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1 **Multi-scale archaeogenetic study of two French Iron Age communities: from internal social- to**
2 **broad-scale population dynamics**

3 Claire-Elise Fischer^{a,*}, Marie-Hélène Pemonge^a, Frédéric Santos^a, Harmony Houzelot^a, Christine
4 Couture-Veschambre^a, Anthony Lefort^b, Stéphane Rottier^a and Marie-France Deguilloux^a

5 ^a De la Préhistoire à l'Actuel, Culture, Environnement, Anthropologie – UMR 5199, CNRS, Université
6 de Bordeaux, Allée Geoffroy Saint-Hilaire, CS 50023, 33615 Pessac Cedex, France

7 ^b Inrap Grand-Ouest, Boulevard de l'Europe, Bourguébus, France

8 [*claire-elise.fischer@u-bordeaux.fr](mailto:claire-elise.fischer@u-bordeaux.fr) (C.-E. Fischer)

9 marie-helene.pemonge@u-bordeaux.fr (M.-H. Pemonge)

10 frederic.santos@u-bordeaux.fr (F. Santos)

11 monyh@hotmail.fr (H. Houzelot)

12 christine.veschambre-couture@u-bordeaux.fr (C. Couture-Veschambre)

13 lefort.anthony@sfr.fr (A. Lefort)

14 stephane.rottier@u-bordeaux.fr (S. Rottier)

15 marie-france.deguilloux@u-bordeaux.fr (M.-F. Deguilloux)

16 **Key words:**

17 Late Iron Age; ancient DNA; social dynamics; phylogeography; French territory

18 **Highlights:**

- 19 • Multidisciplinary study of Late Iron age groups from Northern France
- 20 • Population-scale DNA-based approach permitted the documentation of communities'
21 internal social dynamics
- 22 • Gallic groups were characterised by patrilocal residence and patrilinearity rules
- 23 • Distinct necropolis welcomed distinct biological and social groups

24 • Local-scale communities' features were essential to address broad-scale phylogeographical
25 issues

26

27

28 **Abstract:**

29 Ancient DNA (aDNA) research can address anthropological questions at both the broad continental
30 scale to provide elements of discussion regarding ancient human population dynamics and the very
31 small spatial scale to document population social functioning. In the present study, we propose an
32 original approach combining local- and broad-scale issues, applied to two contemporaneous groups
33 dated from the Late Iron Age period and originating from Northern France. Our analyses targeted
34 uniparental markers (mitochondrial DNA (mtDNA) and the Y chromosome) and permitted the
35 characterization of 43 maternal and 17 paternal lineages for the Urville-Nacqueville necropolis (UN)
36 as well as 27 maternal and 19 paternal lineages for the Gurgy 'Les Noisats' (GLN) tumulus. Data in
37 hand provided a unique opportunity to document Gallic communities' genetic diversities and discuss
38 their internal social dynamics as well as their genetic affinities with other ancient European groups.
39 At the local scale, our study first highlighted patrilocal residence rules and patrilinearity for these
40 Gallic groups, in concordance with textual sources and archaeological data. Second, the gene pool
41 characterization indicated that the UN necropolis welcomed a more cosmopolitan community than
42 did the GLN tumulus and that the funerary space organization in the UN was correlated to the
43 genetic structuration of the community. These local scale characteristics were put into perspective
44 for broad-scale discussions and highlighted different genetic affinities of the UN and GLN
45 communities with ancient European groups. Both communities appeared inserted in distinct
46 exchange networks that may have been responsible for the slight differentiation of their maternal
47 gene pools. Finally, we demonstrated that the sub-groups encountered in the UN necropolis
48 (maternally differentiated) presented very distinct genetic affinities with ancient or
49 contemporaneous human groups from other Western European regions. Consequently, our study
50 reinforces the idea that the identification of genetically differentiated groups within archaeological
51 sites and discussion concerning their specific composition constitute a clear prerequisite before
52 addressing broad-scale phylogeographical issues.

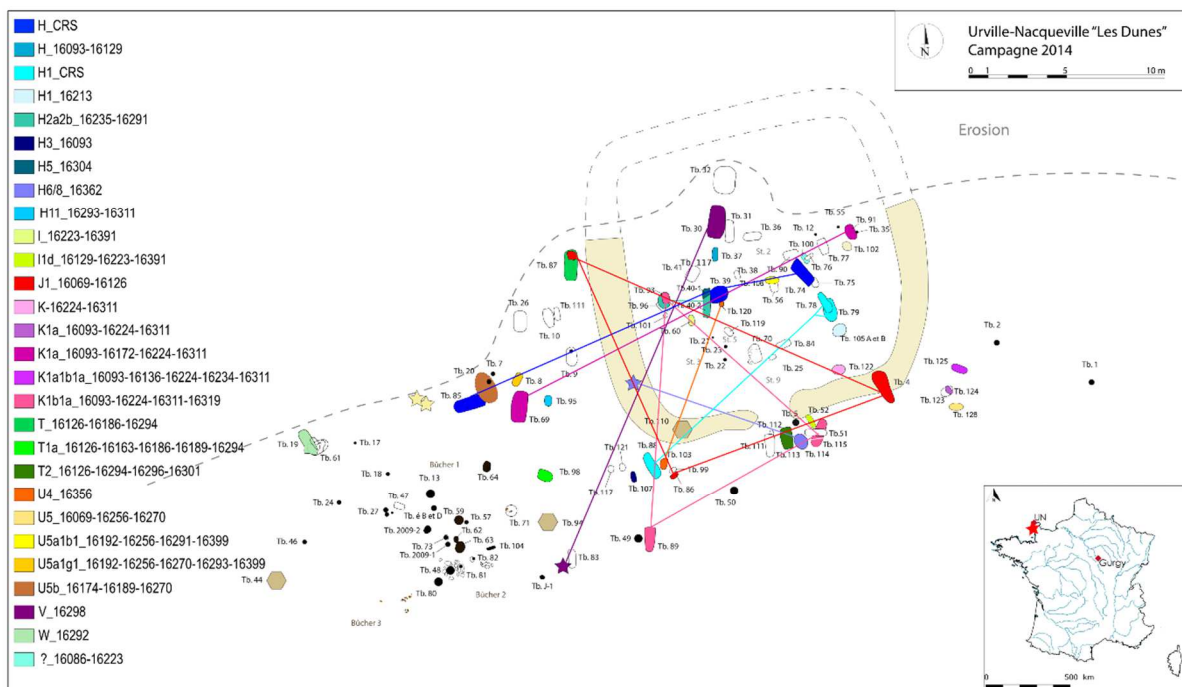
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54 **Introduction**

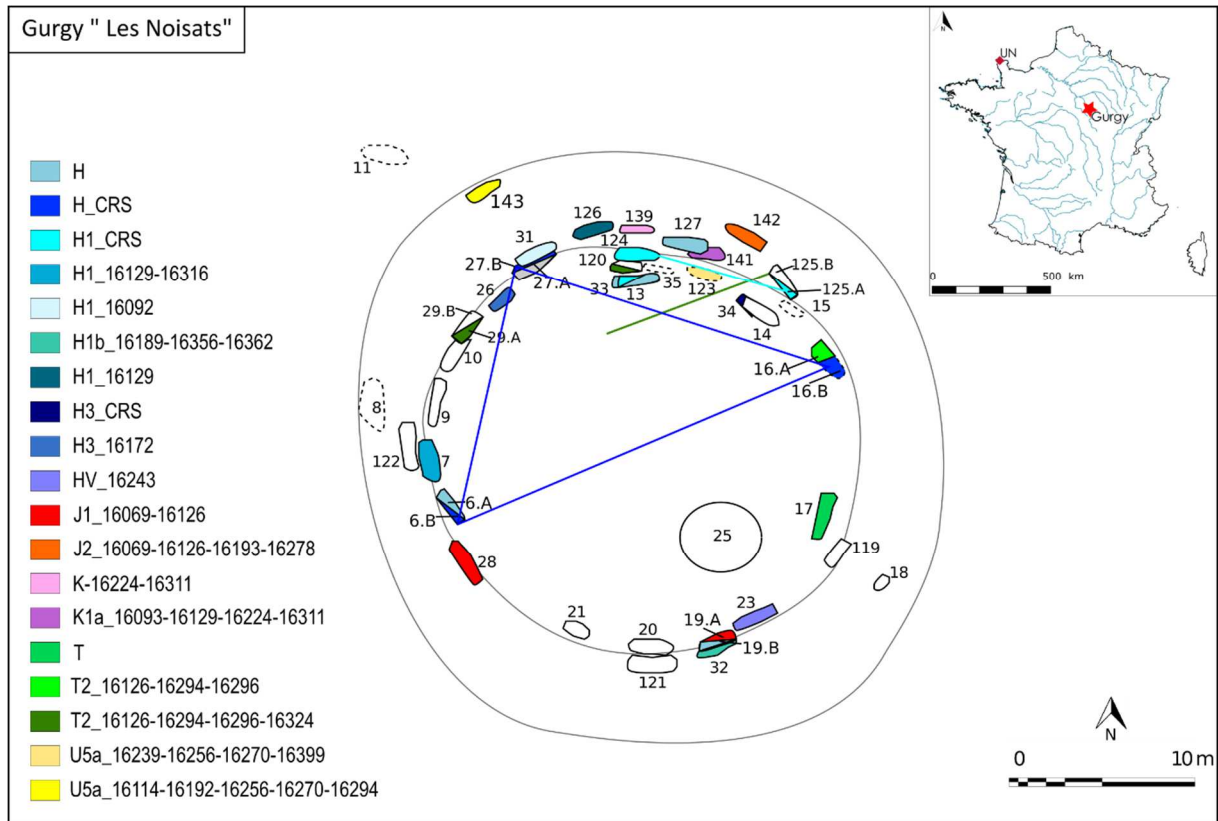
55 Over the past decade, ancient DNA (aDNA) research has addressed archaeological and
56 anthropological questions, whether at the broad continental scale or at the very small spatial scale.
57 The first continental scale has provided major elements of discussion regarding ancient human
58 population migrations, admixture or replacements (for a recent review see Harris, 2017). At the very
59 local scale, the palaeogenetic approach has shed light on specific populations' social functioning, with
60 an emphasis on kinships and matrimonial systems (see for example Keyser-Tracqui et al., 2003 and
61 Haak et al., 2008). The genetic constitution of human populations can be very complex due to social
62 structuration, specific matrimonial or filiation systems. The considerable variability of population
63 gene pools, due to these specific internal social dynamics, implies that the use of a small number of
64 samples to represent largely dispersed archaeological cultures may lead to erroneous interpretation
65 of data. Moreover, the genetically analysed ancient human communities generally originate from
66 specific funerary sites whose access may have been limited to a peculiar group who may not be fully
67 representative of the community. Therefore, considerable variability in the genetic diversity of
68 ancient groups can even be encountered within cemeteries. The precise understanding of both the
69 funerary site functioning and the constitution of the "dead community", addressed through
70 archaeological, anthropological and small-scale aDNA studies, thus constitutes a preliminary process
71 necessary to the appropriate use of the group gene pools for the reconstruction of broad-scale
72 population dynamics (Johannsen et al., 2017; Veeramah, 2018).

73 Thus far, aDNA studies addressing both scales and thus combining local communities' social
74 functioning and phylogeographical issues remain rare (Beau et al., 2017; Knipper et al., 2017; Rivollat
75 et al., 2015; Veeramah, 2018). For the Iron Age, our period of interest, an original study combined
76 biological (osteology, isotopes, DNA) and archaeological data obtained on individuals from a
77 "princely site" in Germany to investigate the social structuration of the local community (Knipper et

78 al., 2014). While the data obtained allowed to discuss individuals' maternal relationships, the small
79 gene pool recovered could not be used to address phylogeographical issues. In the present study, we
80 propose an original approach combining local- and broad-scale issues, applied to two groups dated
81 from the Late Iron Age period and originating from Northern France.
82 Our study targeted two communities corresponding to the famous French "Gauls", according to the
83 Classical and ancient texts, and originating from the second part of the Late Iron Age sites of Urville-
84 Nacqueville (120- 80 BC, Manche) and Gurgy 'Les Noisats' (300-100 BC, Yonne) (Fig 1 and 2). It is
85 important to note that the communities targeted were associated to distinct Celtic Gallic cultures
86 according to texts and historical data: Urville-Nacqueville was associated to the Unelles group
87 whereas Gurgy "Les Noisats" was located in Senons' territory.



88
89 **Figure 1 : Location of the Urville-Nacqueville site and spatial distribution of the mitochondrial**
90 **(mtDNA). Individuals sharing a mtDNA haplotype are linked by a line.**



91

92 **Figure 2 : Location of the Gurgy ‘Les Noisats’ site and spatial distribution of the mitochondrial**
 93 **(mtDNA). Individuals sharing a mtDNA haplotype are linked by a line.**

94

95 Urville-Nacqueville (UN) is a port site located along the Channel seashore **which** is characterized by
 96 the presence of an artisanal sector and a vast cemetery (Lefort et al., 2015). The funerary space,
 97 organized around a square enclosure, included 112 identified burials and at least 120 individuals. **The**
 98 **necropolis of Gurgy Les Noisats is located in the Parisian Basin within the Senon’s territory. Many**
 99 **archaeological sites dated to the Iron Age have been described in the region (Baray, 2016; Duval,**
 100 **1976; Hure, 1931). Although numerous habitats could be identified in the region for the period, non**
 101 **could be associated to the Gurgy necropolis (Delor, 2013). Gurgy ‘Les Noisats’ (GLN) consists of a**
 102 **tumulus approximately 30 metres in diameter that received 40 individuals spread over 35 graves**
 103 **(unpublished).** To document the biological diversity of the UN and GLN groups, our aDNA study
 104 targeted uniparental genetic markers (mitochondrial DNA, mtDNA and the Y chromosome),
 105 permitting the characterization of maternal and paternal lineages. At the very local scale, special

106 attention was paid to the combination of archaeological, anthropological and genetic data (i) to
107 discuss funerary groups' diversity and constitution, (ii) to test for the potential presence of groups
108 genetically differentiated within each necropolis and (iii) to address each community-specific social
109 functioning. The comparison of the results obtained for the partially contemporary sites of UN and
110 GLN permitted us to question potential general social dynamics for the French Late Iron Age context.
111 Interestingly, the European Iron Age is the most ancient archaeological period for which textual
112 documentation is available. The textual sources describing the Gauls and their social habits were not
113 written by the Gauls themselves but by contemporary Romans and Greeks and must consequently
114 provide a distorted view of the French Iron Age groups' cultural diversity or habits. Whatever the
115 case, texts such as the writings of Strabon, Poseidonios d'Apamée or Caesar (*De Bello Gallico*) have
116 survived over time and constitute a unique opportunity to combine archaeological, biological and
117 textual data to better understand Gallic societies. Finally, the elements of discussion obtained at the
118 local scale were put into perspective to address broad scale issues, including (i) the biological
119 affinities of distinct Gaul communities and (ii) the genetic legacy and dynamics of European Iron Age
120 populations.

121 **1. Materials and methods**

122 **1.1 Archaeological samples**

123 The excavations of the Urville-Nacqueville necropolis permitted the discovery of 112 graves
124 (78 burials and 34 cremations) containing the remains of at least 127 individuals (of which 41 were
125 cremated) (Lefort and Rottier, 2014). All aDNA analyses were conducted on individuals recovered
126 from burials (*i.e.*, not cremated) and targeted 51 individuals distributed throughout the entire
127 necropolis. The sample included all individuals published *in* Fischer et al. (Fischer et al., 2018) plus 6
128 newly analysed individuals (S1 Table). To obtain a clear picture of the genetic diversity of sub-groups
129 corresponding to distinct necropolis sectors or funerary practices, we targeted individuals from both
130 outside (N=19) and inside the enclosure (N=32), as well as several individuals from the same small

131 groups of burials. The sample was thus supposed to addressing the genetic variability of intra- and
132 extra-enclosure groups and to test for potential groupings of individuals according to maternal or
133 paternal kinship.

134 Contrary to the Urville-Nacqueville necropolis, which is outstanding for the period and the
135 region, the Gurgy 'Les Noisats' (GLN) site is typical of the necropolises known for the Paris Basin
136 during the Late Iron Age. This site corresponds to a tumulus that grouped a total of 35 graves,
137 containing the remains of at least 40 individuals. Among the graves discovered, 8 correspond to
138 plural tombs, and 5 of them group an adult and an immature. The limited number of individuals
139 allowed to submit all of them to palaeogenetic analyses (S2 Table). The diameter of the tumulus
140 (approximately 30 m) as well as the absence of selection of the deceased according to age or sex or
141 the majority of burials over cremation appeared consistent with necropolises observed for the same
142 context (Baray, 2003; Marion et al., 2009). The combination of these characteristics with a short
143 duration of use of the tumulus (200 years, based on metallic material, unpublished) allowed us to
144 assume that the population recovered in the GLN tumulus was representative of the whole local
145 community.

146 Since both necropolises were used during a short period (less than two hundred years) and because
147 biological studies conducted on both sites have shown the absence of selection of the dead
148 according to age or sex, we expect that the funerary groups were representative of the local
149 communities as a whole. For the specific case of the UN, a change in the funerary treatment could be
150 highlighted as related to age at death since children were usually buried while adults were burnt
151 (Lefort and Rottier, 2014). If burnt adults were not accessible for our aDNA study, the absence of age
152 or sex selection of individuals having access to the necropolis suggests that the gene pool recovered
153 for the buried children group may reflect the population gene pool. Consequently, we consider that
154 the sampling strategy designed in our study was adequate to unravel entire communities' gene pools
155 and to question the presence of groups genetically differentiated within each necropolis.

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1.2 Ancient DNA analyses and descriptive analyses

Most UN samples were collected during excavations (from 2012 to 2014) with all precautions against contaminations. Teeth were then preferentially collected for adults, whereas intact long bones were selected for immature individuals. All sampling performed after 2015 targeted petrous bones according to the recent discovery of the exceptional DNA conservation in this anatomical element (Pinhasi et al., 2015). The GLN human remains were collected for genetic analyses in 2016, 12 years after the excavations (unpublished). We targeted for all GLN individuals, in order of preference, petrous bones then teeth and, finally, bones. Since GLN human remains had been collected without any precautions against contamination and regularly manipulated during post-excavation studies, they were systematically decontaminated before extraction *i.e.*, scraped, cleaned with bleach and subsequently exposed to UV radiation for 20 minutes for each side.

The genetic analyses targeted the uniparental markers permitting the characterization of maternal (mitochondrial DNA, mtDNA) and paternal lineages (Y-chromosome). Our approach combined the analysis of 18 mtDNA and 10 Y-chromosome SNPs (single nucleotide polymorphisms) and the sequencing of the mtDNA Hyper Variable Sequence (HVS-1). Details of all analyses can be found in Rivollat *et al.* (2015). Y-chromosome SNP analyses were conducted on adult individuals identified as males through osteological analyses (determined by the Bruzek (Bruzek, 2002) and DSP (Murail et al., 2005) methods) as well as adults with undetermined sex and all immature individuals.

The genetic diversities of the GLN and UN groups were measured through the computation of Nei genetic diversity (h^2) using Arlequin software (version 3.5.1.2) (Excoffier and Lischer, 2010). Fisher's exact tests were used to test the statistical significance of genetic diversity differences measured between groups or DNA conservation variability observed between sites. The tests were performed with BiostaTGV (<https://biostatgv.sentiweb.fr/?module=tests/fisher>). Resampling analyses were performed with R 3.6.0 (R Core Team, 2019) taking into account sample size heterogeneity between groups for the comparison of Nei's diversity indices (see R script in SI).

182 Adjusted bootstrap confidence interval (Zieffler, Haring, & Long, 2011) were computed for the
183 differences in Nei's indices between the groups under study, using 10000 bootstrap replicates.

184 To discuss the genetic affinities of UN and GLN communities with ancient European human
185 groups, we ran a series of descriptive analyses using the **datas** published by Fischer and colleagues,
186 which includes 1433 mitochondrial sequences dating from the Palaeolithic to the Iron Age (42,500-
187 300 cal. BC), divided into 29 chronological, geographical and cultural groups (Fischer et al., 2018) (S3
188 Table). The proportions of shared mtDNA haplotypes and population-specific pairwise genetic
189 distances (FST) were computed using Arlequin software (version 3.5.1.2)(Excoffier and Lischer, 2010).
190 A principal component analysis (PCA) based on mtDNA haplogroup frequencies was carried out,
191 taking into account the major European haplogroups identified and distinguished in aDNA literature
192 targeting European populations: H, HV, I, J, K, N, T, U4, U5a, U5b, U, V, W, X and "others". The PCA
193 was performed using the R package FactoMineR (Lê et al., 2008).

194

195 **2. Results and Discussion**

196 **2.1 DNA conservation variability among necropolises**

197 Mitochondrial lineages reported for the UN site combined those already published in Fischer
198 *et al.* (2018) and updated (some SNP profiles and HVS-I sequences could be completed), plus those
199 obtained on 6 newly analysed individuals. In the end, 42 mitochondrial haplogroups (determined
200 through SNP analysis) could be characterized over 51 targeted individuals (80.7% success rate), and
201 43 complete and authenticated HVS-1 sequences (mtDNA haplotypes) could be obtained (82.7%
202 success rate) (S1 and S4a Tables). Concerning the Y chromosome, 17 partial or complete SNP profiles
203 were obtained, permitting us to corroborate the sex of 3 adults identified as males through
204 osteological analyses and to unravel the existence of male individuals in the immature group (N= 15)
205 (see details in S4b Table). The analyses conducted on the 40 individuals originating from the GLN
206 necropolis permitted the characterization of 27 mitochondrial haplogroups (67.5% success rate) and

207 23 complete HVS-1 sequences (57.5% success rate). A total of 19 Y-chromosome SNP profiles,
208 complete or partial, were obtained and confirmed the morphological sex of 6 male adults and
209 provided new clues for males identification for 11 individuals (see details in S1, S4c and S4d Table).

210 A higher success rate of HVS-1 sequence recovery could be observed for UN individuals when
211 compared to GLN individuals (UN: 82.7%; GLN:57.5%, statistically significant; p value = 0.00846). The
212 excellent conservation of mitochondrial DNA has already been highlighted for the UN necropolis
213 (Fischer et al., 2018) and could be explained by its location on the edge of the Channel foreshore.
214 Moreover, immature UN individuals were regularly discovered in benches made of plants, confirming
215 the very exceptional conservation parameters in UN. Moreover, this organic material appears to
216 have been responsible for the formation of a crust on the bones that may have protected them from
217 various degradations.

218 Since our sampling targeted petrous bones, teeth and other bones, we tested for differential
219 mitochondrial DNA conservation among these anatomical elements (S1. Figure). Fisher's exact tests
220 revealed significant mtDNA conservation differences among anatomical elements for UN samples,
221 with an easier mtDNA recovery for the teeth compared to other skeletal elements (p value = 0.045).
222 This result is consistent with the recent report of a higher mtDNA/nuclear DNA ratio for teeth
223 compared to petrous bones (Furtwängler et al., 2018). Given the lower number of samples, especially
224 for bones (N=2), we did not perform statistical tests to compare GLN samples. No significant
225 differences in mtDNA recovery could be highlighted between teeth and bones (other than petrous
226 bones), even after merging the UN and GLN results to increase the number of samples. Finally,
227 contrary to that for teeth and bones, we observed a similar mtDNA recovery from GLN and UN
228 petrous bones, whereas the taphonomic environments were very different. This point is in line with
229 studies that demonstrated that DNA was less subject to environmental variations within petrous
230 bones (Gamba et al., 2014; Hansen et al., 2017).

231 Finally, when samples from both sites were merged to increase sample size, mitochondrial DNA
232 appeared to be more preserved for adults than immature individuals. Even if the difference was not

233 significant (p value = 0.478), this observation could be explained by skeletal conservation variation
234 related to age at death. Indeed, it has been clearly shown that the anatomical conservation index
235 (ICA) of immature individuals was lower than that measured for adults, highlighting differential
236 macroscopic conservation according to age at death (Bello et al., 2002).

237

238 **2.2 French Iron Age communities' internal social dynamics**

239 A noticeable variety of mtDNA haplogroups could be characterized for the UN group (N
240 individuals = 43), including K1, J1, H, H1, H2, H3, H5, H6/8, H11, U4, U5a, U5b, I, V, T1 and T2 major
241 lineages (Fig 1). A total of 16 sub-haplogroups and 27 distinct haplotypes could be determined
242 among the UN sample. Among the mtDNA haplotypes discovered, 9 were shown to be shared
243 between at least two distinct individuals, indicating possible maternal kinship (S1 Table). However,
244 several of these shared maternal lineages corresponded to mtDNA haplotypes very frequent within
245 ancient European groups, and their interpretation in terms of kinship determination may be
246 erroneous. This is the case for H (CRS), H1 (CRS), J1 (16069-16126), U4 (163556) and V (16298)
247 lineages shared by 2 to 3 individuals inside the necropolis. More interestingly, some individuals
248 shared infrequent lineages that may thus be more informative in terms of maternal kinship, as this is
249 the case for K1a (16093-16172-16224-16311), K1b1a (16093-16224-16311-16319), H2a2b (16235-
250 16291), H6/8 (16362) and H1 (16213) haplotypes carried by 2 to 3 individuals (Fig 1). It is worth
251 noting that individuals sharing these maternal lineages were discovered both inside and outside the
252 enclosure.

253 The smaller GLN group (N individuals = 27) is unsurprisingly characterized by a smaller number of
254 mtDNA sub-haplogroups (N=9) encompassing lineages H, H1, H3, HV, J1, J2, K, U5a and T2. A total of
255 13 distinct haplotypes could be determined among the GLN sample, of which 3 were shown to be
256 shared between at least 2 individuals. However, maternal lineages shared between GLN individuals
257 all corresponded to very frequent mtDNA haplogroups (H (CRS), H1 (CRS) and T2a1b (16126-16294-
258 16296-16324) haplotypes), impeding any discussion in terms of maternal kinship (Fig 2).

259 For both UN and GLN communities, a striking homogeneity of the Y-chromosome lineages
260 could be observed, all of them corresponding either to R* or R1b (M343) haplogroups. However, we
261 must highlight that the SNP markers used to characterize the individual paternal haplogroups were
262 very low in number and did not permit deep exploration inside the Y-chromosome phylogeny.
263 Furthermore, numerous artefactual alleles regularly appeared in the SNP profiles, complicating
264 lineage determination. The paternal uniformity unravelled for French Iron Age groups is
265 consequently in part the result of the genotyping design. Regardless of the case, we consistently
266 found in our Iron Age samples R* / R1b paternal lineages that are linked to the massive migration
267 from the steppes and dated to the Late Neolithic-to-Bronze Age transition (Haak et al., 2015). This
268 migration was responsible for an impressive genetic turnover in the European populations, with
269 Neolithic haplogroups being replaced by new paternal (R1a and R1b) lineages originating from the
270 eastern regions (see below).

271 The Nei genetic diversity was calculated for each Iron Age group based on maternal markers
272 and provided clues for high maternal diversity for both UN and GLN communities (0.969 and 0.885,
273 respectively). A nonparametric adjusted bootstrap 95% percentile interval was computed for this
274 difference, yielding the range of [-0.2377 ; -0.0026]. This range of values indicates likely candidates
275 for the true value of genetic diversity difference between these two groups. Since this interval does
276 not include the null value, it provides moderate evidence for the hypothesis that there is a higher
277 diversity in the UN group. We propose that the high maternal genetic diversities measured and the
278 variation of diversities observed between our French Iron age communities can be explained by (i)
279 the groups' residence rules and (ii) the constitution of the populations buried in the necropolises.

280

281 **2.2.1 A patrilocal matrimonial system?**

282 The gene pools of societies practising patrilocal residence rules are characterized by a series
283 of specific features, including a low paternal lineage diversity (linked to low mobility of men)
284 combined with a high maternal diversity (related to important mobility of women among groups,

285 introducing new lineages in the recipient population) (Dudar et al., 2003; Oota et al., 2001). Both
286 features could be unravelled for UN and GLN sites and suggested that these communities practised
287 patrilocality residence rules. It is worth noting that aDNA studies have regularly provided arguments
288 permitting the identification of patrilocality residence rules for ancient European groups (Haak et al.,
289 2008; Knipper et al., 2017; Lacan et al., 2011). For example, a study conducted by Knipper et al.
290 (2017) on Bell Beaker and Early Bronze Age societies from Central Europe and based on aDNA and
291 isotopic data highlighted patrilocality residence system as well as exogamy for women. In this specific
292 case, a high mitochondrial diversity ($h^2 = 0.9924$) could be calculated. Because the maternal diversity
293 calculated by Knipper et al. covered 80 individuals spread over 7 distinct archaeological sites dated
294 between 2500 and 1700 BC (representing approximately 27 generations), we believe that the high
295 maternal diversities measured for GLN and UN communities, composed of individuals originating
296 from a unique site and distributed among only 7 generations (approximately 200 years) for GLN and
297 only 3 generations (less than 100 years) for UN, constitute a clear argument for patrilocality.

298 For both UN and GLN necropolises, even if some individuals shared the same mitochondrial
299 lineages, no group of tombs related to maternal lines could be detected (Fig 1 and 2). The absence of
300 visible structuration of the funerary spaces according to maternal affinities may provide argument in
301 favour of patrilinearity. In that case, the paternal homogeneity characterized inside both
302 necropolises may be consistent with a structuration of the necropolises in link with paternal kinships.
303 If it is obvious that more precise genomic data are necessary to confirm this hypothesis, it is
304 nevertheless interesting to note that patrilocality and patrilinearity have both been proposed for
305 Gaulish societies according to textual and archaeological data. In that respect, ancient texts, such as
306 *De Bello Gallico* or Strabon's writings have provided arguments to consider that Gallic societies had
307 practised patrilocality residence rules, with inter-ethnic alliances linked to the exchange of women
308 between *civitas* (the *civitas* being a political entity that included several *pagi*, i.e., group of tribes
309 with a specific ethnic identity; Lewuillon, 1990) . In the same way, according to the work of Lewuillon
310 (1990), Gallic societies may have been built on the fundamental and dominant principle of

311 patrilinearity, with a very strong impact of paternal heredity on communities' internal social
312 structuration. Palaeogenetic data obtained for Late Iron Age UN and GLN communities are thus in
313 line with archaeological or textual arguments. Since the UN group revealed a maternal diversity
314 statistically higher than the one measured for the GLN group, we confronted at the very local scale
315 funerary and genetic traits available to discuss the constitution of each "dead community".

316

317 **2.2.2 Different funerary groups' constitution?**

318 Numerous arguments have permitted the identification of the UN site as an important place
319 of exchange with Southern England. Indeed, the site is located along the Channel coast and faces two
320 port sites of Southern England: Hengistbury Head and Poole Harbour. Exchanges with this region are
321 mirrored by the presence in the UN of cultural elements shared on the both side of the Channel. This
322 is notably the case for circular buildings, the use of lignite as a raw material for the manufacture of
323 bracelets or the position of some buried adults, which evokes the one encountered among the
324 Durotriges group (a contemporary group based in Dorset; Lefort et al., 2015). Obviously, the
325 interpretation of the UN site as a place of human circulation and gene flow along the Channel and
326 the Atlantic coast (as already discussed in Fischer et al., 2018), could explain the higher maternal
327 diversity measured for the community.

328 Since the UN funerary space was clearly organized in different sectors (inside and outside an
329 enclosure), we explored whether this funerary space organization was linked to any genetic
330 differentiation. The observed maternal diversity (h^2) was found to be higher for the group discovered
331 outside the enclosure (0.983) than for the group buried inside the enclosure (0.976). This might
332 suggest that the enclosure constituted a funerary sector that welcomed a special group of deceased.
333 Given the relatively small sample sizes (respectively N=19 inside and N=32 outside the enclosure),
334 the adjusted bootstrap confidence interval, including the null value as a credible candidate for the
335 difference in genetic diversity between these two groups, failed to provide a strong evidence in favor
336 of this hypothesis (extensive results available as Supporting Information online) however, this

337 observation was reinforced by the apparent exclusion of several maternal lineages (notably lineages
338 J1 and T) from the enclosure group (Fig 1). Consequently, we can propose the hypothesis that the
339 enclosure was dedicated to a specific group of the community, characterized by lower genetic
340 diversity. This hypothesis resonates with the propositions offered by archaeological studies. In some
341 necropolises dated to the Late Iron Age, the presence of an enclosure was attributed to the
342 appropriation of the territory by a dominant family, who gathered its deceased members in a
343 dedicated funerary space. The structuration of the funerary space would then reflect the social
344 hierarchy of the community members (Lambot, 2000; Verger, 2009). In the specific case of the UN
345 necropolis, the enclosure may thus have received the members of a dominant family, characterized
346 by lower genetic diversity than the rest of the community, due to its smaller effective size and/or
347 endogamy. The fact that some individuals sharing the same maternal lineage were distributed both
348 inside and outside the enclosure (Fig 1) seems counterintuitive with the hypothesis of a funerary
349 space organized according to family structure. However, since textual sources suggest that social
350 status was inherited through paternal lines (Lewuillon, 1990) and that our genetic data would be in
351 accordance with societies practising patrilinearity, the funerary space should be rather structured
352 alongside Y-chromosome lineages. Unfortunately, our low-resolution analysis of paternal lineages
353 does not permit us to test this point. An alternative hypothesis concerning the constitution of the
354 dead groups having access to the different UN sectors may include chronological evolution from an
355 initial group. Indeed, some archaeological arguments may indicate that the enclosure was used
356 before the rest of the necropolis. Notably, individuals UN-4 and UN-108 were found in graves dug
357 across the enclosure ditch and must therefore have been buried after the enclosure disappearance.
358 This could indicate that the enclosure and the individuals buried in it were more ancient than the
359 individuals found outside. In such a case, the older funerary group found in the enclosure could have
360 corresponded to a smaller founding group (with a lower diversity), which may have been at the origin
361 of a larger community found outside the enclosure or have been replaced by this more recent group.
362 Nevertheless, the chronological succession of genetically differentiated groups must have occurred

363 over only a hundred years *i.e.*, the duration of use of the UN necropolis. Whatever the case, if the
364 processes implied in the genetic differentiation of the groups found inside vs. outside the enclosure
365 in Urville-Nacqueville remain to be determined, the presence in the site of two genetically
366 differentiated groups must be taken into account when addressing broad scale issues including
367 groups' biological affinities, genetic legacies and dynamics.

368 As already mentioned, the combination of these characteristics with a short duration of use of the
369 tumulus (200 years) allowed us to assume that the population recovered in the GLN tumulus was
370 representative of the whole local community. The lower maternal genetic diversity measured for the
371 GLN group could be explained by the fact that the necropolis welcomed the members of a more local
372 community than the cosmopolitan population found in the UN site. According to Gerritsen
373 (Gerritsen, 2006, 2003), a local community includes people who interact daily in a reduced social
374 context in space, such as hamlets or a group of farms, and who can share a common burial place and
375 could therefore be considered a group of affiliated individuals. For other authors, the extended
376 family group is a unit of production, consumption and social interaction in which people participate
377 in collective decisions and defend their own interests and those of their members (Fernández-Götz,
378 2014). For our study, we preferred to use the term local community in the sense defined by
379 Gerritsen.

380 Interestingly, several studies have permitted a better understanding of the local organization of Gaul
381 societies. Notably, Brun's work has permitted to show that, in a rural context, territories were
382 organized into isolated farms distributed every 3 to 5 km (Brun, 2011). This spatial organization of
383 agricultural communities appears to have been established during the second part of the Bronze Age
384 and persisted during the Iron Age. More recent studies have estimated the number of *vici* and
385 *aedificia* composing a *civita* (Lejars and Gruel, 2015; Verger, 2009). These terms refer to various
386 political, spatial and social entities proposed for the Gallic communities. Thus, a *civitas* was a political
387 entity that included several *pagi*, *i.e.*, groups of tribes characterized by specific ethnic identities.
388 *Civitas* were composed of *vici* grouping themselves within several *aedificia* (Fernández-Götz, 2014).

389 The *aedificia* corresponded to both the farm buildings and their inhabitants and could be compared
390 to what Fernandez-Götz called "households" (Fernández-Götz, 2014). For some authors, these
391 households represent the "locus of everyday life and producer of most of the activities and things
392 that archaeologists recover" (Earle and Kristiansen, 2010) and must therefore be distinguished from
393 the nuclear family concept. In this special context, different theoretical types of tomb and habitat
394 configurations have been proposed (Brun, 2011). Among them, the model "grouped tombs and
395 dispersed habitat", *i.e.*, a common funerary site used for several households scattered around the
396 necropolis could correspond to what we found in GLN. While no habitat area is currently known and
397 associated with the GLN tumulus, the moderate number of burials and the lower mitochondrial
398 diversity observed prompt us to propose the hypothesis of the use of the tumulus by a local
399 community distributed among few *aedificia*.

400 The data available for UN and GLN necropolises thus indicated (i) that they welcomed different types
401 of communities (more cosmopolitan for UN vs. more local for GLN) and (ii) that the structuration of
402 the funerary space in UN was linked to a genetic structuration of the community. Consequently, it is
403 necessary to take into account these specificities for the reconstruction of broad-scale population
404 dynamics.

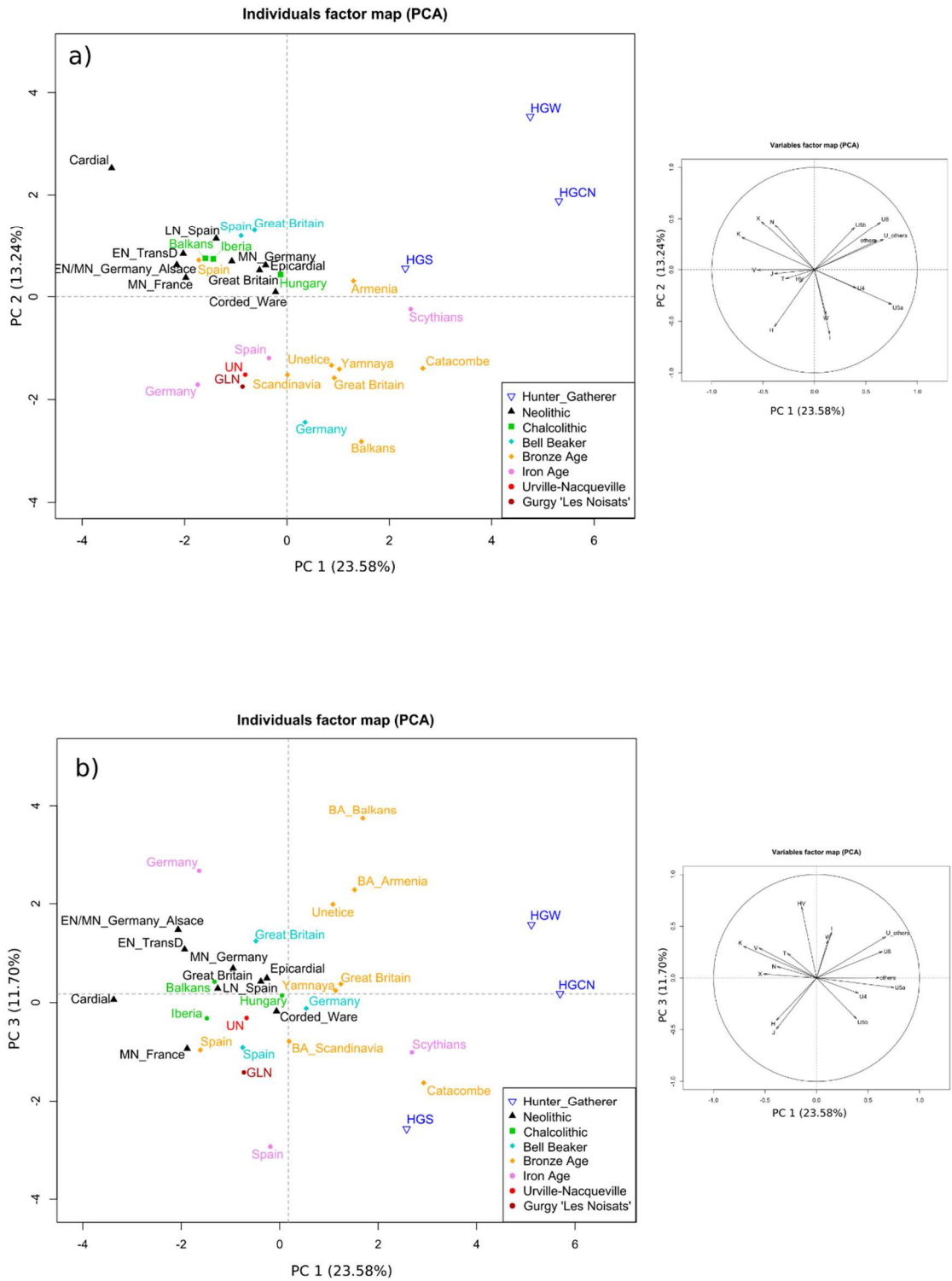
405

406 **2.3 French Iron Age communities' affinities and dynamics**

407 **2.3.1 A common maternal legacy but distinct exchange networks**

408 We first conducted descriptive analyses taking into account the gene pools of whole UN and
409 GLN groups. A principal component analysis (PCA) based on mtDNA haplogroup frequencies was
410 computed after the merging of the UN and GLN gene pools with those of available ancient groups
411 dated from the Palaeolithic to the Iron Age (database published in Fischer *et al.* 2018). Since
412 potential maternal kinship within both UN and GLN necropolises has been previously noted (which
413 may bias haplogroup frequency estimations), we carried out PCA either considering all the

414 individuals (Fig 3) or only one individual per haplotype (S2 Fig). As the exclusion of potentially
415 maternally related individuals had no significant effect on the PCA structure, we decided in the main
416 text to present the PCA obtained for the entire UN and GLN groups.



417

418 **Figure 3: Principal component analysis (PCA) on the ancient mtDNA dataset. A) PCA**

419 **performed on haplogroup frequencies, built with PC1 and PC2 B) PCA performed on haplogroup**

420 **frequencies, built with PC1 and PC3. HGCN: Hunter-gatherers from Central Europe; HGW: Hunter-**
421 **gatherers from Western Europe; HGS: Hunter-gatherers from Southern Europe; CAR: Cardial; EN:**
422 **Early Neolithic; MN: Middle Neolithic; LN: Late Neolithic; UN: Urville-Nacqueville; GLN: Gurgy ‘Les**
423 **Noisats’.**

424

425 The PCA built with PC1 and PC2 (23.58% and 13.24%, respectively) (Fig 3a) confirmed that
426 most of the variations in mtDNA haplogroup frequencies lies between ancient European hunter-
427 gatherers, Neolithic and Bronze Age groups. In this PCA, the UN and GLN samples grouped with other
428 Iron Age groups from Spain and Germany, and this western European Iron Age cluster showed clear
429 affinities with Bronze Age groups, indicating global maternal continuity between groups from both
430 periods. The first important outcome of our analyses was then the demonstration of a coherent
431 western European Iron Age group (composed of populations from Germany, France and Spain),
432 notably characterized by a high proportion of haplogroup H (UN = 38.63%, GLN = 58.6%, IA_Spain =
433 37.5% and IA_Germany = 36.36%)(S6 Table). Such proportions of haplogroup H are close to the
434 values observed for current European populations. Since it has been demonstrated that the major
435 genetic ancestral components of current European populations were introduced during the Bronze
436 Age (Allentoft et al., 2015; Haak et al., 2015), the resemblance between Iron Age groups and extant
437 European populations was expected. The second important outcome of our analyses was directly
438 linked to the previous one and corresponded to the characterization of a clear maternal steppe
439 legacy in both UN and GLN communities. Distinct lines of evidence supported this point. First, the UN
440 and GLN position in the PCA appeared linked to high frequencies of maternal lineage H and a
441 noticeable proportion of haplogroups U4 (for UN group) and I, three characteristics shared with
442 European Bronze Age groups bearing an important steppe legacy (S6 Table). Second, clear affinities
443 between our French Late Iron Age communities and Yamnaya pastoralist groups or groups
444 presenting a major steppe-ancestry component (*i.e.*, groups linked to Corded Ware Culture (CWC),
445 groups associated with Bell Beaker in Germany (BBC_GER), Great Britain (BBC_GB) or Spain

446 (BBC_Spain), and Early Bronze Age groups from Great Britain (EBA_GB)) could be consistently
447 supported through (i) the study of shared informative haplotype frequencies (S7 Table) or (ii) the
448 measurement of close genetic distances (FST; S8 Table). Lastly, the partial data obtained for Y-
449 chromosome lineages in UN and GLN revealed a striking majority of haplogroups R*/R1b that were
450 mainly associated with the arrival of steppe migrants in central Europe after 3000 BC (Allentoft et al.,
451 2015; Haak et al., 2015; Mathieson et al., 2015).

452 If shared maternal legacy could be unravelled for both French Late Iron Age groups, we could identify
453 some divergences in terms of genetic affinities with distinct regional ancient groups. The second PCA,
454 computed with PC1 and PC3 (respectively 23.58% and 11.70%) (Fig 3b), tended to associate groups
455 dated from the Neolithic to the Iron Age, found within each European region. In this PCA, it is worth
456 noting that the GLN group held a specific position close to the Middle Neolithic group from the same
457 location (MN_France; Rivollat et al., 2015) and to ancient groups from Spain associated with Bell
458 Beaker culture or dated to the Early Bronze Age. The maternal affinities between GLN and ancient
459 groups from Spain were also supported by low FST values (all in the range of 0.02; S8 Table) as well
460 as noticeable shared haplotype rates with the Spanish group associated with the Epicardial (6.67%)
461 or dated to the Bronze Age (6.67%) (S7 Table). If similar maternal affinities could be identified
462 between the UN group and groups from Spain (through the study of both shared informative
463 haplotype frequencies (S7 Table) or genetic distances (S8 Table)), they were always found in
464 combination with affinities with groups from Great Britain, associated with Bell Beaker culture or
465 dated to the Early Bronze Age. For the UN group, these maternal links with Great Britain and Spain
466 may be explained by genetic exchanges along the Atlantic coast either during the Neolithic or the
467 Bronze Age periods (as already discussed in Fischer et al. 2018). In sum, the different geographical
468 positions of the UN and GLN communities, inserted in distinct exchange networks, may have been
469 responsible for the slight differentiation of their maternal gene pools and affinities.

470

471 **2.3.2 Distinct funerary groups - distinct maternal legacy ?**

472 Because we could demonstrate that the Urville-Nacqueville funerary group was composed of two
473 maternally differentiated sub-groups (corresponding either to two socially distinct groups and/or to a
474 chronological evolution from an initial group), we tested for potential distinct maternal legacy. We
475 consequently performed all the same descriptive analyses (PCA, FST, shared haplotypes), separating
476 groups buried inside the enclosure (“UN_intra_enclos”) vs. groups found outside the enclosure
477 (“UN_extra_enclos”). Interestingly, the results of these analyses revealed different maternal affinities
478 depending on the group considered. Notably, we observed in PCA computed with either PC1 and PC2
479 (23.03% and 13.5%) or PC1 and PC3 (23.03% and 11.72%) that “UN_intra_enclos” and
480 “UN_extra_enclos” groups were systematically placed in very distinct positions. In the first PCA, the
481 group originating from the enclosure notably held a very special outlier position, whereas the group
482 buried outside the enclosure was found to be very close to the GLN group. This first analysis may
483 indicate a very special maternal constitution of the group having access to the UN enclosure.
484 However, the results obtained through subsequent analyses were more difficult to interpret. Indeed,
485 the second PCA (S3 Fig) indicated affinities between the group buried outside the enclosure and
486 Neolithic groups of Germany, Spain and Great Britain, while the group found inside the enclosure
487 was determined to be closer to the groups from Spain dated from the Late Neolithic or the
488 Chalcolithic periods. The FST calculated for the distinct funerary groups also pointed out different
489 affinities, with the group from the enclosure being closer to the Channel / Atlantic coast groups
490 (EBA_GB = 0.01625; Cardial = 0.01823; BBC_Spain = 0.01848; CH_Iberia = 0.02099) while the group
491 outside the enclosure presented more affinities with French groups from the Paris basin dated from
492 the Neolithic and Iron Ages (MNF = 0.00865; GLN = 0.01039) as well as with various groups from
493 Central Europe (EN_MN_Germany_Alsace = 0.01716; EN_transDanubia = 0.0863 and IA_Germany =
494 0.01963) (Table S9). Finally, affinities regarding eastern groups differentiated the two UN funerary
495 groups. Notably, maternal affinities with the Yamnaya pastoralist groups were stronger for the group
496 outside the enclosure in regard to the group buried inside the enclosure (FST 0.02755 and 0.04687,
497 respectively; shared haplotypes 14.634% and 2.439%). All data in hand consequently tended to show

498 that the group having access to a specific funerary structure in the UN necropolis, an enclosure, was
499 characterized by a special maternal gene pool, showing affinities with ancient groups distributed
500 along the Channel or the Atlantic region (Spain). In contrast, the group buried outside the enclosure
501 may have resembled the typical French Gaul community found in GLN. These elements of discussion
502 would reinforce the idea of a social structuration linked to the funerary organization found in the UN
503 necropolis and/or support the hypothesis of a founding group, partly originating from an
504 allochthonous region, establishing the necropolis and having access to the enclosure. Then, this
505 group may have opened this matrimonial system and this funerary space to some populations, which
506 are more similar to the one observed at GLN. Although these hypotheses need to be tested through
507 more precise palaeogenomic analyses, the results obtained highlight the fact that genetically
508 differentiated groups can be encountered within cemeteries and that these groups may present very
509 distinct genetic affinities with ancient or contemporaneous human groups from other regions. The
510 identification of these genetically differentiated funerary groups and discussions concerning their
511 specific composition constitute a clear prerequisite before addressing broad-scale phylogeographical
512 issues.

513 **3. Conclusion**

514 The ancient DNA results obtained for two human groups of the French Late Iron Age are in total
515 accordance with textual sources or archaeological data describing both paternal residence rules and
516 patrilinearity for Gaulish societies. Beyond these common internal social dynamics, the comparison
517 of genetic, osteological and archaeological data permitted us to note that the necropolises analysed
518 welcomed communities with distinct compositions. Indeed, the Urville-Nacqueville necropolis,
519 located along the Channel seashore and linked to a port, appeared to host a more cosmopolitan
520 community than the Gurgy 'Les Noisats' tumulus that may have received the deceased of a local
521 community. Moreover, the fine-scale analysis of both communities revealed that the organization of
522 the funerary space in the UN necropolis was directly linked to a genetic structuration of the funerary

523 group. Indeed, data in hand permitted us to propose that the enclosure discovered in this site may
524 have either received the members of a dominant family or a smaller funding group that may have
525 been at the origin of a larger community found outside the enclosure. Finally, we demonstrated that
526 genetically differentiated groups found within the UN necropolis presented very distinctive signals
527 concerning genetic affinities with contemporary or more ancient groups. These results highlight how
528 fine-scale analyses of ancient groups permit a better understanding of community establishment or
529 internal social functioning necessary for a correct assessment of broad-scale genetic affinities.

530 **Conflicts of interest**

531 The authors declare that they have no conflicts of interest.

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539

540 **Data Availability Statement:**

541 The sequences were deposited in the GenBank database (<http://www.ncbi.nlm.nih.gov/genbank/>;
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543

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559

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716 **Supplementary data**

717 **S1 Percentage of mitochondrial DNA recovery depending on sites and skeletal elements**

718 **S2 Fig. PCA taking into account potential kinship between individuals**

719 **S3 Fig. PCA considering UN as two groups**

720 **S1. Script. R-Script used for genetic diversity computation as well as resampling tests (.txt)**

721 **S1 Table. Biological and genetic data compiled for Urville-Nacquerville individuals targeted in our**
722 **study. (XLSX)**

723 **S2 Table. Biological and genetic data compiled for Gurgy ‘Les Noisats’ individuals targeted in our**
724 **study. (XLSX)**

725 **S3 Table. Details and references of the ancient populations dataset. (XLSX)**

726 **S4 Table. Details of the mtDNA and Y-chromosome SNPs analysed on Urville-Nacquerville and Gurgy**
727 **‘Les Noisats’ human remains. (XLSX)**

728 **S5 Table. Genetic diversity indices measured on ancient groups. (XLSX)**

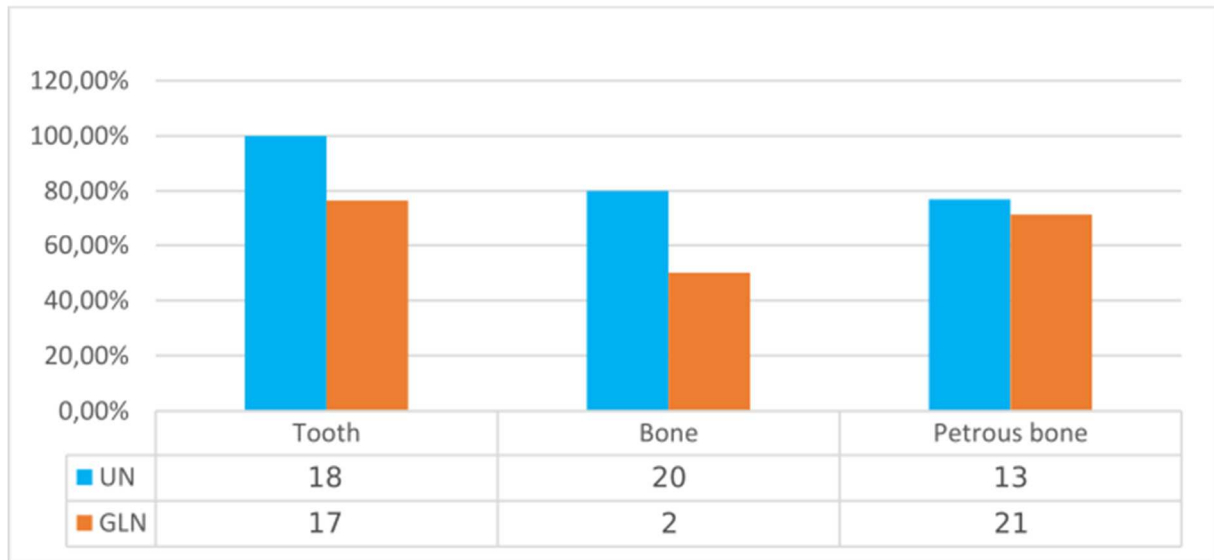
729 **S6 Table. MtDNA haplogroups frequencies for ancient groups (XLSX)**

730 **S7 Table. Mitochondrial haplotypes shared between UN and GLN communities and ancient**
731 **European groups. (XLSX)**

732 **S8 Table. Fst values measured between ancient European groups (XLSX)**

733 **S9 Table. Mitochondrial haplotypes shared between UN and GLN communities and ancient groups**
734 **and Fst values measured between ancient European groups if UN is considered as two groups**
735 **(XLSX)**

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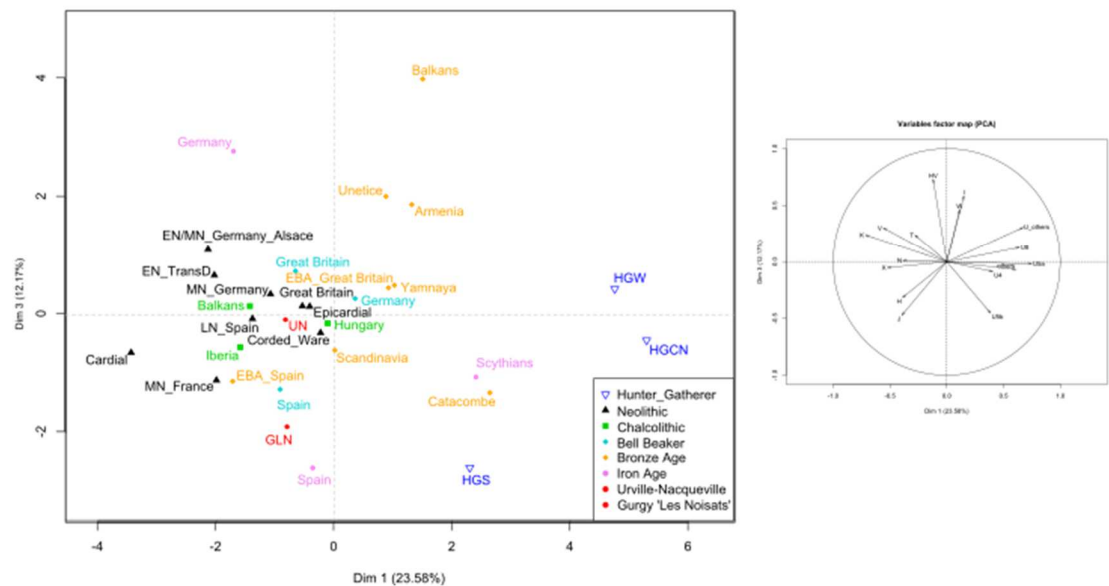
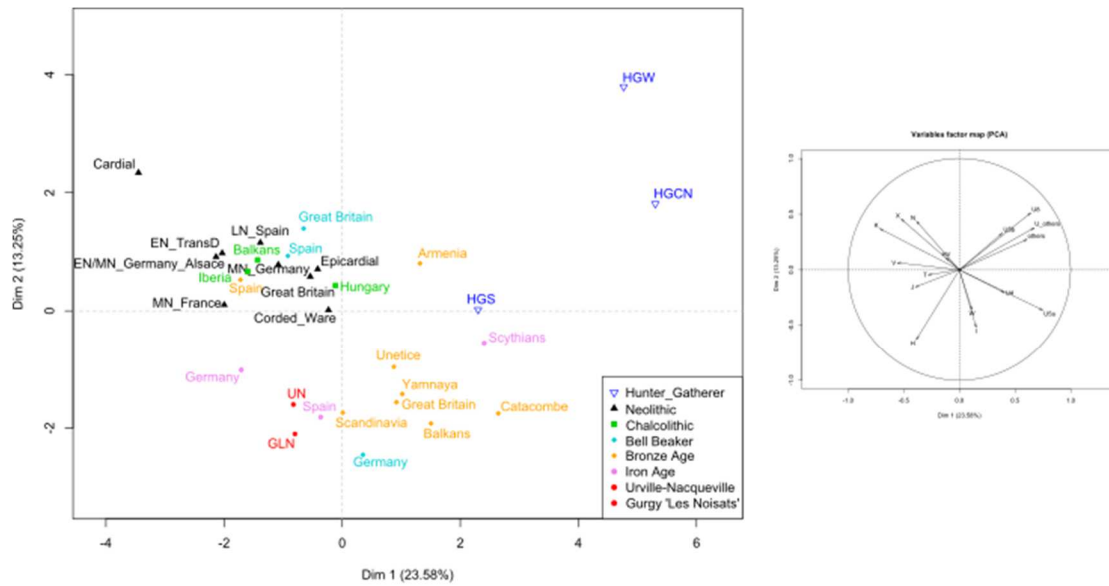
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Figure S1 : Success rate in recovering mitochondrial DNA, according to site and anatomical

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elements. In blue UN: Urville-Nacquerville and in orange GLN: Gurgy 'Les Noisats'



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Figure S3 : Principal component analysis (PCA) on the ancient mtDNA dataset, taking into

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account potential maternal kinship. A) PCA performed on haplogroup frequencies, built with PC1

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and PC2 B) PCA performed on haplogroup frequencies, built with PC1 and PC3. HGCN: Hunter-

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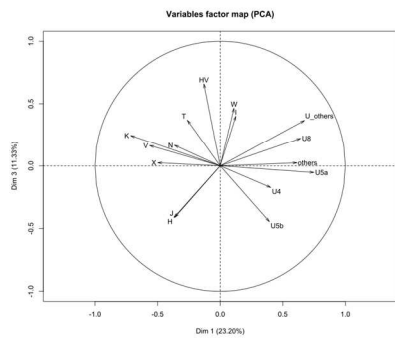
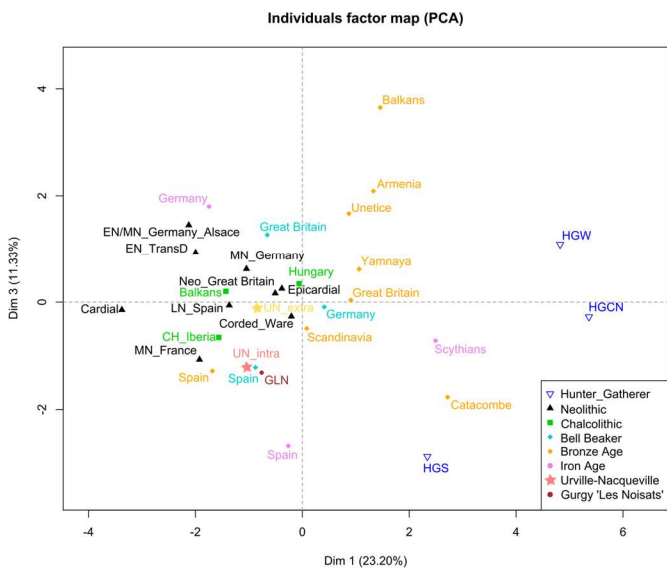
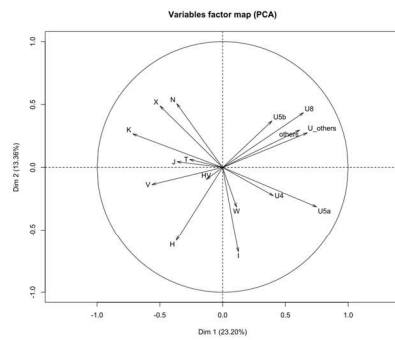
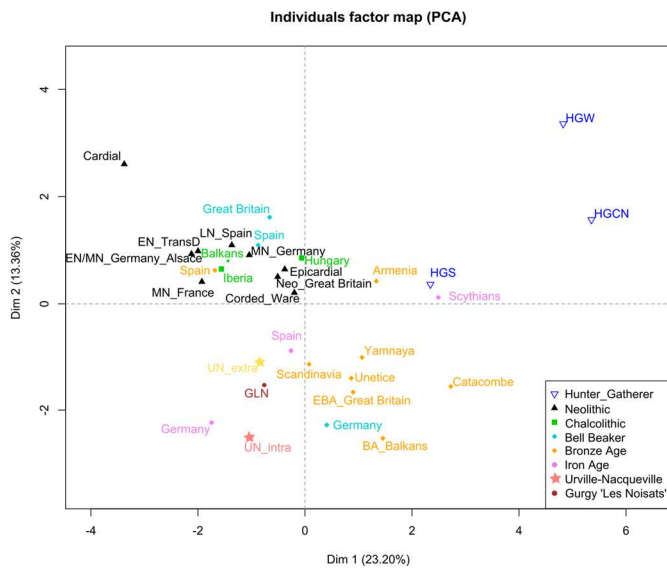
gatherers from Central Europe; HGW: Hunter-gatherers from Western Europe; HGS: Hunter-

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gatherers from Southern Europe; CAR: Cardial; EN: Early Neolithic; MN: Middle Neolithic; LN: Late

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Neolithic; UN: Urville-Nacqueville; GLN: Gurgy 'Les Noisats'.



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Figure S3 : Principal component analysis (PCA) on the ancient mtDNA dataset, considering

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UN as two groups. A) PCA performed on haplogroup frequencies, built with PC1 and PC2 B) PCA

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performed on haplogroup frequencies, built with PC1 and PC3. HGCN: Hunter-gatherers from

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Central Europe; HGW: Hunter-gatherers from Western Europe; HGS: Hunter-gatherers from

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Southern Europe; CAR: Cardial; EN: Early Neolithic; MN: Middle Neolithic; LN: Late Neolithic;

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UN_intra: Urville-Nacqueville intra enclosure; UN_extra: Urville-Nacqueville extra-enclosure ; GLN:

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Gurgy 'Les Noisats'.