination Anatolia EN Barcin and Iran EN Ganj Dareh.

430 **Materials and Methods**

431 **aDNA analysis.** All pre-amplification laboratory work was performed in dedicated clean rooms (82) at the
432 Max Planck Institute (MPI) for the Science of Human history (SHH) in Jena and MPI for Evolutionary
433 Anthropology (EVA) in Leipzig, Germany. At the MPI-SHH the individuals were sampled for bone or
434 tooth powder, originating from various skeletal elements (e.g. petrous, molars, teeth, humerus, phalange,
435 tibia, see Data file 1). The outer layer of the skeletal elements was removed with high-pressured powdered
436 aluminium oxide in a sandblasting instrument, and the element was irradiated with ultraviolet (UV) light
437 for 15 minutes on all sides. The elements were then sampled using various strategies, including grinding
438 with mortar and pestle or cutting and followed by drilling into denser regions (Data file 1). Subsequently,
439 for each individual 1-8 extracts of 100uL were generated from ~50mg powder per extract, following a
440 modified version of a silica-based DNA extraction method (83) described earlier (50) (Data file 1). At the
441 MPI-SHH, 20uL undiluted extract aliquots were converted into double-indexed double stranded (ds-)
442 libraries following established protocols (40, 84), some of them with a partial uracil-DNA glycosylase ('ds
443 UDG-half') treatment (85) and others without ('ds non-UDG'). At the MPI-EVA, 30uL undiluted extract
444 aliquot was converted into double-indexed single-stranded (ss-) libraries (86) with minor modifications
445 detailed in (87), without UDG treatment ('ss non-UDG') (Data file 1). At the MPI-SHH, all the ds- and ss-
446 libraries were shotgun sequenced to check for aDNA preservation, and subsequently enriched using in-
447 solution capture probes following a modified version of (19) (described in (25)) for ~1240k single
448 nucleotide polymorphisms (SNPs) in the nuclear genome (17, 18, 54) and independently for the complete
449 mitogenome. Then the captured libraries were sequenced on an Illumina 224 HiSeq4000 platform using
450 either a single end (1x75bp reads) or paired end configuration (2x50bp reads).

451 The sequenced reads were demultiplexed according to the expected index pair for each library, allowing
452 one mismatch per 7 bp index, and subsequently processed using EAGER v1.92.21 (88). We used
453 AdapterRemoval v2.2.0 (89) to clip adapters and Ns stretches of the reads. We merged paired end reads
454 into a single sequence for regions with a minimal overlap of 30 bp, and single end reads smaller than 30 bp

455 in length were discarded. The reads obtained from the nuclear capture were aligned against the human
456 reference genome (hg19), and those from the mitogenome captured against the revised Cambridge
457 Reference Sequence (rCRS). For mapping we used the Burrows-Wheeler Aligner (BWA v0.7.12) *aln* and
458 *samse* programs (90) with a lenient stringency parameter of ‘-n 0.01’ that allows more mismatches, and ‘-l
459 16500’ to disable seeding. We excluded reads with Phred-scaled mapping quality (MAPQ) <25. Duplicate
460 reads, identified by having identical strand orientation, start and end positions, were removed using DeDup
461 v.0.12.1 (88).

462 **adDNA authentication and quality control.** We assessed the authenticity and contamination levels in our
463 ancient DNA libraries (unmerged and merged per-individual) in several ways. First, we checked the
464 cytosine deamination rates at the end of the reads (91) using DamageProfiler v0.3
465 (<https://github.com/apeltzer/DamageProfiler>). After merging the libraries for each individual, we observed
466 21-52% C>T mismatch rates at the first base in the terminal nucleotide at the 5'-end, an observation that is
467 compatible with the presence of authentic ancient DNA molecules. Second, we tested for contamination of
468 the nuclear genome in males based on the X-chromosomal polymorphism rate. We determined the genetic
469 sex by calculating the X-rate (coverage of X-chromosomal SNPs/ coverage of autosomal SNPs) and Y-rate
470 (coverage of Y-chromosomal SNPs/ coverage of autosomal SNPs) (16). Four individuals for which the
471 libraries showed a Y-rate ≥ 0.49 we assigned the label ‘male’ and 14 individuals with Y-rates ≤ 0.07 as
472 ‘female’. The individual *UZZ26.cont* with an intermediate Y-rate of 0.17 we excluded from further genetic
473 analyses. Then we tested for heterozygosity of the X-chromosome using ANGSD v0.910 (92) (≥ 200 X-
474 chromosomal SNPs, covered at least twice (16). We found a nuclear contamination of 1.7-5.3% for the four
475 male individuals (Data file 1), based on new Method1 (93). Third, we obtained two mtDNA contamination
476 estimates for genetic males and females, using ContaMix v1.0.10 (19) and Schmutzi v1.0 (94) (Data file
477 1). Before running Schmutzi, we realigned the reads to the rCRS using CircularMapper v1.93.4 filtering
478 with MAPQ < 30. After removing duplicate reads, we downsampled to ~30,000 reads per library. With
479 Schmutzi we found low contamination estimates of 1-3% for all individuals with sufficient coverage (Data

480 file 1). ContaMix returned estimates in the range of 0.0-5.6% for all individuals except for *UZZ69* (3.7-
481 10.6%) and the lower coverage individual *UZZ096* (0.3-13.5%).

482 **Dataset.** For genotyping we extracted reads with high mapping quality ($\text{MAPQ} \geq 37$) to the autosomes
483 using samtools v1.3. The DNA damage plots indicated that misincorporations could extend up to 10 bp
484 from the read termini in non-UDG treated and up to 3bp in UDG-half treated libraries. We hence clipped
485 the reads accordingly, thereby removing G>A transitions from the terminal read ends in ds-libraries and
486 C>T transitions in both ss- and ds-libraries. For each individual, we randomly chose a single base per SNP
487 site as a pseudo-haploid genotype with our custom program ‘pileupCaller’
488 (<https://github.com/stschiff/sequenceTools>). We intersected our data with a global set of high-coverage
489 genomes from the Simon Genome Diversity Project (SGDP) for ~1240k nuclear SNP positions (21),
490 including previously reported ancient individuals from (15-17, 21-51). To minimize the effects of residual
491 ancient DNA damage, we removed ~300k SNPs on CpG islands from the data set. CpG dinucleotides,
492 where a cytosine is followed by a guanine nucleotide, are frequent targets of DNA methylation (95). Post-
493 mortem cytosine deamination was shown to occur more frequently at methylated than unmethylated CpGs
494 (20) resulting in excess of CpG \rightarrow TpG conversions. The final data set includes 868,755 intersecting
495 autosomal SNPs for which our newly reported individuals cover 53,352-796,174 SNP positions with an
496 average read depth per SNP of 0.09-9.39X (Data file 1). For principal component analyses (PCA) we
497 intersected our data and published ancient genomes with a panel of worldwide present-day populations,
498 genotyped on the Affymetrix Human Origins (HO) (37, 57). After filtering out CpG dinucleotides this data
499 set includes 441,774 SNPs.

500 **Kinship relatedness and individual assessment.** We determined pairwise mismatch rates (PMMRs) (34,
501 96) for pseudo-haploid genotypes to check for genetic duplicate individuals and first-degree relatives. If
502 two individuals show similar low PMMRs for inter- and intra-individual library comparisons, then this
503 indicates a genetic duplicate. Moreover, the expected PMMR for two first-degree related individuals falls
504 approximately in the middle of the baseline values for comparison between genetically unrelated and

505 identical individuals (97). We found a genetic triplicate (UZZ44, -45, -46) and quintuplicate (UZZ50-54),
506 and merged the respective libraries into *UZZ4446* and *UZZ5054*, respectively. In addition, *UZZ79* and
507 *UZZ81* showed an elevated PMMR indicative of a kinship relation (Data file 4).

508 **Mitogenome haplogroup determination.** We could reconstruct the mitochondrial genomes for 17
509 individuals (Data file 1). To obtain an automated mitochondrial haplogroup assignment we imported the
510 consensus sequences from Schmutzi into HaploGrep2 v2.1.1 ((98); available via:
511 <https://haplogrep.uibk.ac.at/>) based on phylotree (99) (mtDNA tree build 17, available via
512 <http://www.phylotree.org/>). In parallel, we manually haplotyped the reconstructed mitogenomes, based on
513 a procedure described in (52). We imported the bam.files for the merged libraries into Geneious v.9.0.5
514 (<http://www.geneious.com>) (100). After reassembling the reads against the revised Cambridge Reference
515 Sequence (rCRS) we called SNP variants with a minimum variant frequency of 0.7 and 2.0X coverage.
516 Using phylotree, we double-checked whether the called variants matched the expected diagnostic ones
517 based on the automated HaploGrep assignment. We did not consider known unstable nucleotide positions
518 309.1C(C), 315.1C, AC indels at 515-522, 16093C, 16182C, 16183C, 16193.1C(C) and 16519. We
519 extracted the consensus sequences based on a minimum of 75% base similarity. Using this approach, we
520 identified a total of twelve lineage-specific and private variants in the high coverage *UZZ5054* mitogenome.
521 Four of the lineage-specific variant positions were covered by only one or two reads in the low coverage
522 *UZZ96* and *OrienteC* genomes, and hence fell initially below our frequency threshold for variant detection.
523 However, since these variants were covered by a large number of reads in the closely related *UZZ5054*
524 mitogenome, for *UZZ96* and *OrienteC* we based the variant calls at these positions on the few reads
525 available and adjusted their consensus sequences accordingly (table S7.3).

526 **Y-chromosome haplogroup determination.** To determine the Y chromosome haplogroup for genetic
527 males we used the *yHaplo* program ((101), available via: <https://github.com/23andMe/yhaplo>). We based
528 our haplogroup assignment on 13,581 strand-unambiguous ancestry informative SNPs from the ISOGG
529 (International Society of Genetic Genealogy) data set. We called genotypes for these SNP sites by randomly

530 choosing one allele with ‘pileupCaller’ (<https://github.com/stschiff/sequenceTools>). Using an in-house
531 script (Choongwon Jeong) the genotypes were converted to an input format for *yHaplo*. In ancient genomes,
532 missing data for key diagnostic sites may halt the automated search before the most derived haplogroup is
533 reached. We therefore manually checked the coverage for informative SNPs further downstream for the
534 haplogroup that was assigned to each individual. Also, our sequence reads from the non-UDG treated ss-
535 libraries have an expected 3-5% C->T mismatches due to residual ancient damage. C->T mismatches at
536 diagnostic SNP positions may result *yHaplo* to incorrectly assign a more derived haplogroup. We therefore
537 checked whether the ancestral state variants matched those that are expected for the assigned haplogroup.

538 **Principal component analysis (PCA).** We computed principal components from individuals from 43
539 modern West Eurasian groups in the Human Origin panel (37, 57) using the *smartpca* program in the
540 EIGENSOFT package v6.0.1 (102) with the parameter ‘numeroutlieriter:0’. Ancient individuals were
541 projected using ‘lsqproject:YES’ and ‘shrinkmode:YES’.

542 ***f*-statistics.** We performed *f*-statistics on the 1240k data set using ADMIXTOOLS (57). For f_3 -outgroup
543 statistics (103) we used *qp3Pop* and for f_4 -statistics *qpDstat* with *f4mode:YES*. Standard errors (SEs) were
544 determined using a weighted block jackknife over 5Mb blocks. F_3 -outgroup statistics of the form $f_3(O;A,B)$
545 test the null hypothesis that *O* is a true outgroup to *A* and *B*. The strength of the f_3 -statistic is a measure for
546 the amount of genetic drift that *A* and *B* share after they branched off from a common ancestor with *O*,
547 provided that *A* and *B* are not related by admixture. F_4 -statistics of the form $f_4(X,Y; A,B)$ test the null
548 hypothesis that the unrooted tree topology $((X,Y)(A,B))$, in which (X,Y) form a clade with regard to (A,B) ,
549 reflects the true phylogeny. A positive value indicates that either *X* and *A*, or *Y* and *B*, share more drift than
550 expected under the null hypothesis. A negative value indicates that the tree topology under the null-
551 hypothesis is rejected into the other direction, due to more shared drift between *Y* and *A*, or *X* and *B*.

552 **Multidimensional scaling (MDS).** We performed MDS using the R package *cmdscale*. Euclidean
553 distances were computed from the genetic distances among West-Eurasian HGs, as measured by $f_3(Mbuti$;
554 *HG1, HG2)* for all possible pairwise combinations (16). The first two principal components are plotted. We

555 restricted the analyses to individuals with >30,000 autosomal SNPs covered. Relevant previously published
556 West Eurasian HGs were pooled in groups according to their geographical or temporal context, following
557 their initial publication labels (Data file 1). We deviated from the original labels with regard to Iron Gates
558 HGs from Serbia by splitting them into an early and late subgroup, labelled here as ‘Iron Gates HG Serbia
559 I’ (RC date: 10,000-7,500 calBCE) and ‘Iron Gates HG Serbia II’ (RC date: 7,500-5,700 calBCE) (17).

560 **Nucleotide diversity.** We selected a total of 120 West-Eurasian HGs with >100k SNPs covered, of which
561 103 were previously published (Data file 1), from four broad geographical regions “western” (n=18),
562 “south-western” (n=7), “southern-central” (n=33), and “(south)-eastern” (n=62) Europe. We subgrouped
563 the individuals further based on similar ¹⁴C-dates and genetic cluster assignment (for an overview of the
564 HG groups, see (Data file 1). E.g. we analysed the individuals associated with the Villabruna cluster and
565 those high in Magdalenian-related ancestry in separate groups. We determined the nucleotide diversity (π)
566 from pseudo-haploid genotypes by calculating the proportion of nucleotide mismatches for overlapping
567 autosomal SNPs covered by at least one read in both individuals. We hence determined π from all possible
568 combinations of individual pairs, rather than from all possible chromosome pairs, within a given group. We
569 filtered out individual pairs that shared less than 30,000 SNPs covered. We calculated an average over all
570 the individual pairs within a group and determined standard errors from block jackknives over 5Mb
571 windows and 95% confidence intervals (95CIs) from 1,000 bootstraps

572 **Inference of mixture proportions.** To characterize the ancestry of the ancient Sicilians we used the
573 qpWave (54) and qpAdm (36) programs from the Admixtools v3.0 package, with the ‘allsnps: YES’ option.
574 qpWave tests whether a set of *Left* populations is consistent with being related via as few as N streams of
575 ancestry to a set of *Outgroup* populations. qpAdm tries to fit a *Target* as a linear combination of the
576 *Left/Source* populations, and estimates the respective ancestry proportions that each of the *Left* populations
577 contributed to the *Target*. Both qpWave and qpAdm are based on f_4 -statistics of the form $f_4(X, O1; O2, O3)$,
578 where *O1*, *O2*, *O3* are all the triplet combinations of the *Outgroup* populations, and *X* is a *Target* or
579 *Left/Source* population. We used an *Outgroup* set from Mathieson et al. (17): *El Miron*, *Mota*, *Mbuti*, *Ust*

580 *Ishim, Mal'ta, AfontovaGora3, GoyetQ116, Villabruna, Kostenki14, Vestonice16, Karitiana, Papuan, Onge.*
581 We grouped individuals with a similar ancestry for Sicily EM, Sicily LM, EHG and CHG (Data file 1).
582 Since missing data may inflate the P-values for this test, we required a test result to be smaller (less extreme)
583 than $P = 0.1$ in order to reject the null-hypothesis of a full ancestry fit between the *Target* and the *Left/Source*
584 population(s). Prior to running qpAdm we used qpWave to check whether the pairs of *Left/Source*
585 populations are not equally related to the *Outgroups*.

586 **Phylogeny modelling.** We used the qpGraph program (57) to construct a phylogeny of ancestry lineages
587 found among Palaeolithic and Mesolithic West-Eurasian HGs to clarify the genetic history of Sicily EM
588 and LM HGs. For our modelling we used the parameters 'useallsnps: YES', 'forcezmode: YES', 'terse:
589 NO'. We built the phylogeny models with increasing complexity by fitting representative West Eurasian
590 HG ancestry lineages in the order: 1) Mbuti, 2) *Ust Ishim*, 3) *Kostenki14*, 4) *Mal'ta*, 5) *Vestonice16*, 6)
591 *GoyetQ2*, 7) *AfontovaGora3*, 8) *Villabruna* or Sicily EM, 9) Sicily EM or *Villabruna* (Supplementary
592 Section S5). We fitted the lineages one by one by adding them to all possible nodes as a branch without
593 admixture or as a binary admixture between two branches. We preferred the former over the latter if both
594 models fitted the observed f -statistics equally well. We selected models that did not include trifurcations or
595 0% ancestry stream estimates, and for which the difference between the observed and fitted f -statistics were
596 less extreme than 3.5 SEs.

597 **Direct AMS ^{14}C bone dates.** For 15 individuals we obtained a direct ^{14}C date from the skeletal element
598 that was used for genetic analysis (Data file 1). All bone samples were pretreated at the Department of
599 Human Evolution at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA), Leipzig,
600 Germany, using the method described in (104). For each skeletal element, 200-500mg of bone/tooth powder
601 was decalcified in 0.5M HCl at room temperature ~4 hours until no CO_2 effervescence was observed. To
602 remove humics, in a first step 0,1M NaOH was added for 30 minutes, followed by a final 0.5M HCl step
603 for 15 minutes. The resulting solid was gelatinized following a protocol of (105) at pH 3 in a heater block
604 at 75°C for 20h. The gelatin was then filtered in an Eeze-Filter™ (Elkay Laboratory Products (UK) Ltd.)

605 to remove small (> 80mm) particles, and ultrafiltered (106) with Sartorius “VivaspinTurbo” 30 KDa
606 ultrafilters. Prior to use, the filter was cleaned to remove carbon containing humectants (107). The samples
607 were lyophilized for 48 hours. In order to monitor contamination introduced during the pre-treatment stage,
608 a sample from a cave bear bone, kindly provided by D. Döppes (MAMS, Germany), was extracted along
609 with the batch from La Ferrassie samples (108). In marine environments the radiocarbon is older than the
610 true age, usually by ~400 years (marine reservoir effect). The specimens for which a correction was
611 necessary are UZZ4446 (40±10% marine), UZZ81 (45±10% marine), UZZ69, UZZ79 and UZZ80 (50±10%
612 marine). Corrections were made using the reservoir correction estimated for the Mediterranean Basin by
613 (109), which is $\Delta R = 58 \pm 85 \text{ }^{14}\text{C yr}$.

614 **Isotope analysis.** For 14 individuals we determined the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values
615 for dietary inference (Data file 1). To assess the preservation of the collagen yield, C:N ratios, together with
616 isotopic values are evaluated following the limits of (110).

617 **H2: Supplementary Materials**

618 Section S1. Grotta dell'Uzzo: archaeology and stratigraphic sequence

619 Section S2. Genetic grouping and substructure of the ancient Sicilians

620 Section S3. Elevated lineage-specific genetic drift in the Sicilian Early Mesolithic

621 Section S4. Characterizing the Sicilian Mesolithic HGs ancestry using F-statistics

622 Section S5. Investigating the phylogenetic position of the Early Mesolithic Sicilian HGs

623 Section S6. Characterizing the Sicilian early farmer ancestry using F-statistics

624 Section S7. Uniparental marker haplotyping

625 Data file S1. Summary table results ancient Sicilians, labels used in analyses, data in Supplementary

626 Sections

627 Data file S2. Data underlying Fig. 1

628 Data file S3. Data underlying Fig. 2

629 Data file S4. Data underlying Fig. 3

630 Data file S5. Data underlying Fig. 4

631 Data file S6: Data underlying Fig. 5.

632 Data file S7. Admixture models for ancient Sicilians and West Eurasian HGs

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634 **References and Notes**

- 635 1. D. Binder, P. Lanos, L. Angeli, L. Gomart, J. Guilaine, C. Manen, R. Maggi, I. M. Muntoni, C.
636 Panelli, G. Radi, C. Tozzi, D. Arobba, J. Battentier, M. Brandaglia, L. Bouby, F. Briois, A. Carré, C.
637 Delhon, L. Gourichon, P. Marinval, R. Nisbet, S. Rossi, P. Rowley-Conwy, S. Thiébaud, Modelling the
638 earliest north-western dispersal of Mediterranean Impressed Wares: new dates and Bayesian chronological
639 model. *Documenta Praehistorica* 44, 54-77 (2017).
- 640 2. O. García-Puchol, A. A. Diez Castillo, S. Pardo-Gordo, *Timing the Western Mediterranean Last*
641 *Hunter-Gatherers and First Farmers*. O. García-Puchol, D. C. Salazar García, Eds., Times of Neolithic
642 Transition along the Western Mediterranean, Fundamental Issues in Archaeology (Springer, New York,
643 2017).
- 644 3. Í. García-Martínez de Lagrán, Recent Data and Approaches on the Neolithization of the Iberian
645 Peninsula. *European Journal of Archaeology* 18, 429-453 (2015).
- 646 4. H. Martins, F. X. Oms, L. Pereira, A. W. G. Pike, K. Rowsell, J. Zilhão, Radiocarbon Dating the
647 Beginning of the Neolithic in Iberia. *Journal of Mediterranean Archaeology* 28, 105-131 (2015).
- 648 5. J. Zilhão, Radiocarbon evidence for maritime pioneer colonization at the origins of farming in west
649 Mediterranean Europe. *PNAS* 98, 14180-14185 (2001).
- 650 6. J. Guilaine, *Premiers bergers et paysans de l'Occident méditerranéen*. Études rurales (Mouton,
651 Paris, 1976), pp. 145.
- 652 7. J. Guilaine, A personal view of the neolithisation of the Western Mediterranean. *Quaternary*
653 *International* 470 211-225 (2018).
- 654 8. E. Natali, V. Forgia, The beginning of the Neolithic in Southern Italy and Sicily. *Quaternary*
655 *International* 470, 253-269 (2018).

- 656 9. S. Forenbaher, P. T. Miracle, The spread of farming in the Eastern Adriatic. *Documenta*
657 *Praehistorica* 33, 89-100 (2006).
- 658 10. M. A. Fugazzola Delpino, V. Tiné, Le statuine fittili femminili del Neolitico italiano. Iconografia
659 e contesto culturale. *Bullettino di Paletnologia Italiana (Roma)* 93-94, 19-51 (2002-2003).
- 660 11. C. A. T. Malone, The Italian Neolithic: A Synthesis of Research. *Journal of World Prehistory* 17,
661 235-312 (2003).
- 662 12. M. A. Mannino, S. Talamo, A. Tagliacozzo, I. Fiore, O. Nehlich, M. Piperno, S. Tusa, C. Collina,
663 R. Di Salvo, V. Schimmenti, M. P. Richards, Climate-driven environmental changes around 8.200 years
664 ago favoured increases in cetacean strandings and Mediterranean hunter-gatherers exploited them. *Sci. Rep.*
665 5, 1-12 (2015).
- 666 13. M. A. Mannino, K. D. Thomas, M. J. Leng, M. Piperno, S. Tusa, A. Tagliacozzo, Marine resources
667 in the Mesolithic and Neolithic at the Grotta dell'Uzzo (Sicily): evidence from isotope analyses of marine
668 shells. *Archaeometry* 49, 117-133 (2007).
- 669 14. A. Tagliacozzo, *Archeozoologia della Grotta dell'Uzzo, Sicilia. Da un'economia di caccia ad*
670 *un'economia di pesca ed allevamento*. I. P. e. Z. d. Stato, Ed., Supplemento al *Bullettino di Paletnologia*
671 *Italiana* (Istituto poligrafico e zecca dello Stato, Roma, 1993), vol. 84.
- 672 15. G. Catalano, P. F. Fabbri, D. Lo Vetro, S. Mallick, Late Upper Palaeolithic hunter-gatherers in the
673 Central Mediterranean: new archaeological and genetic data from the Late Epigravettian burial Oriente C
674 (Favignana, Sicily). *bioRxiv*, (2019).
- 675 16. Q. Fu, C. Posth, M. Hajdinjak, M. Petr, S. Mallick, D. Fernandes, A. Furtwängler, W. Haak, M.
676 Meyer, A. Mittnik, B. Nickel, A. Peltzer, N. Rohland, V. Slon, S. Talamo, I. Lazaridis, M. Lipson, I.
677 Mathieson, S. Schiffels, P. Skoglund, A. P. Derevianko, N. Drozdov, V. Slavinsky, A. Tsyvabkov, R.
678 Grifoni Cremonesi, F. Mallegni, B. Gély, E. Vacca, M. R. González Morales, L. G. Straus, C. Neugebauer-

- 679 Maresch, M. Teschler-Nicola, S. Constantin, O. T. Moldovan, S. Benazzi, M. Peresani, D. Coppola, M.
680 Lari, S. Ricci, A. Ronchitelli, F. Valentin, C. Thevenet, K. Wehrberger, D. Grigorescu, H. Rougier, I.
681 Crevecoeur, D. Flas, P. Semal, M. A. Mannino, C. Cupillard, H. Bocherens, N. J. Conard, K. Harvati, V.
682 Moiseyev, D. G. Drucker, J. Svoboda, M. P. Richards, D. Caramelli, R. Pinhasi, J. Kelso, N. Patterson, J.
683 Krause, S. Pääbo, D. Reich, The genetic history of Ice Age Europe. *Nature* 534, 200-205 (2016).
- 684 17. I. Mathieson, S. Alpaslan-Roodenberg, C. Posth, A. Szécsényi-Nagy, N. Rohland, S. Mallick, I.
685 Olalde, N. Broomandkoshbacht, F. Candilio, O. Cheronet, D. Fernandes, M. Ferry, B. Gamarra, G. Fortes,
686 W. Haak, E. Harney, E. Jones, D. Keating, B. Krause-Kyora, I. Kucukkalipci, M. Michel, A. Mittnik, K.
687 Nägele, M. Novak, J. Oppenheimer, N. Patterson, S. Pfrengle, K. Sirak, K. Stewardson, S. Vai, S.
688 Alexandrov, K. Alt, R. Andreescu, D. Antonović, A. Ash, N. Atanassova, K. Bacvarov, M. Gusztáv, H.
689 Bocherens, M. Bolus, A. Boroneanț, Y. Boyadzhiev, A. Budnik, J. Burmaz, S. Chohadzhiev, N. Conard,
690 R. Cottiaux, M. Čuka, C. Cupillard, D. Drucker, N. Elenski, M. Francken, B. Galabova, G. Ganetsovski,
691 B. Gély, T. Hajdu, V. Handzhyiska, K. Harvati, T. Higham, S. Iliev, I. Janković, I. Karavanić, D. Kennett,
692 D. Komšo, A. Kozak, D. Labuda, M. Lari, C. Lazar, M. Leppek, K. Leshtakov, D. Vetro, D. Los, I.
693 Lozanov, M. Malina, F. Martini, K. McSweeney, H. Meller, M. Mendušić, P. Mirea, V. Moiseyev, V.
694 Petrova, T. Price, A. Simalcsik, L. Sineo, M. Šlaus, V. Slavchev, P. Stanev, A. Starović, T. Szeniczey, S.
695 Talamo, M. Teschler-Nicola, C. Thevenet, I. Valchev, F. Valentin, S. Vasilyev, F. Veljanovska, S.
696 Venelinova, E. Veselovskaya, B. Viola, C. Virag, J. Zaninović, S. Zäuner, P. Stockhammer, G. Catalano,
697 R. Krauß, D. Caramelli, G. Zariņa, B. Gaydarska, M. Lillie, A. Nikitin, I. Potekhina, A. Papathanasiou, D.
698 Borić, C. Bonsall, J. Krause, R. Pinhasi, D. Reich, The genomic history of southeastern Europe. *Nature*
699 555, 197-203 (2018).
- 700 18. Q. Fu, M. Hajdinjak, O. T. Moldovan, S. Constantin, S. Mallick, P. Skoglund, N. Patterson, N.
701 Rohland, I. Lazaridis, B. Nickel, T. B. Viola, K. Prüfer, M. Meyer, J. Kelso, D. Reich, S. Pääbo, An early
702 modern human from Romania with a recent Neanderthal ancestor. *Nature* 524, 216-219 (2015).

- 703 19. Q. Fu, M. Meyer, X. Gao, U. Stenzel, H. A. Burbano, J. Kelso, S. Pääbo, DNA analysis of an early
704 modern human from Tianyuan Cave, China. *Proc. Natl. Acad. Sci. U.S.A* **110**, 2223-2227 (2013).
- 705 20. A. Seguin-Orlando, C. A. Hoover, S. K. Vasiliev, N. D. Ovodov, B. Shapiro, A. Cooper, E. M.
706 Rubin, E. Willerslev, L. Orlando, Amplification of TruSeq ancient DNA libraries with AccuPrime Pfx:
707 consequences on nucleotide misincorporation and methylation patterns. *STAR* **1**, 1-9 (2015).
- 708 21. S. Mallick, H. Li, M. Lipson, I. Mathieson, M. Gymrek, F. Racimo, M. Zhao, N. Chennagiri, S.
709 Nordenfelt, A. Tandon, P. Skoglund, Lazaridis I, Sankararaman S, Q. Fu, N. Rohland, G. Renaud, Y. Erlich,
710 T. F. Willems, C. Gallo, J. Spence, Y. Song, G. Poletti, F. Balloux, G. van Driem, P. de Knijff, I. Romero,
711 A. Jha, D. Behar, C. Bravi, C. Capelli, T. Hervig, A. Moreno-Estrada, O. Posukh, E. Balanovska, O.
712 Balanovsky, S. Karachanak-Yankova, H. Sahakyan, D. Toncheva, L. Yepiskoposyan, C. Tyler-Smith, Y.
713 Xue, M. Abdullah, A. Ruiz-Linares, C. Beall, A. Di Rienzo, C. Jeong, E. Starikovskaya, E. Metspalu, J.
714 Parik, R. Villems, B. Henn, U. Hodoglugil, R. Mahley, A. Sajantila, G. Stamatoyannopoulos, J. Wee, R.
715 Khusainova, E. Khusnutdinova, S. Litvinov, G. Ayodo, D. Comas, M. Hammer, T. Kivisild, W. Klitz, C.
716 Winkler, D. Labuda, M. Bamshad, L. Jorde, S. A. Tishkoff, W. Watkins, M. Metspalu, S. Dryomov, R.
717 Sukernik, L. Singh, K. Thangaraj, S. Pääbo, J. Kelso, N. Patterson, D. Reich, The Simons Genome Diversity
718 Project: 300 genomes from 142 diverse populations. *Nature* **538**, 201-206 (2016).
- 719 22. M. Allentoft, Sikora M, S. KG, Rasmussen S, Rasmussen M, Stenderup J, Damgaard PB, Schroeder
720 H, Ahlström T, Vinner L, Malaspinas AS, Margaryan A, Higham T, Chivall D, Lynnerup N, Harvig L,
721 Baron J, Della Casa P, Dąbrowski P, Duffy PR, Ebel AV, Epimakhov A, Frei K, Furmanek, Gralak T,
722 Gromov A, Gronkiewicz S, Grupe G, Hajdu T, Jarysz R, Khartanovich V, Khokhlov A, Kiss V, Kolář J,
723 Kriiska A, Lasak I, Longhi C, McGlynn G, Merkevcicius A, Merkyte I, Metspalu M, Mkrtchyan R,
724 Moiseyev V, Paja L, Pálfi G, Pokutta D, Pospieszny Ł, Price TD, Saag L, Sablin M, Shishlina N, Smrčka
725 V, Soenov VI, Szeverényi V, Tóth G, Trifanova SV, Varul L, Vicze M, Yepiskoposyan L, Zhitenev V,
726 Orlando L, Sicheritz-Pontén T, Brunak S, Nielsen R, K. K, W. E, Population genomics of Bronze Age
727 Eurasia. *Nature* **522**, 167-172 (2015).

- 728 23. F. Broushaki, M. G. Thomas, V. Link, S. López, L. van Dorp, K. Kirsanow, J. Burger, Early
729 Neolithic genomes from the eastern Fertile Crescent. *Science* 353, 499-503 (2016).
- 730 24. P. de Barros Damgaard, R. Martiniano, J. Kamm, J. V. Moreno-Mayar, G. Kroonen, M. Peyrot, G.
731 Barjamovic, S. Rasmussen, C. Zacho, N. Baimukhanov, V. Zaibert, V. Merz, A. Biddanda, I. Merz, V.
732 Loman, V. Evdokimov, E. Usmanova, B. Hemphill, A. Seguin-Orlando, F. E. Yediay, I. Ullah, K. G.
733 Sjögren, K. H. Iversen, J. Choin, C. de la Fuente, M. Ilardo, H. Schroeder, V. Moiseyev, A. Gromov, A.
734 Polyakov, S. Omura, S. Y. Senyurt, H. Ahmad, C. McKenzie, A. Margaryan, A. Hameed, A. Samad, N.
735 Gul, M. H. Khokhar, O. I. Goriunova, V. I. Bazaliiskii, J. Novembre, A. W. Weber, L. Orlando, M. E.
736 Allentoft, R. Nielsen, K. Kristiansen, M. Sikora, A. K. Outram, R. Durbin, E. Willerslev, The first horse
737 herders and the impact of early Bronze Age steppe expansions into Asia. *Science* 360, eaar7711 (2018).
- 738 25. M. Feldman, E. Fernández-Domínguez, L. Reynolds, D. Baird, J. Pearson, I. Hershkovitz, H. May,
739 N. Goring-Morris, M. Benz, J. Gresky, R. Bianco, A. Fairbairn, G. Mustafaoğlu, P. W. Stockhammer, C.
740 Posth, W. Haak, C. Jeong, J. Krause, Late Pleistocene human genome suggests a local origin for the first
741 farmers of central Anatolia. *Nat. Commun.* 10, 1218 (2019).
- 742 26. R. Fregel, F. Méndez, Y. Bokbot, D. Martín-Socas, M. Camalich-Massieu, M. J. Santana J5, M.
743 Ávila-Arcos, P. Underhill, B. Shapiro, G. Wojcik, M. Rasmussen, A. Soares, J. Kapp, A. Sockell, F.
744 Rodríguez-Santos, A. Mikdad, A. Trujillo-Mederos, C. D. Bustamante, Ancient genomes from North Africa
745 evidence prehistoric migrations to the Maghreb from both the Levant and Europe. *Proc Natl Acad Sci U S*
746 *A* 115, 6774-6779 (2018).
- 747 27. Q. Fu, H. Li, P. Moorjani, F. Jay, S. Slepchenko, A. Bondarev, P. Johnson, A. Aximu-Petri, K.
748 Prüfer, C. de Filippo, M. Meyer, N. Zwyns, D. Salazar-García, Y. Kuzmin, S. Keates, P. Kosintsev, D.
749 Razhev, M. Richards, N. Peristov, M. Lachmann, K. Douka, T. Higham, M. Slatkin, J. Hublin, D. Reich,
750 J. Kelso, T. Viola, S. Pääbo, Genome sequence of a 45,000-year-old modern human from western Siberia.
751 *Nature*. . *Nature* 514, 445-459 (2014).

- 752 28. M. Gallego Llorente, E. R. Jones, A. Eriksson, V. Siska, K. Arthur, M. Curtis, J. T. Stock, M.
753 Coltorti, P. Pieruccini, S. Stretton, F. Brock, T. F. G. Higham, Y. Park, M. Hoffreiter, D. G. Bradley, J.
754 Bhak, R. Pinhasi, A. Manica, Ancient Ethiopian genome reveals extensive Eurasian admixture in Eastern
755 Africa. *Science* 350, 820-822 (2015).
- 756 29. C. Gamba, E. R. Jones, M. D. Teasdale, R. McLaughlin, L. G. Gonzales-Fortes, V. Mattiangeli, L.
757 Domboróczki, I. Kővári, I. Pap, A. Anders, A. Whittle, J. Dani, P. Raczky, T. F. G. Higham, M. Hofreiter,
758 D. G. Bradley, R. Pinhasi, Genome flux and stasis in a five millennium transect of European prehistory.
759 *Nat. Commun.* 5, 5257-5265 (2014).
- 760 30. Z. Hofmanová, S. Kreutzer, G. Hellenthal, C. Sell, Y. Diekmann, D. Díez-del-Molino, L. van Dorp,
761 S. López, A. Kousathanas, A. Link, K. Kirsanow, L. M. Cassidy, R. Martiniano, M. Strobel, A. Scheu, A.
762 Kotsakis, P. Halstead, P. Triantaphyllou, N. Kyparissi-Apostolika, N. Urem-Kotsou, C. Ziota, F.
763 Adaktylou, F. Gopalan, D. M. Bobo, L. Winkelbach, J. Blöcher, M. Unterländer, C. Leuenberger, Ç.
764 Çilingiroğlu, B. Horejs, B. Gerritsen, S. J. Shennan, D. G. Bradley, M. Currat, K. R. Veeramah, D.
765 Wegmann, M. G. Thomas, C. Papageorgopoulou, J. Burger, Early farmers from across Europe directly
766 descended from Neolithic Aegeans. *Proc. Natl. Acad. Sci. USA* 113, 6886-6891 (2016).
- 767 31. E. Jones, G. Zarina, V. Moiseyev, E. Lightfoot, P. Nigst, A. Manica, R. Pinhasi, D. Bradley, The
768 Neolithic Transition in the Baltic Was Not Driven by Admixture with Early European Farmers. *Curr Biol.*
769 27, 576-582 (2017).
- 770 32. E. R. Jones, G. Gonzalez-Fortes, S. Connell, V. Siska, A. Eriksson, R. Martiniano, R. McLaughlin,
771 L. M. Gallego Llorente, L. Cassidy, C. Gamba, T. Meshveliani, O. Bar-Yosef, W. Müller, A. Belfer-Cohen,
772 Z. Matskevich, N. Jakeli, T. F. G. Higham, M. Currat, D. Lordkipanidze, M. Hofreiter, A. Manica, R.
773 Pinhasi, D. G. Bradley, Upper Palaeolithic genomes reveal deep roots of modern Eurasians. *Nat. Commun.*
774 6, 8912-8919 (2015).

- 775 33. A. Keller, A. Graefen, M. Ball, M. Matzas, V. Boisguerin, F. Maixner, P. Leidinger, C. Backes, R.
776 Khairat, M. Forster, B. Stade, A. Franke, J. Mayer, J. Spangler, S. McLaughlin, M. Shah, C. Lee, T. T.
777 Harkins, A. Sartori, A. Moreno-Estrada, B. Henn, M. Sikora, O. Semino, J. Chiaroni, S. Rootsi, N. M.
778 Myres, V. M. Cabrera, P. A. Underhill, C. D. Bustamante, E. E. Vigl, M. Samadelli, G. Cipollini, J. Haas,
779 H. Katus, B. D. O'Connor, M. R. Carlson, B. Meder, N. Blin, E. Meese, C. M. Pusch, A. Zink, New insights
780 into the Tyrolean Iceman's origin and phenotype as inferred by whole-genome sequencing. *Nat. Commun.*
781 3, 698 (2012).
- 782 34. G. Kılınç, A. Omrak, F. Özer, T. Günther, A. Büyükkarakaya, E. Bıçakçı, D. Baird, H. Dönertaş,
783 A. Ghalichi, R. Yaka, D. Koptekin, S. Açıkan, P. Parvizi, M. Krzewińska, E. Daskalaki, E. Yüncü, N. Dağtaş,
784 A. Fairbairn, J. Pearson, G. Mustafaoğlu, Y. Erdal, Y. Çakan, İ. Togan, M. Somel, J. Storå, M. Jakobsson,
785 A. Götherström, The Demographic Development of the First Farmers in Anatolia. *Curr Biol.* 26, 2659-
786 2666 (2016).
- 787 35. I. Lazaridis, A. Mittnik, N. Patterson, S. Mallick, N. Rohland, S. Pfrengle, A. Furtwängler, A.
788 Peltzer, C. Posth, A. Vasilakis, P. J. P. McGeorge, E. Konsolaki-Yannopoulou, G. Korres, H. Martlew, M.
789 Michalodimitrakis, M. Özşait, N. Özşait, A. Papanasiou, M. Richards, S. A. Roodenberg, Y. Tzedakis,
790 R. Arnott, D. M. Fernandes, J. R. Hughey, D. M. Lotakis, P. A. Navas, Y. Maniatis, J. A.
791 Stamatoyannopoulos, K. Stewardson, P. Stockhammer, R. Pinhasi, D. Reich, J. Krause, G.
792 Stamatoyannopoulos, Genetic origins of the Minoans and Mycenaeans. *Nature* 548, 214-218 (2017).
- 793 36. I. Lazaridis, D. Nadel, G. Rollefson, D. Merrett, N. Rohland, S. Mallick, D. Fernandes, M. Novak,
794 B. Gamarra, K. Sirak, S. Connell, K. Stewardson, E. Harney, Q. Fu, G. Gonzales-Fortes, E. R. Jones, S.
795 Roodenberg, G. Lengyel, F. Bocquentin, B. Gasparian, J. Monge, M. Gregg, V. Eshed, A. Mizrahi, C.
796 Meiklejohn, F. Gerritsen, L. Bejenaru, M. Blüher, A. Campbell, G. Cavellari, D. Comas, P. Froguel, E.
797 Gilbert, S. Kerr, P. Kovacs, J. Krause, D. McGettigan, M. Merrigan, D. Merriwether, S. O'Reilly, M. B.
798 Richards, O. Semino, M. Shamoon-Pour, G. Stefanescu, M. Stumvoll, A. Tönjes, A. Torroni, J. Wilson, L.

- 799 Yengo, N. Hovhannisyán, N. Patterson, R. Pinhasi, D. Reich, Genomic insights into the origin of farming
800 in the ancient Near East. *Nature* 536, 419–424 (2016).
- 801 37. I. Lazaridis, N. Patterson, A. Mittnik, G. Renaud, S. Mallick, K. Kirsanow, P. Sudmant, J.
802 Schraiber, S. Castellano, M. Lipson, B. Berger, C. Economou, R. Bollongino, Q. Fu, K. I. Bos, S.
803 Nordenfelt, H. Li, C. de Filippo, K. Prüfer, S. Sawyer, C. Posth, W. Haak, F. Hallgren, E. Fornander, N.
804 Rohland, D. Delsate, M. Francken, J. Guinet, J. Wahl, G. Ayodo, H. Babiker, G. Baillel, E. Balanovska, O.
805 Balanovsky, R. Barrantes, G. Bedoya, H. Ben-Ami, J. Bene, F. Berrada, C. Bravi, F. Brisighelli, G. Busby,
806 F. Cali, M. Churnosov, D. Cole, D. Corach, van Driem G, L. Damba, Dryomov S, Dugoujon JM, Fedorova
807 SA, Gallego Romero I, Gubina M, Hammer M, Henn BM, Hervig T, Hodoglugil U, Jha AR, Karachanak-
808 Yankova S, Khusainova R, Khusnutdinova E, Kittles R, Kivisild T, Klitz W, Kučinskas V, Kushniarevich
809 A, Laredj L, Litvinov S, Loukidis T, Mahley RW, Melegh B, Metspalu E, Molina J, Mountain J,
810 Näkkäläjärvi K, Nesheva D, Nyambo T, Osipova L, Parik J, Platonov F, Posukh O, Romano V,
811 Rothhammer F, Rudan I, Ruizbakiev R, Sahakyan H, Sajantila A, Salas A, Starikovskaya EB, Tarekegn A,
812 Toncheva D, Turdikulova S, Uktveryte I, Utevska O, Vasquez R, Villena M, Voevoda M, Winkler CA,
813 Yepiskoposyan L, Zalloua P, Zemunik T, Cooper A, Capelli C, Thomas MG, Ruiz-Linares A, Tishkoff SA,
814 Singh L, Thangaraj K, VILLEMS R, Comas D, Sukernik R, Metspalu M, Meyer M, Eichler EE, Burger J, M.
815 Slatkin, Pääbo S, Kelso J, Reich D, K. J., Ancient human genomes suggest three ancestral populations for
816 present-day Europeans. *Nature* 513, 409–413 (2014).
- 817 38. M. Lipson, A. Szécsényi-Nagy, S. Mallick, A. Pósa, B. Stégmár, V. Keerl, N. Rohland, K.
818 Stewardson, M. Ferry, M. Michel, J. Oppenheimer, N. Broomandkhoshbacht, E. Harney, S. Nordenfelt, B.
819 Llamas, B. Gusztáv Mende, K. Köhler, K. Oross, M. Bondár, T. Marton, A. Oszttás, J. Jakucs, T. Paluch,
820 F. Horváth, P. Csengeri, J. Koós, K. Sebök, A. Anders, P. Raczky, J. Regenye, J. Barna, S. Fábíán, G.
821 Serlegi, Z. Toldi, E. Gyöngyvér Nagy, J. Dani, E. Molnár, G. Pálfi, L. Márk, B. Melegh, Z. Bánfai, L.
822 Domboróczki, J. Fernández-Eraso, J. Antonio Mujika-Alustiza, C. Alonso Fernández, J. Jiménez
823 Echevarría, R. Bollongino, J. Orschiedt, K. Schierhold, H. Meller, A. Cooper, J. Burger, E. Bánffy, K. Alt,

- 824 C. Lalueza-Fox, W. Haak, D. Reich, Parallel palaeogenomic transects reveal complex genetic history of
825 early European farmers. *Nature* 551, 368-372 (2017).
- 826 39. I. Mathieson, I. Lazaridis, N. Rohland, S. Mallick, N. Patterson, S. A. Roodenberg, H. Eadaoin, K.
827 Stewardson, D. Fernandes, M. Novak, K. Sirak, C. Gamba, E. R. Jones, B. Llamas, S. Dryomov, J. Pickrell,
828 J. L. Arsuaga, J. M. Bermúdez de Castro, E. Carbonell, F. Gerritsen, A. Khokhlov, P. Kuznetsov, M.
829 Lozano, H. Meller, O. Mochalov, V. Moiseyev, M. A. R. Guerra, J. Roodenberg, J. M. Vergès, J. Krause,
830 A. Cooper, K. W. Alt, D. Brown, D. Anthony, C. Lalueza-Fox, W. Haak, R. Pinhasi, D. Reich, Genome-
831 wide patterns of selection in 230 ancient Eurasians. *Nature* 528, 499–503 (2015).
- 832 40. M. Meyer, M. Kircher, M.-T. Gansauge, H. Li, F. Racimo, S. Mallick, J. Schraiber, F. Jay, K.
833 Prüfer, C. de Filippo, P. Sudmant, C. Alkan, Q. Fu, R. Do, N. Rohland, A. Tandon, M. Siebauer, R. Green,
834 K. Bryc, A. Briggs, U. Stenzel, J. Dabney, J. Shendure, J. Kitzman, M. Hammer, M. Shunkov, A.
835 Derevianko, N. Patterson, A. Andrés, E. Eichler, M. Slatkin, D. Reich, J. Kelso, S. Pääbo, A high-coverage
836 genome sequence from an archaic Denisovan individual. *Science* 338, 222-226 (2012).
- 837 41. A. Mittnik, C. C. Wang, S. Pfrengle, M. Daubaras, G. Zariņa, F. Hallgren, R. Allmäe, V.
838 Khartanovich, V. Moiseyev, M. Törv, A. Furtwängler, V. Andrades, A. M. Feldman, C. Economou, M.
839 Oinonen, A. Vasks, E. Balanovska, D. Reich, R. Jankauskas, W. Haak, S. Schiffels, J. Krause, The genetic
840 prehistory of the Baltic Sea region. *Nat Commun.* 9, (2018).
- 841 42. I. Olalde, M. E. Allentoft, F. Sánchez-Quinto, G. Santpere, C. W. Chiang, M. DeGiorgio, J. Prado-
842 Martinez, J. A. Rodríguez, S. Rasmussen, J. Quilez, O. Ramírez, U. M. Marigorta, M. Fernández-Callejo,
843 M. E. Prada, J. M. Encinas, R. Nielsen, M. G. Netea, J. Novembre, R. A. Sturm, P. Sabeti, T. Marquès-
844 Bonet, A. Navarro, E. Willerslev, C. Lalueza-Fox, Derived immune and ancestral pigmentation alleles in a
845 7,000-year-old Mesolithic European. *Nature.* 507, 225-228 (2014).
- 846 43. I. Olalde, S. Brace, M. E. Allentoft, I. Armit, K. Kristiansen, T. Booth, N. Rohland, Mallick, A.
847 Szécsényi-Nagy, A. Mittnik, E. Altena, M. Lipson, I. Lazaridis, T. K. Harper, N. Patterson, N.

848 Broomandkhoshbacht, Y. Diekmann, Z. Faltyskova, D. Fernandes, M. Ferry, E. Harney, P. de Knijff, M.
849 Michel, J. Oppenheimer, K. Stewardson, A. Barclay, K. W. Alt, C. Liesau, P. Ríos, C. Blasco, J. V. Miguel,
850 R. M. García, A. A. Fernández, E. Bánffy, M. Bernabò-Brea, D. Billoin, C. Bonsall, L. Bonsall, T. Allen,
851 L. Büster, S. Carver, L. C. Navarro, O. E. Craig, G. T. Cook, B. Cunliffe, A. Denaire, K. E. Dinwiddy, N.
852 Dodwell, M. Ernée, C. Evans, M. Kuchařik, J. F. Farré, C. Fowler, M. Gazenbeek, R. G. Pena, M. Haber-
853 Uriarte, E. Haduch, G. Hey, N. Jowett, T. Knowles, K. Massy, S. Pfrengle, P. Lefranc, O. Lemercier, A.
854 Lefebvre, C. H. Martínez, V. G. Olmo, A. B. Ramírez, J. L. Maurandi, T. Majó, J. I. McKinley, K.
855 McSweeney, B. G. Mende, A. Modi, G. Kulcsár, V. Kiss, A. Czene, R. Patay, A. Endrődi, K. Köhler, T.
856 Hajdu, T. Szeniczey, J. Dani, Z. Bernert, M. Hoole, O. Cheronet, D. Keating, P. Velemínský, M. Dobeš, F.
857 Candilio, F. Brown, R. F. Fernández, A. M. Herrero-Corral, S. Tusa, E. Carnieri, L. Lentini, A. Valenti, A.
858 Zanini, C. Waddington, G. Delibes, E. Guerra-Doce, B. Neil, M. Brittain, M. Luke, R. Mortimer, J.
859 Desideri, M. Besse, G. Brücken, M. Furmanek, A. Hałuszko, M. Mackiewicz, A. Rapiński, S. Leach, I.
860 Soriano, K. T. Lillios, J. L. Cardoso, M. P. Pearson, P. Włodarczak, T. D. Price, P. Prieto, P. J. Rey, R.
861 Risch, G. Rojo, M. A. A. Schmitt, J. Serralongue, A. M. Silva, V. Smrčka, L. Vergnaud, J. Zilhão, D.
862 Caramelli, T. Higham, M. G. Thomas, D. J. Kennett, H. Fokkens, V. Heyd, A. Sheridan, K. G. Sjögren, P.
863 W. Stockhammer, J. Krause, R. Pinhasi, W. Haak, I. Barnes, C. Lalueza-Fox, D. Reich, The Beaker
864 phenomenon and the genomic transformation of northwest Europe. *Nature* 555, 190-119 (2018).

865 44. I. Olalde, H. Schroeder, M. Sandoval-Velasco, L. Vinner, I. Lobón, O. Ramirez, S. Civit, B. García,
866 P, D. C. Salazar-García, S. Talamo, F. María, J. O. Xavier, F, M. Pedro, P. Martínez, M. Sanz, J. Daura, J.
867 Zilhão, T. Marquès-Bonet, M. T. Gilbert, C. Lalueza-Fox, A common genetic origin for early farmers from
868 Mediterranean Cardial and Central European LBK cultures. *Mol Biol Evol.* 32, 3132-3142 (2015).

869 45. A. Omrak, T. Günther, C. Valdiosera, E. M. Svensson, H. Malmström, H. Kiesewetter, W.
870 Aylward, J. Storå, M. Jakobsson, A. Götherström, Genomic Evidence Establishes Anatolia as the Source
871 of the European Neolithic Gene Pool. *Curr Biol.* 26, 270-275 (2016).

- 872 46. M. Raghavan, P. Skoglund, K. E. Graf, M. Metspalu, A. Albrechtsen, I. Moltke, M. Rasmussen, T.
873 J. Stafford, L. Orlando, E. Metspalu, M. Karmin, K. Tambets, S. Rootsi, R. Mägi, P. Campos, E.
874 Balanovska, O. Balanovsky, E. Khusnutdinova, S. Litvinov, L. Osipova, S. Fedorova, M. Voevoda, M.
875 DeGiorgio, T. Sicheritz-Ponten, S. Brunak, S. Demeshchenko, T. Kivisild, R. Villems, R. Nielsen, M.
876 Jakobsson, E. Willerslev, Upper Palaeolithic Siberian genome reveals dual ancestry of Native Americans.
877 *Nature* 505, 87–91 (2014).
- 878 47. M. Sikora, A. Seguin-Orlando, V. C. Sousa, A. Albrechtsen, T. S. Korneliussen, A. Ko, S.
879 Rasmussen, I. Dupanloup, P. R. Nigst, M. D. Bosch, G. Renaud, M. E. Allentoft, A. Margaryan, S. V.
880 Vasilyev, E. V. Veselovskaya, S. B. Borutskaya, T. Deviese, D. Comeskey, T. Higham, A. Manica, R.
881 Foley, D. J. Meltzer, R. Nielsen, L. Excoffier, M. Mirazon-Lahr, L. Orlando, E. Willerslev, Ancient
882 genomes show social and reproductive behavior of early Upper Paleolithic foragers. *Science* 358, 659-662
883 (2017).
- 884 48. P. Skoglund, H. Malmström, A. Omrak, M. Raghavan, C. Valdiosera, T. Günther, P. Hall, K.
885 Tambets, J. Parik, K. Sjögren, J. Apel, E. Willerslev, J. Storå, A. Götherström, M. Jakobsson, Genomic
886 diversity and admixture differs for Stone-Age Scandinavian foragers and farmers. *Science* 344, 747-750
887 (2014).
- 888 49. C. Valdiosera, T. Günther, J. C. Vera-Rodríguez, I. Ureña, E. Iriarte, R. Rodríguez-Varela, L. G.
889 Simões, R. M. Martínez-Sánchez, E. M. Svensson, H. Malmström, L. Rodríguez, d. Bermúdez, Castro, J.M,
890 E. Carbonell, A. Alday, V. Hernández, J.A, A. Götherström, J. M. Carretero, J. L. Arsuaga, C. I. Smith, M.
891 Jakobsson, Four millennia of Iberian biomolecular prehistory illustrate the impact of prehistoric migrations
892 at the far end of Eurasia. *Proc Natl Acad Sci U S A.* 115, 3428-3433 (2018).
- 893 50. V. Villalba-Mouco, M. S. van de Loosdrecht, C. Posth, R. Mora, J. Martínez-Moreno, M. Rojo-
894 Guerra, D. C. Salazar-García, J. I. Royo-Guillén, M. Kunst, H. Rougier, I. Crevecoeur, H. Arcusa-
895 Magallón, C. Tejedor-Rodríguez, I. García-Martínez de Lagrán, R. Garrido-Pena, K. W. Alt, C. Jeong, S.

- 896 Schiffels, P. Utrilla, J. Krause, W. Haak, Survival of Late Pleistocene Hunter-Gatherer Ancestry in the
897 Iberian Peninsula. *Current Biology* 29, 1169-1177 (2019).
- 898 51. L. Saag, L. Varul, C. L. Scheib, J. Stenderup, M. E. Allentoft, L. Saag, L. Pagani, M. Reidla, K.
899 Tambets, E. Metspalu, A. Kriiska, E. Willerslev, T. Kivisild, M. Metspalu, Extensive Farming in Estonia
900 Started through a Sex-Biased Migration from the Steppe. *Curr Biol.* 27, 2185-2193 (2017).
- 901 52. C. Posth, G. Renaud, A. Mittnik, D. G. Drucker, H. Rougier, C. Cupillard, F. Valentin, C. Thevenet,
902 A. Furtwängler, C. Wißing, M. Francken, M. Malina, M. Bolus, M. Lari, E. Gigli, G. Capecchi, I.
903 Crevecoeur, C. Beauval, D. Flas, M. Germonpré, J. Van der Plicht, R. Cottiaux, B. Gély, A. Ronchitelli, K.
904 Wehrberger, D. Grigorescu, J. Svoboda, P. Semal, Caramelli D, H. Bocherens, K. Harvati, N. Conard, W.
905 Haak, A. Powell, J. Krause, Pleistocene mitochondrial genomes suggest a single major dispersal of non-
906 Africans and a Late Glacial population turnover in Europe. *Current Biology* 26, 827-833 (2016).
- 907 53. B. Bramanti, M. Thomas, W. Haak, M. Unterlaender, P. Jores, K. Tambets, I. Antanaitis-Jacobs,
908 M. Haidle, R. Jankauskas, C. Kind, F. Lueth, T. Terberger, J. Hiller, S. Matsumura, P. Forster, B. Joachim,
909 Genetic discontinuity between local hunter-gatherers and central Europe's first farmers. *Science* 326, 137-
910 140 (2009).
- 911 54. W. Haak, I. Lazaridis, N. Patterson, N. Rohland, S. Mallick, B. Llamas, G. Brandt, S. Nordenfelt,
912 E. Harney, K. Stewardson, Q. Fu, A. Mittnik, E. Bánffy, C. Economou, M. Francken, S. Friederich, R.
913 Pena, F. Hallgren, V. Khartanovich, A. Khokhlov, M. Kunst, P. Kuznetsov, H. Meller, O. Mochalov, V.
914 Moiseyev, N. Nicklisch, S. Pichler, R. Risch, M. Rojo Guerra, C. Roth, A. Szécsényi-Nagy, J. Wahl, M.
915 Meyer, J. Krause, D. Brown, D. Anthony, A. Cooper, K. W. Alt, D. Reich, Massive migration from the
916 steppe was a source for Indo-European languages in Europe. *Nature* 522, 207-211 (2015).
- 917 55. G. Brandt, W. Haak, C. J. Adler, C. Roth, A. Szécsényi-Nagy, S. Karimnia, S. Möller-Rieker, H.
918 Meller, R. Ganslmeier, S. Friederich, V. Dresely, N. Nicklisch, J. K. Pickrell, F. Sirocko, D. Reich, A.

- 919 Cooper, K. W. Alt, The Genographic Consortium. Ancient DNA Reveals Key Stages in the Formation of
920 Central European Mitochondrial Genetic Diversity. *Science* 342, 257-261 (2013).
- 921 56. I. Lazaridis, A. Belfer-Cohen, S. Mallick, N. Patterson, O. Cheronet, N. Rohland, G. Bar-Oz, O.
922 Bar-Yosef, N. Jakeli, E. Kvavadze, D. Lordkipanidze, Z. Matzkevich, T. Meshveliani, B. J. Cullen, D. J.
923 Kennett, R. Pinhasi, D. Reich, Paleolithic DNA from the Caucasus reveals core of West Eurasian ancestry.
924 *BioRxiv*, (2018).
- 925 57. N. Patterson, P. Moorjani, Y. Luo, S. Mallick, N. Rohland, Y. Zhan, T. Genschoreck, T. Webster,
926 D. Reich, Ancient Admixture in Human History. *Genetics* 192, 1065-1093 (2012).
- 927 58. M. Piperno, *Papers in Italian Archaeology IV. Part II. Prehistory* C. Malone, S. Stoddart, Eds.,
928 International Series 244 (British Archaeological Reports, Oxford, 1985).
- 929 59. S. Tusa, *Papers in Italian Archaeology IV. Part II. Prehistory*. C. Malone, S. Stoddart, Eds.,
930 International Series 244 (British Archaeological Reports, Oxford, 1985).
- 931 60. S. Tusa, *Early Societies in Sicily: New developments in archaeological research* R. Leighton, Ed.,
932 (Accordia Specialist Studies on Italy 5, London, 1996).
- 933 61. G. N. Feliner, Southern European glacial refugia: A tale of tales. *Taxon* 60, 365-372 (2011).
- 934 62. T. Schmitt, Molecular biogeography of Europe: Pleistocene cycles and postglacial trends. *Frontiers*
935 *in Zoology* volume 4, 11 (2007).
- 936 63. P. Soares, A. Achilli, O. Semino, W. Davies, V. Macaulay, B. H.J, A. Torroni, M. B. Richards, The
937 archaeogenetics of Europe. *Curr Biol.* 20, R174-183 (2010).
- 938 64. F. Antonioli, V. Lo Presti, M. Gasparo Morticelli, B. Laura, M. Mannino, M. R. Palombo, G.
939 Sannino, L. Ferranti, S. Furlani, K. Lambeck, S. Canese, R. Catalano, F. Chiocci, G. Mangano, G.
940 Scicchitano, R. Tonielli, Timing of the emergence of the Europe–Sicily bridge (40–17 cal ka BP) and its

- 941 implications for the spread of modern humans. *Geological Society London Special Publications* 411, 111-
942 144 (2014).
- 943 65. G. Di Maida, M. A. Mannino, B. Krause-Kyora, T. Z. T. Jensen, S. Talamo, Radiocarbon dating
944 and isotope analysis on the purported Aurignacian skeletal remains from Fontana Nuova (Ragusa, Italy).
945 *PLoS ONE* 14, e0213173 (2019).
- 946 66. M. Mussi, *Earliest Italy. An Overview of the Italian Palaeolithic and Mesolithic*. European Journal
947 of Archaeology (Springer US, New York, 2001), vol. 5, pp. 402.
- 948 67. P. Biagi, *The Widening Harvest. The Neolithic Transition in Europe: Looking Forward, Looking*
949 *Back*. A. J. Ammerman, P. Biagi, Eds., Aia Colloquia & Conference Papers (Book 6) (Archaeological
950 Institute of America, Boston, 2003), pp. 365.
- 951 68. D. Vetro, F. Martini, Mesolithic in Central-Southern Italy: Overview of lithic productions. *Quat.*
952 *Int* 423, 279-302 (2016).
- 953 69. C. Collina, *Le Neolithique ancien en Italie due sud: Evolution des industries lithiques entre VIIe et*
954 *VIe millenaire*. (Archaeopress Archaeology, Oxford, 2015), pp. 508.
- 955 70. D. Binder, C. Collina, R. Guilbert, T. Perrin, O. Garcia-Puchol, in *The emergence of pressure blade*
956 *making: From origin to modern experimentation* P. M. Desrosiers, Ed. (Springer Verlag, 2012), chap. 7,
957 pp. 199-218.
- 958 71. P. Biagi, D. Kiosak, The Mesolithic of the northwestern Pontic region New AMS dates for the
959 origin and spread of the blade and trapeze industries in southeastern Europe. *Eurasia Antiqua* 16, 21-41
960 (2010).
- 961 72. P. Biagi, E. Starnini, *The Origin and Spread of the Late Mesolithic Blade and Trapeze Industries*
962 *in Europe: Reconsidering J. G. D. Clark's Hypothesis Fifty Years After*. S. Terna, B. Govedarica, Eds.,

- 963 Interactions, changes and meanings. Essays in honour of Igor Manzura on the occasion of his 60th birthday.
964 (Kishinev, 2016).
- 965 73. D. Gronenborn, *Migrations before the Neolithic? The Late Mesolithic blade-and-trapeze horizon*
966 *in central Europe and beyond*. Migration and Integration from Prehistory to the Middle Age (Tagungen des
967 Landesmuseums für Vorgeschichte Halle, Saale, 2017), vol. 17.
- 968 74. M.-L. Inizan, *The Emergence of Pressure Blade Making. From Origin to Modern Experimentation*.
969 P. M. Desrosiers, Ed., (Springer-Verlag, New York, 2012), pp. 536.
- 970 75. G. Marchand, T. Perrin, Why this revolution? Explaining the major technical shift in Southwestern
971 Europe during the 7th millennium cal. BC. *Quat. Int* 428, 73-85 (2017).
- 972 76. T. Perrin, D. Binder, paper presented at the La transition néolithique en Méditerranée, Paris, 2014.
- 973 77. T. Günther, C. Valdiosera, H. Malmström, I. Ureña, R. Rodriguez-Varela, Ó. O. Sverrisdóttir, E.
974 A. Daskalaki, P. Skoglund, T. Naidoo, E. M. Svensson, J. M. Bermúdez de Castro, E. Carbonell, M. Dunn,
975 J. Storå, E. Iriarte, J. L. Arsuaga, J.-M. Carretero, A. Götherström, M. Jakobsson, Ancient genomes link
976 early farmers from Atapuerca in Spain to modern-day Basques. *Proc Natl Acad Sci U S A*. 112, 11917–
977 11922 (2015).
- 978 78. C. Bonsall, R. Vasić, A. Boroneanț, M. Roksandic, A. Soficaru, K. McSweeney, A. Evatt, Ü.
979 Agurajua, C. Pickard, V. Dimitrijević, T. Higham, D. Hamilton, G. Cook, New AMS 14C Dates for Human
980 Remains from Stone Age Sites in the Iron Gates Reach of the Danube, Southeast Europe. *Radiocarbon* 57,
981 33-46 (2015).
- 982 79. D. Borić, D. Price, Strontium isotopes document greater human mobility at the start of the Balkan
983 Neolithic. *PNAS* 110, 3298-3303 (2013).
- 984 80. V. Tine, S. Tusa, paper presented at the Atti della XLI Riunione Scientifica, 16-19 novembre 2006,
985 San Cipirello (PA), 2012.

- 986 81. C. Collina, *Sistemi tecnici e chaînes opératoires alla grotta dell'Uzzo (Trapani): analisi*
987 *tecnologica delle industrie litiche dai livelli mesolitici e neolitici*. D. c. a. e. s. a. e. t. n. S. P. e, Protostorica,
988 Eds., (Istituto Italiano di Preistoria e Protostoria, San Cipirello 2012), vol. Atti della XLI Riunione
989 Scientifica, pp. 268.
- 990 82. M. Gilbert, H. Bandelt, M. Hofreiter, I. Barnes, Assessing ancient DNA studies. *Trends Ecol. Evol.*
991 20, 541–544 (2005).
- 992 83. J. Dabney, M. Knapp, I. Glocke, M.-T. Gansauge, A. Weihmann, B. Nickel, C. Valdiosera, N.
993 García, S. Pääbo, J.-L. Arsuaga, M. Meyer, Complete mitochondrial genome sequence of a Middle
994 Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proc. Natl. Acad. Sci. U.S.A* 110,
995 15758–15763 (2013).
- 996 84. M. Meyer, M. Kircher, Illumina sequencing library preparation for highly multiplexed target
997 capture and sequencing. *Cold Spring Harb Protoc.* 6, pdb.prot5448 (2010).
- 998 85. N. Rohland, E. Harney, S. Mallick, S. Nordenfelt, D. Reich, Partial uracil–DNA–glycosylase
999 treatment for screening of ancient DNA. *Phil. Trans. R. Soc. B* 370, 20130624 (2015).
- 1000 86. M.-T. Gansauge, T. Gerber, I. Glocke, P. Korlevic, L. Lippik, S. Nagel, L. Riehl, A. Schmidt, M.
1001 Meyer, Single-stranded DNA library preparation from highly degraded DNA using T4 DNA ligase. *Nucleic*
1002 *Acids Res.* 45, e79 (2017).
- 1003 87. V. Slon, C. Hopfe, C. L. Weiß, F. Mafessoni, M. de la Rasilla, C. Lalueza-Fox, A. Rosas, M.
1004 Soressi, M. Knul, R. Miller, J. Stewart, A. P. Derevianko, Z. Jacobs, B. Li, R. Roberts, M. Shunkov, H. de
1005 Lumley, C. Perrenoud, I. Gušić, Ž. Kućan, P. Rudan, A. Aximu-Petri, E. Essel, S. Nagel, B. Nickel, A.
1006 Schmidt, K. Prüfer, J. Kelso, H. A. Burbano, S. Pääbo, M. Meyer, Neandertal and Denisovan DNA from
1007 Pleistocene sediments. *Science* 356, 605-608 (2017).

- 1008 88. A. Peltzer, G. Jäger, A. Herbig, A. Seitz, C. Kniep, J. Krause, K. Nieselt, EAGER: efficient ancient
1009 genome reconstruction. *Genome Biol.* 17, 60-73 (2016).
- 1010 89. M. Schubert, S. Lindgreen, L. Orland, AdapterRemoval v2: rapid adapter trimming, identification,
1011 and read merging. *BMC Res. Notes* 9, 88-93 (2016).
- 1012 90. H. Li, R. Durbin, Fast and accurate short read alignment with Burrows–Wheeler transform.
1013 *Bioinformatics* 26, 589-595 (2009).
- 1014 91. A. W. Briggs, U. Stenzel, P. L. F. Johnson, R. E. Green, J. Kelso, K. Prüfer, M. Meyer, J. Krause,
1015 M. T. Ronan, M. Lachmann, S. Pääbo, Patterns of damage in genomic DNA sequences from a Neandertal.
1016 *Proc. Natl. Acad. Sci. U.S.A* 104, 14616–14621 (2007).
- 1017 92. T. S. Korneliussen, A. Albrechtsen, R. Nielsen, ANGSD: Analysis of Next Generation Sequencing
1018 Data. *BMC Bioinformatics* 15, 356-368 (2014).
- 1019 93. M. Rasmussen, X. Guo, Y. Wang, K. Lohmueller, S. Rasmussen, A. Albrechtsen, L. Skotte, S.
1020 Lindgreen, M. Metspalu, T. Jombart, T. Kivisild, W. Zhai, A. Eriksson, A. Manica, L. Orlando, F. De La
1021 Vega, S. Tridico, E. Metspalu, K. Nielsen, M. Ávila-Arcos, J. Moreno-Mayar, C. Muller, J. Dortch, M.
1022 Gilbert, O. Lund, A. Wesolowska, M. Karmin, L. Weinert, B. Wang, J. Li, S. Tai, F. Xiao, T. Hanihara, G.
1023 van Driem, A. Jha, F. Ricaut, P. de Knijff, A. Migliano, I. Gallego Romero, K. Kristiansen, D. Lambert, S.
1024 Brunak, P. Forster, B. Brinkmann, O. Nehlich, M. Bunce, M. Richards, R. Gupta, C. Bustamante, A. Krogh,
1025 R. Foley, M. Lahr, F. Balloux, T. Sicheritz-Pontén, R. Villems, R. Nielsen, J. Wang, E. Willerslev, An
1026 Aboriginal Australian Genome Reveals Separate Human Dispersals into Asia. *Science* 334, 94-98 (2011).
- 1027 94. G. Renaud, V. Slon, A. T. Duggan, J. Kelso, Schmutzi: estimation of contamination and
1028 endogenous mitochondrial consensus calling for ancient DNA. *Genome Biol.* 16, 224-241 (2015).
- 1029 95. E. Li, Y. Zhang, DNA methylation in mammals. *Cold Spring Harb Perspect Biol.* 6, a019133
1030 (2014).

- 1031 96. D. J. Kennett, S. Plog, R. J. George, B. J. Culleton, A. S. Watson, P. Skoglund, N. Rohland, S.
1032 Mallick, K. Stewardson, L. Kistler, S. A. LeBlanc, P. M. Whiteley, D. Reich, G. H. Perry, Archaeogenomic
1033 evidence reveals prehistoric matrilineal dynasty. *Nat. Commun.* 8, 14115 (2017).
- 1034 97. M. van de Loosdrecht, A. Bouzouggar, L. Humphrey, C. Posth, N. Barton, A. Aximu-Petri, B.
1035 Nickel, S. Nagel, E. Talbi, M. El Hajraoui, S. Amzazi, J. Hublin, S. Pääbo, S. Schiffels, M. Meyer, W.
1036 Haak, C. Jeong, J. Krause, Pleistocene North African genomes link Near Eastern and sub-Saharan African
1037 human populations. *Science* 360, 548-552 (2018).
- 1038 98. H. Weissensteiner, D. Pacher, A. Kloss-Brandstätter, L. Forer, G. Specht, H. J. Bandelt, F.
1039 Kronenberg, A. Salas, S. Schönherr, *Nucleic Acids Res.* 44, W58-63 (2016).
- 1040 99. M. van Oven, M. Kayser, Updated comprehensive phylogenetic tree of global human mitochondrial
1041 DNA variation. *Hum Mutat.* 30, E386-394 (2009).
- 1042 100. M. Kearse, R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper,
1043 S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Meintjes, A. Drummond, Geneious Basic: An integrated
1044 and extendable desktop software platform for the organization and analysis of sequence data.
1045 *Bioinformatics* 28, 1647–1649 (2012).
- 1046 101. G. D. Poznik, Y. Xue, F. L. Mendez, T. F. Willems, T. G. P. Consortium, C. D. Bustamante, C.
1047 Tyler-Smith, Punctuated bursts in human male demography inferred from 1,244 worldwide Y-chromosome
1048 sequences. *Nat. Genet.* 48, 593–599 (2016).
- 1049 102. N. Patterson, A. L. Price, D. Reich, Population Structure and Eigenanalysis. *PLoS Genet* 2, e190
1050 (2006).
- 1051 103. D. Reich, K. Thangaraj, N. Patterson, A. L. Price, L. Singh, Reconstructing Indian population
1052 history. *Nature* 461, 489-494 (2009).

- 1053 104. S. Talamo, M. Richards, A Comparison of Bone Pretreatment Methods for AMS Dating of Samples
1054 >30,000 BP. *Radiocarbon* 53, 443-449 (2011).
- 1055 105. R. Longin, New Method of Collagen Extraction for Radiocarbon Dating. *Nature* 230, 241-242
1056 (1971).
- 1057 106. T. A. Brown, D. E. Nelson, J. S. Vogel, J. R. Southon, Improved Collagen Extraction by Modified
1058 Longin Method. *Radiocarbon* 30, 171-177 (1988).
- 1059 107. F. Brock, C. Bronk Ramsey, T. Higham, Quality assurance of ultrafiltered bone dating.
1060 *Radiocarbon* 49, 187–192 (2007).
- 1061 108. P. Korlević, S. Talamo, M. Meyer, A combined method for DNA analysis and radiocarbon dating
1062 from a single sample. *Scientific Reports* 8, (2018).
- 1063 109. P. Reimer, G. McCormac, Marine Radiocarbon Reservoir Corrections for the Mediterranean and
1064 Aegean Seas. *Radiocarbon* 44, 159 (2002).
- 1065 110. G. van Klinken, J. Bone Collagen Quality Indicators for Palaeodietary and Radiocarbon
1066 Measurements. *Journal of Archaeological Science* 26, 687-695 (1999).
- 1067 111. G. Mannino, Il riparo dell'Uzzo. *Sicilia Archeologica (VI)* 23, 21-39 (1973).
- 1068 112. L. Conte, S. Tusa, Approfondimento stratigrafico alla Grotta dell'Uzzo. *Atti della XLI Riunione
1069 Scientifica dell'Istituto Italiano di Preistoria e Protostoria*, 437-445 (2012).
- 1070 113. M. Piperno, S. Scali, A. Tagliacozzo, Mesolitico e Neolitico alla Grotta dell'Uzzo (Trapani). Primi
1071 dati per un'interpretazione paleoeconomica. *Quaternaria* 22, 275-300 (1980).
- 1072 114. M. Piperno, S. Tusa, Relazione preliminare sulla seconda campagna di scavi alla Grotta dell'Uzzo
1073 (Trapani). *Sicilia Archeologica (VI)* 21, 39-42 (1976).

- 1074 115. M. Piperno, S. Tusa, I. Valente, Campagne di scavo 1977 e 1978 alla Grotta dell'Uzzo (Trapani).
1075 Relazione preliminare e datazione dei livelli mesolitici e neolitici. *Sicilia Archeologica (VI)* 42, 49-64
1076 (1980).
- 1077 116. S. M. Borgognini Tarli, A. Canci, M. Piperno, E. Repetto, Dati archeologici e antropologici sulle
1078 sepolture mesolitiche della Grotta dell'Uzzo (Trapani). *Bullettino di Paletnologia Italiana* 84, 85-179
1079 (1993).
- 1080 117. R. Di Salvo, M. A. Mannino, V. Schimmenti, L. Sineo, K. D. Thomas, paper presented at the Atti
1081 della XLI Riunione Scientifica dell'Istituto Italiano di Preistoria e Protostoria, 2012.
- 1082 118. S. M. Borgognini Tarli, E. Repetto, Dietary patterns in the Mesolithic samples from Uzzo and
1083 Molara caves (Sicily): the evidence of teeth. *Journal of Human* 14, 241-254 (1985).
- 1084 119. A. Guerreschi, F. Fontana, paper presented at the Atti della XLI Riunione Scientifica dell'Istituto
1085 Italiano di Preistoria e Protostoria, 2012.
- 1086 120. D. Lo Vetro, F. Martini, paper presented at the Atti della XLI Riunione Scientifica dell'Istituto
1087 Italiano di Preistoria e Protostoria, 2012.
- 1088 121. L. Costantini, M. Piperno, S. Tusa, *La néolithisation de la Sicile occidentale d'après les résultats*
1089 *des fouilles a la grotte de l'Uzzo (Trapani)*. J. Guilaine, J. Courtin, J.-L. Roudil, J.-L. Vernet, Eds.,
1090 Premières Communautés Paysannes en Méditerranée Occidentale (CNRS Editions, Montpellier, 1987).
- 1091 122. M. A. Mannino, K. D. Thomas, M. Piperno, S. Tusa, A. Tagliacozzo, Fine-tuning the radiocarbon
1092 chronology of the Grotta dell'Uzzo (Trapani). *Atti della Società per la Preistoria e Protostoria della*
1093 *Regione Friuli-Venezia Giulia* 15, 17-31 (2006).
- 1094 123. M. Piperno, Scoperta di una sepoltura doppia epigravettiana nella Grotta dell'Uzzo (Trapani).
1095 *Kokalos* 22-23, 734-760 (1976-77).
- 1096 124. C. Bronk Ramsey, Bayesian analysis of radiocarbon dates. *Radiocarbon* 51, 337-370 (2009).

- 1097 125. P. J. Reimer, E. Bard, A. Bayliss, J. W. Beck, P. G. Blackwell, C. Bronk Ramsey, P. M. Grootes,
1098 T. P. Guilderson, H. Hafliðason, I. Hajdas, C. Hatté, T. J. Heaton, D. L. Hoffmann, A. G. Hogg, K. A.
1099 Hughen, K. F. Kaiser, B. Kromer, S. W. Manning, M. Niu, R. W. Reimer, D. A. Richards, E. M. Scott, J.
1100 R. Southon, R. A. Staff, C. S. M. Turney, J. van der Plicht, IntCal13 and Marine13 radiocarbon age
1101 calibration curves 0–50,000 years cal BP. *Radiocarbon* 55, 1869–1887 (2013).
- 1102 126. K. Prüfer, snpAD: An ancient DNA genotype caller. *Bioinformatics* 34, 4165-4171 (2018).
- 1103 127. A. Seguin-Orlando, T. S. Korneliussen, M. Sikora, A. S. Malaspinas, A. Manica, I. Moltke, A.
1104 Albrechtsen, A. Ko, A. Margaryan, V. Moiseyev, T. Goebel, M. Westaway, D. Lambert, V. Khartanovich,
1105 J. D. Wall, P. R. Nigst, R. A. Foley, M. M. Lahr, R. Nielsen, L. Orlando, E. Willerslev, Genomic structure
1106 in Europeans dating back at least 36,200 years. *Science* 346, 1113-1118 (2014).
- 1107 128. Q. Fu, P. Rudan, S. Pääbo, J. Krause, Complete Mitochondrial Genomes Reveal Neolithic
1108 Expansion into Europe. *PLoS ONE* 7, e32473 (2012).
- 1109 129. M. Pala, A. Achilli, A. Olivieri, B. Hooshiar Kashani, U. Perego, D. Sanna, E. Metspalu, K.
1110 Tambets, E. Tamm, M. Accetturo, V. Carossa, H. Lancioni, F. Panara, B. Zimmermann, G. Huber, N. Al-
1111 Zahery, F. Brisighelli, S. R. Woodward, P. Francalacci, W. Parson, A. Salas, D. Behar, R. Villems, O.
1112 Semino, H. J. Bandelt, A. Torroni, Mitochondrial haplogroup U5b3: a distant echo of the epipaleolithic in
1113 Italy and the legacy of the early Sardinians. *Am J Hum Genet.* 84, 814-821 (2009).
- 1114 130. T. Günther, H. Malmström, E. M. Svensson, A. Omrak, F. Sánchez-Quinto, G. M. Kılınc, M.
1115 Krzewińska, G. Eriksson, M. Fraser, H. Edlund, A. R. Munters, A. Coutinho, L. G. Simões, M. Vicente, A.
1116 Sjölander, B. Jansen Sellevold, R. Jørgensen, P. Claes, M. D. Shriver, C. Valdiosera, M. G. Netea, J. Apel,
1117 K. Lidén, B. Skar, J. Storå, A. Götherström, M. Jakobsson, Population genomics of Mesolithic Scandinavia:
1118 Investigating early postglacial migration routes and high-latitude adaptation. *PLoS Biol.* 16, e2003703
1119 (2018).

- 1120 131. C. Gamba, E. Fernández, M. Tirado, M. F. Deguilloux, M. H. Pemonge, P. Utrilla, M. Edo, M.
1121 Molist, R. Rasteiro, L. Chikhi, A.-P. E., Ancient DNA from an Early Neolithic Iberian population supports
1122 a pioneer colonization by first farmers. *Mol. Ecol.* 21, 45-56 (2012).
- 1123 132. A. Szécsényi-Nagy, C. Roth, G. Brandt, C. Rihuete-Herrada, C. Tejedor-Rodríguez, P. Held, Í.
1124 García-Martínez-de-Lagrán, M. H. Arcusa, S. Zesch, C. Knipper, E. Bánffy, S. Friederich, H. Meller, R. P.
1125 Bueno, B. R. Barroso, B. R. de Balbín, A. M. Herrero-Corral, F. R. Flores, F. C. Alonso, E. J. Jiménez, L.
1126 Rindlisbacher, C. Oliart, M. I. Fregeiro, I. Soriano, O. Vicente, R. Micó, V. Lull, D. J. Soler, P. J. A. López,
1127 M. C. Roca de Togores, P. M. S. Hernández, M. F. J. Jover, M. J. Lomba, F. A. Avilés, K. Lillios, A. Silva,
1128 R. M. Magalhães, L. M. Oosterbeek, C. Cunha, A. J. Waterman, J. Roig Buxó, A. Martínez, M. J. Ponce,
1129 O. M. Hunt, J. C. Mejías-García, E. J. C. Pecero, B. R. Cruz-Auñón, T. Tomé, B. E. Carmona, J. Cardoso,
1130 A. Araújo, C. Liesau von Lettow-Vorbeck, B. B. C, M. P. Ríos, A. Pujante, J. I. Royo-Guillén, M. A.
1131 Esquembre Beviá, V. M. Dos Santos Goncalves, R. Parreira, H. E. Morán, I. E. Méndez, M. J. Vega Y, G.
1132 R. Mendiña, C. V. Martínez, J. O. López, J. Krause, S. L. Pichler, R. Garrido-Pena, M. Kunst, R. Risch,
1133 M. A. Rojo-Guerra, W. Haak, K. W. Alt, The maternal genetic make-up of the Iberian Peninsula between
1134 the Neolithic and the Early Bronze Age. *Sci. Rep.* 7, 15644 (2017).
- 1135 133. W. Haak, O. Balanovsky, J. J. Sanchez, S. Koshel, V. Zaporozhchenko, C. J. Adler, C. S. I. Der
1136 Sarkissian, G. Brandt, C. Schwarz, N. Nicklisch, V. Dresely, B. Fritsch, E. Balanovska, R. Villems, H.
1137 Meller, K. W. Alt, A. Cooper, C. the Genographic, Ancient DNA from European Early Neolithic Farmers
1138 Reveals Their Near Eastern Affinities. *PLOS Biology* 8, e1000536 (2010).
- 1139 134. W. Haak, P. Forster, B. Bramanti, S. Matsumura, G. Brandt, M. Tänzer, R. Villems, C. Renfrew,
1140 D. Gronenborn, K. Alt, J. Burger, Ancient DNA from the first European farmers in 7500-year-old Neolithic
1141 site. *Science* 310, 1016-1018 (2005).
- 1142 135. T. Kivisild, The study of human Y chromosome variation through ancient DNA. *Hum. Genet.* 137,
1143 863 (2017).

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1160 Read Archive (accession number X) and consensus mitogenome sequences (FASTA format) in GenBank
1161 (accession numbers X to X).