Origin and mobility of Iron Age Gaulish groups in present-day France revealed through archaeogenomics

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16 Summary

17 The Iron Age period occupies an important place in French history, as the Gauls are 18 regularly presented as the direct ancestors of the extant French population. We documented here the genomic diversity of Iron Age communities originating from six French regions. The 19 20 49 acquired genomes permitted us to highlight an absence of discontinuity between Bronze Age and Iron Age groups in France, lending support to a cultural transition linked to 21 22 progressive local economic changes rather than to a massive influx of allochthone groups. 23 Genomic analyses revealed strong genetic homogeneity among the regional groups associated 24 with distinct archaeological cultures. This genomic homogenisation appears to be linked to

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25 individuals' mobility between regions as well as gene flow with neighbouring groups from

26 England and Spain. Thus, the results globally support a common genomic legacy for the Iron

Age population of modern-day France that could be linked to recurrent gene flow between

28 culturally differentiated communities.

29 Introduction

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31 The French Iron Age holds an important place in French history, as Gaulish 32 communities are regularly presented to the general public as the direct ancestors of French 33 populations. This major interest has led to an impressive number of archaeological studies 34 describing Iron Age communities through their material culture and funerary practices and 35 questioning their cultural origins and affinities. Despite this interest, questions concerning the 36 cultural and biological processes underlying the emergence and expansion of Iron Age 37 cultures remain intensely debated. Thus, the transition between the Bronze Age (BA) and the 38 Iron Age (IA) was first linked to the rapid shift from bronze to iron technologies between 39 Hallstatt B3 and Hallstatt C (approximately 800 BC). However, this clear cut-off does not 40 appear to reflect the regional archaeological reality that there was a gradual transition to the 41 use of iron instead of a rapid substitution (Verger, 2015). Moreover, the cultural 42 transformations associated with the transition span over two centuries encompassing the late 43 Bronze Age and the first phase of the Iron Age and appear to have followed different rhythms 44 that varied by region (Verger, 2015). Debates also concern the modes of emergence of the Late Iron Age culture La Tène, associated with groups generally referred to as 'Celts' and 45 46 spread over a large part of Europe, spanning from Bohemia to the Atlantic (Roure, 2020). 47 Thus, some authors propose an advent of this cultural entity in Central Europe and Bohemia 48 before its expansion through the migration of groups bringing cultural developments from the northern Alpine area to the rest of Europe (Kruta, 2000; Brun, 2017). Other authors propose a 49 50 multiregional origin of the La Tène culture through the evolution of a mosaic of cultural 51 complexes ('multipolar genesis in networks'; Milcent, 2006) connected by common markers 52 such as art without implying major migration. According to this view, the 'Celts' would be 53 defined as a multitude of related people with different cultural practices (Lejars and Gruel, 54 2015).

55 The great amount of archaeological data available for Iron Age groups from the 56 French territory strikingly contrasts with the near absence of genomic data for the human 57 groups concerned. In the archaeology of death, as well as in the study of ancient human group dynamics, palaeogenetic analyses have led to considerable advances. From the Palaeolithic to 58 59 the Bronze Age periods, ancient DNA (aDNA) studies have provided arguments 60 complementary to the archaeological evidence to reconstruct the dynamics of the groups at 61 the European macroregional scale (see Liu et al., 2021 for a recent review), as well as 62 discussions on the social functioning of communities at the local scale (documenting, for 63 example, residence rules or filiation systems; e.g. Mittnik et al., 2019). Despite the considerable increase in palaeogenomic analyses over the last decade, some territories or 64 65 periods remain poorly documented. In that respect, the French territory remained neglected in palaeogenomic studies in Europe until the very recent publication of three studies targeting 66 this key crossroad region in western Europe (Brunel et al., 2020; Rivollat et al., 2020; 67 Seguin-Orlando et al., 2021). Nevertheless, genetic and genomic data for IA period from 68 69 French territory remain scarce, with mitochondrial data for 91 individuals and low-coverage 70 genomes for 19 individuals (Fischer et al., 2018, 2019; Brunel et al., 2020). To date, the 71 underrepresentation of IA populations in palaeogenomic studies, compared with prior 72 periods, can be extended to the European scale, with a total of 44 mitochondrial sequences from Germany, Spain and Italy (Knipper *et al.*, 2014, Núñez *et al.*, 2016, Serventi *et al.*,
2018) and a total of 27 genomic data points from England (Martiniano *et al.*, 2016; Schiffels *et al.*, 2016), Bulgaria (Mathieson *et al.*, 2018), Croatia (Mathieson *et al.*, 2018), Spain
(Olalde *et al.*, 2019), Hungary (Gamba *et al.*, 2014), Montenegro (Allentoft *et al.*, 2015),
Estonia (Saag *et al.*, 2019) and Germany (Furtwängler *et al.*, 2020).

78 These observations are particularly frustrating given that only the acquisition of 79 representative palaeogenomic data for French Iron Age groups and their comparison with 80 archaeological data can allow to directly characterise the biological processes potentially 81 involved in the cultural transformations documented between the Bronze Age and Iron Age 82 or between the Early and the Late Iron Age periods. Furthermore, compelling genomic data 83 for these ancient communities provide the only way to test for correlation between the 84 cultural and biological diversities of groups and question modes of exchanges between 85 populations. Finally, genomic data obtained at the local scale can provide major insights into 86 the social organisation of communities. For older periods, whether the Neolithic or Bronze 87 Age, palaeogenomic studies have revealed recurrent patrilocal residence rules, patrilineal 88 filiation systems or differences in social level (see, for example, Lacan et al., 2011; Mittnik et 89 al., 2019). For the Iron Age, the indirect testimonies left by Greeks and Romans (such as De 90 Bello Gallico from Julius Caesar, even if they must be considered with caution) mentioned a 91 very hierarchical society characterised by a patrilineal system of filiation. Thus, obtaining 92 genomic data for the Iron Age communities represents a unique opportunity to compare 93 biological, archaeological and textual data.

94 The outstanding questions presented above and the great potential of the combination 95 of archaeological, textual and genomic data in an attempt to resolve them motivated us to better document the genomic diversity of the Gaulish populations. For this purpose, we 96 97 targeted 145 individuals from 27 sites spread over the extant French territory and distributed 98 throughout the IA period to optimise our chance of documenting the gene pool of a 99 representative set of French Iron Age individuals. The wide chronological distribution of the 100 dataset permitted us to address questions of origin and evolution of the groups, whereas the 101 wide geographical distribution of the samples allowed us to test for interregional gene flow. 102 Notably, some archaeological evidence highlighted particular exchange networks with the groups from the surrounding areas, such as the example of the necropolis of Urville-103 Nacqueville, sharing clear archaeological features (roundhouses, Durotrigian burials, etc.) 104 105 with contemporaneous groups from Britain (Lefort et al., 2015). Finally, we also targeted 106 sites associated with different funerary practices to better understand the biological identity 107 and potential selection of the individuals buried.

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109 **Results**

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111 The Iron Age genomic dataset from France

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113 A total of 145 individuals were targeted for palaeogenomic analyses (Table S1). DNA 114 was extracted, and DNA libraries were built with a partial uracil-DNA glycosylase treatment, 115 allowing for the assessment of postmortem deamination patterns (2% to 29%) expected for 116 ancient DNA data. Initial screening via shotgun sequencing of 1 to 2 million reads was used to select libraries with an amount of endogenous DNA above 15%, leading to the exclusion 117 of 92 individuals. For the remaining individuals who passed these quality criteria, we 118 sequenced the libraries to an average depth of 0.178X (Table S2). We found overall 119 120 negligible level of contamination in our dataset by testing for heterozygosity of polymorphic 121 sites on the X chromosome in males (Table S3). The dataset resulting from these successive 122 quality selections encompasses low-coverage genomes for 49 individuals originating from 27 123 sites, dating from the Bronze Age (N = 2) and the Iron Age periods (N = 47). We compiled 124 the IA data with 18 low-coverage genomes already published for IA groups from France 125 (Brunel et al., 2020), leading to a total of 65 low-coverage genomes distributed in 6 geographical areas: Alsace (N = 20), Champagne (N = 5), Normandy (N = 3), North (N = (N = 3)) 126 127 10), South (N = 18) and Paris Basin (N = 9) (see Figure 1A, STAR Methods and Tables S1 128 and S3). The IA dataset is unbalanced in terms of the chronological distribution of the 129 individuals, with 11 individuals dated to the Early Iron Age and 54 dated to the Late Iron Age 130 period (Figure 1B). This can be partly explained by the funerary treatment and the use of 131 cremation (see, for example, Dedet, 2004 for southern France). The few humans remains (from southern or north-western France) available for genomic analyses represent deceased 132 133 who escaped cremation and benefited from non-ordinary funerary practices. Therefore, the 134 corpus available for genomic analysis may not be representative of the entire population 135 living at the time. For instance, for southern France, genetically analysed individuals correspond to severed heads (see STAR Methods. site of Le Cailar) or to neonates buried in 136 137 settlements (see STAR Methods, site Le Plan de la Tour). The dataset is also unbalanced in 138 terms of regional representativeness, with the Normandy region providing the lowest number 139 of genomes due to the low DNA conservation in the coastal Urville-Nacqueville necropolis 140 targeted (Table S1). Finally, among the 65 individuals, if 33 were males and 32 were females, 141 the sex ratio within each region was unbalanced, with notably more females in Alsace and 142 more males in the South (Table S2). With this frame in mind, we analysed our data with 143 published ancient individuals (n = 5225) genotyped on the 1240k panel (Mathieson *et al.*, 144 2015) as well with modern (n = 6461) individuals from a panel of modern-day worldwide populations genotyped on the Affymetrix Human Origins (HO) panel. From the present 145 146 study's dataset, 65 individuals with more than 20,000 SNPs on the 1240k panel were used for 147 the downstream genome-wide analyses (see STAR Methods and Table S2). We found no first-degree relatives among IA individuals from present-day France allowing us to keep the 148 149 full dataset for downstream analyses (see STAR Methods, Table S3 and Figure S4).

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151 We first explored our data qualitatively using principal component analysis (PCA) by 152 projecting the ancient genomes onto the genetic variation of an HO set of west Eurasians 153 (Figure 1C and S1). French IA individuals fall within the genomic variability of the modern-154 day French population. IA samples from Spain and Great Britain also fall within modern-day 155 populations from the same region, highlighting a certain degree of continuity from the Iron 156 Age to modern-day populations in western Europe, confirming previous results based on 157 mitochondrial DNA (Fischer et al., 2018). The PCA also shows a clinal distribution of our IA 158 French samples according to their latitudinal position: the northern samples are closer to the 159 extant Great Britain population, and the southern samples are closer to the Spanish population 160 (Figure S1). These observations are fully consistent with genomic studies conducted on modern Europeans and highlight a geographically and genomic intermediate position of the 161 162 French groups between north-western and south-western European populations (Novembre et 163 al., 2008).

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166 To test further the genomic variability of the new IA genomes, we grouped the 167 individuals among different chrono-cultural groups, i.e., according to their region of origin 168 and, when possible, to their dating (Early vs. Late Iron Age): EIA_Alsace (from 800 BC to 169 450 BC), LIA_Alsace (from 450 BC to 50 BC), IA_Champagne, IA_Normandy, IA_North, 170 IA_Paris_Basin and IA_South. We then carried out a *qpWave* analysis iterated over all 171 individuals in the pool, testing for significant evidence of heterogeneity relative to the

172 remaining chrono-cultural group (see STAR Methods and Figure 2). Individuals were 173 considered genomic outliers from the chronological-cultural group from which they originate when the *qpWave* p value was < 0.05 (Fernandes *et al.*, 2020). This resulted in the 174 175 identification of six individuals as outliers: BES1248, PECH3 and PEY163 stand as outliers 176 from the IA South group, CROI11 from the EIA Alsace group, COL239 from the 177 LIA Alsace group and GDF1341 from the IA Paris Basin group. The analyses at the 178 regional level were consequently conducted separately on these individuals and their chrono-179 cultural groups. The outlier status of these special individuals will be further discussed.

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182 Genomic continuity from the Bronze Age to the Iron Age

184 The PCA highlighting Bronze and Iron Age samples from Europe shows relative genomic continuity between groups from the two periods (Figure 1C). To further explore this 185 continuity, we performed a *qpWave* analysis to test whether the regional Bronze and Iron Age 186 187 groups form a clade. Analyses permitted us to demonstrate an absence of discontinuity (no 188 significant differentiation) between the BA and IA groups in southern France but not in 189 Alsace or in the Paris Basin (Figure 2). The scarcity of data available for the Bronze Age in 190 the Paris Basin (N = 2) might not reflect the diversity of the BA population of this region, 191 which could explain this result. Nevertheless, the absence of continuity between both periods 192 in Alsace is documented by a satisfying number of samples and may be linked to notable 193 gene flow in this crossroads region during both periods. Interestingly, the EIA Alsace and 194 LIA_Alsace groups form a clade, which is consistent with some genetic continuity between 195 periods yet recognising important cultural transformations (see STAR Methods). Moreover 196 when looking at the three main ancestral components that contributed to the genomic 197 composition of western European populations, i.e., pre-Neolithic western Hunter-Gatherers 198 (WHG component), Early Neolithic farmers (Anatolia_N) and steppe-legacy brought by Bell 199 Beaker groups (Russia_EMBA_Yamnaya; Haak et al., 2015) with qpAdm modelling, we 200 observe no significant differences for the last two components between BA and IA 201 populations of southern and northern France (Figure 3 A and B and Figure S7) while 202 differences exist at the regional level (Figure S8). This indicates the absence of major genetic input from populations with different genetic legacy in the genetic make-up of French IA 203 204 groups. We then performed *apAdm* analyses to assess whether the regional Iron Age groups 205 in France could be only explained with the French Bronze Age groups or with supplementary 206 BA groups as sources (see STAR Methods and Table S4). We tested different models and 207 found that all French IA groups could be explained by one or two French BA groups as 208 sources. Notably, the fact that the EIA Alsace and LIA Alsace group gene pools could be 209 explained by a combination of local BA_Alsace and nonlocal BA_South groups as sources 210 reinforces the status of the region as a gene flow crossroad. Although alternative models involving BA sources from other European regions (Table S5) are also statistically possible, 211 212 following a principle of parsimony, we preferentially suggest that the French IA groups 213 directly derive from the previous French BA groups.

214 However, when considering uniparental markers, the genetic continuity between the 215 BA and IA groups from French territory can be only partially identified. A total of 86 mitochondrial and 33 Y chromosome lineages were compiled for the French IA sample (see 216 217 STAR Methods). Despite a great diversity of mitochondrial lineages among French IA 218 groups, nearly 26% of the individuals could be characterised as belonging to haplogroup H. 219 Even though important regional variability in haplogroup frequencies must be pointed out, 220 haplogroup H represents almost 50% of the lineages in IA North but less than 30% in 221 IA_South groups (Table S3). Notable increases in haplogroup H and J frequencies between

222 French BA and IA can also be highlighted (Figure S2). Regarding the Y chromosome 223 lineages, we observed an increase in Y chromosome diversity in the Iron Age. We identified 224 four major haplogroups in the French IA dataset: haplogroups I1, I2, and G2, which were 225 dominant during the Neolithic in western Europe, and the overrepresented R1b1a haplogroup 226 associated with steppe-related migration (69%) (Table S3 and Figure S3), while BA males 227 carry only R1b (or R*) haplogroups (Brunel et al., 2020). Nevertheless, it remains to be seen 228 whether the variations observed between BA and IA periods are related to the small amount 229 of data available or to maternal/paternal gene pool shifts linked to specific microevolution 230 processes.

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232 Overall, the compiled results reinforce the archaeological hypothesis that explains the 233 transition from the Bronze Age to the Iron Age by political and economic crisis combined 234 with social changes rather than by major migration or population turnover for the territory of 235 present-day France. These genomic results are in line with more recent archaeological 236 hypotheses that have tended to rule out the involvement of major invasion/migration in the 237 cultural transition (Garcia and Le Bras, 2017). Recent re-evaluations of the archaeological 238 data have indeed indicated progressive cultural evolution during these periods, such as the 239 gradual use of iron (instead of an abrupt substitution from one material to another) or the progressive evolution of pottery (Guilaine and Garcia, 2018; Verger, 2015). Complicating the 240 241 scenario, recent archaeological studies have even revealed different cultural evolution 242 rhythms depending on the regions or on the type of material studied (Milcent, 2009; Verger, 243 2015). Finally, the genomic data gathered for the Early and Late Iron Age in the Alsace region is consistent with genetic continuity throughout the Iron Age period. Even if the data 244 245 in hand are restricted to the Alsace region, they support the view that the emergence of the La 246 Tène culture was not necessarily linked to a major influx of populations/genes.

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Genomic and cultural diversity among the Gauls

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250 As previously mentioned, the PCA performed on the French IA dataset highlighted a 251 clear latitudinal distribution of individuals (Figure 1C). The genetic differentiation projected 252 on the PC2 axis is positively correlated with the latitudinal position of the sites where were found the samples in France ($r^2=0.59$, Pearson). This correlation even increases when adding 253 IA individuals from Iberian Peninsula and England (Figure 3C, $r^2=0.628$). However, the f3 254 255 statistic applied in the form f3(Mbuti, Ind1, Ind2) showed no clear grouping of individuals in 256 relation to their region of origin (Figure S5). To better characterise the genomic variability 257 perceived between French IA individuals, we ran an f3 statistic in the form f3(Mbuti, X, Ind), ancestral 258 where Х represents an component (WHG. Anatolia N and 259 Russia_EMBA_Yamnaya). The results clearly pointed out differences between regions of 260 France with a greater affinity between IA_South and the Anatolia_N component, whereas IA groups from northern French (notably Normandy) regions present more affinity with the 261 262 Steppe-legacy component (Figure S6 and Table S6). To more precisely quantify these gradual affinities, we performed a *qpAdm* analysis modelling the IA French groups with these three 263 components as source populations (Table S7). The modelling results clearly confirm that a 264 265 decreasing north to south gradient in the steppe-related component among IA French groups is inversely correlated with an increase in the early farmer component (Figure 3A and S8). 266 267 The scarcity of data from Bronze Age periods did not allow us to compare these differential 268 affinities at a fine regional scale for this period, but it is worth noting that the distribution of 269 available data into two separated groups, North vs. South, permitted us to observe the same 270 tendency (Figure 3B and S7). This steppe-related ancestry gradient is well established for modern-day European populations (Haak *et al.*, 2015) and appears to be well established in
French territory, at least since the BA period.

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274 To test for specific genomic affinities between IA French regional groups or individuals, we 275 performed f3-outgroup statistics in the form f3(Mbuti, Region, Region), where Region 276 represents the individuals grouped by geographical affinities (without the previously defined 277 outliers), and in the form f3(Mbuti, X, X), where X represents individuals from the study 278 (Figure S5). Neither type of test permitted the detection of any specific affinity between 279 regional groups or individuals. Finally, we also computed f3 statistics in the form f3 (Mbuti, 280 Site, Site), where Site represents all the individuals discovered within the same archaeological 281 site, and, once again, we did not detect any affinity between funerary groups. We then 282 performed an MDS based on the genetic distance (1-f3(Mbuti, Site, Site)) and did not detect 283 any correlation between genetic and geographical distances between sites. A Mantel test comparing a matrix of genetic distances (1-f3) and a matrix of geographical distances 284 285 between the sites, with the assumption (H_0) being "there is no correlation between the two 286 matrices", permitted us to confirm the absence of statistical correlation between both types of 287 distances (p value = 0.3931607).

288 All the statistical tests performed on IA French groups consequently highlighted an 289 extremely gradual genetic structuration of populations distributed across the present-day 290 French territory, complicating the demonstration of statistically significantly differentiated 291 groups. This major observation supports the hypotheses of a common genomic legacy of the 292 populations dispersed throughout this vast area (Collis, 2003; Roure, 2020). This very weak 293 large-scale genomic pattern contrasts with the cultural variability documented among the 294 regions concerned, which remained important enough during the whole Iron Age period for 295 archaeologists to propose to differentiate the Mediterranean, Atlantic, Hallstattian and 296 Latenian Celts (Bouffier and Garcia, 2012; Garcia, 2006). A recent archaeological scenario implies a multipolar cultural evolution of regional groups sharing some common cultural 297 298 traits, such as language, religion, and social relations, as well as ornaments and metal 299 furniture (Milcent, 2006, 2009). Combined with the lack of genetic discontinuity pointed out 300 between BA and IA French groups and the global low genetic structuration of groups 301 throughout the IA period, data clearly reinforce a scenario in which regional groups linked through a rich network of cultural and biological exchanges evolve. 302

303 Interestingly, biological exchanges between regional French IA groups could be 304 reinforced by the recurrent characterisation of genetic outliers, grouping both men and 305 women (see Table S2), which could demonstrate individual interregional mobility. We 306 performed an f3 statistic analysis in the form f3 (Mbuti, Individual, Region) to assess a 307 possible region of origin for each outlier, and we plot the results in Figure 4. The results 308 indeed highlighted genomic affinities between these outliers and French IA groups from other 309 regions representing possible regions of origin of the individuals or possible origins of their direct ancestors. These affinities are also visible through the *qpWave* analysis (Figure 2). 310 311 Interestingly, from an archaeological point of view, nothing distinguishes the genetically 312 defined outlier individuals from the others discovered at the same site. This would indicate 313 the full cultural integration of individuals originating from distinct regions. Nevertheless, two exceptions can be pointed out for outlier BES1248 and PECH3. The individual BES1248, 314 315 from the Bessan site, was found in a single burial, whereas cremation was the predominant 316 funerary practice in southern France during this period (Dedet, 2004). However, the other 317 only adult buried in Bessan (BES1249) does not appear as a genetic outlier and, therefore, 318 impedes drawing any conclusion about the link between outlier status and special funerary 319 features in this case. PECH3 was found in the filling of a ditch associated with the remains of 320 equids contemporary with the ritual phase following the destruction of the Pech Maho site

321 (see STAR Methods for site description). The possibility of an exogenous origin for this 322 individual is particularly interesting as it could reinforce the historical hypothesis of the 323 destruction of the site in relation to the Second Punic War between Rome and Carthage. 324 Interestingly, Olalde et al. (2019) also found a genetic outlier (individual I3326; Figure 3C) 325 in the Ullastret site on the Iberian Peninsula, where many Latenian swords, locally produced, 326 were discovered. This evidence reinforces the idea of important exchanges of goods, people 327 and skills among IA communities. On the other hand, at the Cailar site, where archaeologists have highlighted the practice of severed heads (Ciesielski et al., 2014; STAR Methods; 328 329 Ghezal et al., 2019), as at Ullastret and Pech Maho, all the individuals analysed form a 330 genetically homogeneous group and fall within the genetic diversity observed for southern 331 France. Therefore, no genetic element supports the hypothesis of a distant origin for these 332 individuals, whose heads were probably used as trophies. All these specific cases highlight 333 the impressive variability and complexity of interrelation between IA individuals genetic and 334 archaeological identities.

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- 336
- 337 <u>Interactions between western European contemporaneous groups</u>

338 Given the gene flow characterised between French IA groups, we tested for 339 equivalent biological interactions with groups from other western European areas. We have 340 seen that PCA and *qpAdm* analyses highlighted special affinities between IA groups from 341 southern France and Spain and from north-western France and England (Figure 1C and S8). 342 We, therefore, explored these specific affinities through an f3 statistic in the form f3(Mbuti,343 IA France, IA other), where IA other represents IA groups from regions other than French 344 territory and considering either individuals, sites or regions (see STAR methods). 345 Unfortunately, palaeogeneomic data are still poor or missing for several bordering regions, 346 such as Germany, which limits this part of our study. The performed test did not permit us to significantly differentiate any specific genetic affinities with IA from the European regions 347 348 documented, surely linked to the very low genomic differentiation of all the groups 349 concerned. *qpWave* analyses performed between regional groups and other European 350 contemporaneous groups highlight clustering of northern France and north Europe (England 351 and Sweden) IA groups, while the Gauls of southern France stand out from this cluster but appear closer to the Celtiberians from Iberian Peninsula (Figure 2). Finally, no genetic 352 353 affinity was found between Greece or Italy and the populations of the IA of the current 354 French territory. Genomic affinities perceived between IA groups from south-western France 355 and northern Spain are expected since they belong to the same cultural entity called ibero-356 languedocian (Gailledrat, 1997; Py, 1993). Similar types of ceramics, as well as weapons, are 357 indeed found on both sides of the Pyrenees during the IA. Moreover, the settlements and 358 fortifications found in respective regions are quite similar, and some scholars have even 359 proposed the shared use of the Iberian language by the concerned groups (Mullen, 2019). Similarly, the genomic affinity detected between the IA groups from north-western France 360 361 and England is not surprising. Indeed, the north-western French groups are represented by 362 individuals originating from the Urville-Nacqueville necropolis (Normandy), where specific archaeological features, such as roundhouses, are clearly related to the English IA cultural 363 sphere (Lefort et al., 2015). Moreover, Normandy and South England are part of a well-364 documented network of exchanges during the Bronze Age (Atlantic BA and Manche-Mer du 365 366 Nord Complex; Marcigny et al., 2017) and the Iron Age periods (part of the medio-Atlantic 367 Iron Age; Milcent, 2006). It is finally worth adding that the three individuals from Urville-368 Nacqueville that provided genomic data are three males, all buried in the so-called "Durotrigian" position, which is well known in Dorset (Fitzpatrick, 2011; Lefort et al., 2015). 369 370 Consequently, we cannot exclude that these individuals might originate from southern 371 England and may not be representative of the whole population buried at Urville-Nacqueville 372 (Fischer et al., 2018, 2019). Regardless of the case, the correlation between exogenous 373 material, cultural variations, and gene flow with groups from other regions found in these 374 specific contexts cannot be extended to the full IA archaeological landscape. This is notably the case for the necropolis of Peyrou (southern France, 6th-4th centuries BC), where the 375 funerary treatment of the deceased and the material deposited in the tombs provided clear 376 377 evidence of the establishment of Greek settlers in the region after an intermittent phase of 378 contacts. However, none of the individuals analysed (N = 3, male or female) from the 379 necropolis show peculiar genetic affinity with Greece or the Mediterranean Basin. 380 Interestingly, the individual who stands as an outlier (PEY163) seems to have more affinities 381 with the Paris Basin and did not point out to the Mediterranean area (Figure 2 and 4). As our 382 study is not exhaustive for this site, it is quite possible that the analysis of a larger number of 383 individuals would allow to highlight the presence of Greek settlers in this necropolis. Indeed, Greek colonies are a very particular environment, where the surrounding native population 384 385 can live among the Greek settlers (Dedet, 2015). However, this example once again 386 demonstrates that funerary practices and/or exogenous material do not constitute reliable 387 evidence of allochthonous individuals, as already described for other periods/regions 388 (O'Sullivan et al., 2018).

389 An important result is also the greater dispersion of IA Alsace individuals in the 390 PCA, overlapping groups from IA South, IA North, IA Paris Basin or IA Champagne. 391 This dispersion points to higher genetic diversity within this regional group, which could be 392 evidence of higher gene flow (Figure 1C). The Alsace region is regularly characterised as a 393 "crossroads", an axis of transit and exchange, due to the presence of the Rhine River, which 394 has constituted a major communication link between western and central Europe through 395 history. Nevertheless, the genetic exchanges characterised for the IA period do not appear to 396 find a special echo in the material culture. During the Early Iron Age, archaeological records 397 suggest material exchanges between southern Alsace and southwestern Germany (Bavaria, 398 Baden-Württemberg), while northern Alsace shared contacts with the Lower Rhine Valley. If 399 the arrival during the Hallstatt period of material described as exogenous (amber from the 400 Baltic region, coral from the Mediterranean, Etruscan imports, etc.) could testify to a notable 401 increase in north-south trade, this kind of material remains very occasional. Therefore, even if cultural exchanges with neighbouring regions are verified, contributions from further 402 403 distances remain apparently limited.

404

405 <u>Functioning of communities</u>

406 To start documenting the local functioning of French IA groups, we performed an 407 analysis to detect long runs of homozygosity (ROH, Ringbauer et al., 2021). We observed 408 that the number of ROHs of 4-8 cM tended to decrease during the Iron Age following the 409 general tendency observed since the Mesolithic, a result explained by a progressive increase in the mating populations and/or an increase in long-distance gene flow (Figure S10). Few 410 411 archaeological studies have focused on the IA population demography, nonetheless, a study 412 conducted on funerary data by Isoardi (2008) found an increase in population size at the end of the Early Iron Age in the southern Alps, Provence and probably in the Rhone and Saone 413 valleys, followed by a slight decrease around the mid-4th century BC. They also noted that 414 415 population size tended to increase during the second half of the 3rd century BC. Various 416 studies have also demonstrated the importance of exchange networks at varying distances 417 during the Iron Age, as evidenced, for example, by the Greek bronze crater in the tomb of 418 Vix (Early Iron Age, Joffroy, 1954) or the Roman amphorae discovered at Urville-419 Nacqueville (Late Iron Age, Lefort et al., 2015), but we found no evidence of such longdistance exchanges in our data. Such events might have been restricted to a few individualsplaying an important role in Iron Age society but having a limited impact on the genetic pool.

422 Finally, we detected multiple long ROH on different chromosomes in one individual, 423 COL 336 (Alsace), who can be interpreted as the offspring of a first-degree incestuous union (parent-offspring or full siblings) (Figure S11). Intriguingly, the Colmar site includes several 424 425 burials in pits without any grave goods or weapons accompanying the deceased while the 426 main funerary practice for this period and this region is the inhumation in small funerary complexes of tumuli. Therefore, even if the observed funerary treatment of COL 336 does not 427 428 differ from that of any other individuals from the site, it could be considered as a relegation-429 type burial. This could be linked to a rejection by the IA society of this incestuous practice. This is in opposition to what has been described at the site of Newgrange for Neolithic period 430 431 (Cassidy et al., 2020), where the presence of consanguineous individual on one of the most 432 spectacular Megalithic mount of Europe was interpreted as the evidence of a high hierarchical society with complex chiefdoms. To explore more in details the social 433 434 organisation of IA groups and compare it with historical sources, a more exhaustive genomic 435 dataset would be necessary.

436

438

437 **Discussion**

439 In this study, we recovered 49 genomes from BA and IA individuals widely distributed within present-day France. With this valuable dataset in hand, we were unable to 440 441 detect a genetic discontinuity between the Bronze and Iron Age communities of France, as 442 already mentioned by Brunel et al. (2020). Our dataset also highlighted a north to south 443 gradient for steppe-related ancestry inversely correlated with the Early Neolithic Farmer one. Moreover, the distribution and proportion of these legacy components remain stable between 444 445 Bronze and Iron Age periods. This is perfectly in line with recent archaeological evidence 446 considering that the transition from the Bronze to the Iron Age was a consequence of social 447 and political changes from the 8th century BC onwards. If no evidence of migration event 448 could be highlighted since the BA, although events of this type involving populations with 449 the same genetic characteristics are hard to perceive, we were able to detect mobility at the individual scale between regions as well as gene flow with neighbouring groups from 450 451 England and Spain. Of great interest, these genetic outliers were not always distinguishable 452 from an archaeological perspective, which could mean that they were fully integrated within 453 the community. Although analyses allow us to propose a possible region of origin for these 454 outliers, Sr isotope analyses would be of great interest to complete the individual mobility 455 scenario. Interestingly, these networks are visible not only in the French territory but also on 456 the western European scale. Indeed, we were able to detect specific affinities between 457 northern/north-western France and England IA communities as well as between southern 458 France and Spain communities. This result is consistent with archaeological evidence, such as 459 the presence of roundhouses and so-called 'Durotrigian' buried in Urville (Normandy) and the definition of the 'Ibero-languedocian' complex in the South. Globally, the results proposed 460 461 reinforce the idea that 'Celts' derived from local BA populations that evolved progressively 462 between regional groups sharing some common cultural traits and linked through a network of cultural and biological exchanges. 463

464

465 Limitations of study

466 Due to the extensive use of cremation in the period considered, the highly variable 467 DNA preservation among sites and the unequal distribution of archaeological discoveries 468 among regions, the genomic dataset obtained remains differentially distributed among 469 regions and periods.

470

471 Acknowledgements

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489 490

491 **Author contributions**

- 492 Conceptualisation: CEF, MFD, MP
- 493 Data curation: CEF, MHP, ID, MFD, MP
- 494 Resources: HBE, AB, EC, BD, SD, FC, EG, SG, AG, AB, GK, FL, AL, AM, FM, SO, CP,
- 495 EP, SP, IR, MRZ, RR, CT, YT and SR
- 496 Formal analysis: CEF, MFD, MP
- 497 Funding acquisition: SR, MFD, MP
- 498 Writing original draft: CEF, MFD, MP
- 499 Writing review & editing: all
- 500
- 501 **Declaration of interests**
- 502 The authors declare no competing interests.
- 503
- 504 Inclusion and diversity statement
- 505
- 506
- 507 Main figure titles and legends
- 508
- 509

Figure 1- Overview of our dataset. Each colour represents a region, and each symbol represents a site. (A) Location of samples included in the study. (B) Timeline of BA and IA individuals with genomic data for the territory corresponding to present-day France. Circles without black outline represent previously published samples. (C) Principal component analysis of western samples from the Neolithic until the Iron Age projected onto the genomic variability of present-day populations.

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Figure 2- Pairwise *qpWave* testing to detect outliers. Grey-coloured models have a p value of less than 0.05 and were rejected, pink-coloured models have a p value of more than 0.05. Orange circles represent outliers from the chronological-cultural group from which they originate (p value < 0.05).

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527 Figure 3- Distribution and average level of ancestral components in IA samples from western 528 Europe. Each colour corresponds to a region (France) or a country. (A) Triplot of *qpAdm* 529 values for the Anatolia Neolithic (NEO), steppe and western Hunter-Gatherer components 530 (WHG) for individuals from the Neolithic to the Bronze Age from France (B) Triplot of 531 *qpAdm* values for the Anatolia Neolithic (NEO), steppe and western Hunter-Gatherer components (WHG) for individuals from Iron Age from France. (C) Evolution of qpAdm 532 533 values for the Steppe related ancestry component in southern and northern French regions, 534 between the Bronze and Iron Age periods. (D) Relation between the latitudinal position of the 535 archaeological sites where western Europe IA individuals were found and PC2 values (PCA 536 calculated on the genetic variation of an HO set of west Eurasians).

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- 538 539

540 **Figure 4** – Plot results of the f3-outgroup statistic in the form f3 (Mbuti, Outlier, Region), 541 where "region" corresponds to Iron Age individuals grouped according to their region of 542 origin.

543

544 Legends of Supplemental Tables

- Table S1: Description of the samples analysed in this study and in Brunel et al., 2020, relatedto STAR Methods
- 547 Table S2: Sequencing and alignment informations, related to STAR Methods
- 548 Table S3: Genetic information from individuals with low coverage genome newly acquired
- and from Brunel et al., 2020, related to STAR Methods
- 550 Tables S4: *qpAdm* values for two sources model with BA groups from France, related to
- 551 STAR Methods
- 552 Tables S5: *qpAdm* values for three sources model with BA groups from Europe, related to
- 553 STAR Methods
- Table S6: Value of statistical test in the form *f4 (Mbuti, Yamnaya, PopA, PopB)*, related to STAR Methods
- 556 Table S7: qpAdm values for three sources model (Yamnaya, Anatolian Neolithic and western
- 557 European Hunter-Gatherers, related to Figure 3
- 558

559 STAR+METHODS

560

561 **RESOURCE AVAILABILITY:**

- 562 Lead contact:
- 563 Further information and requests for resources and reagents should be directed to and will be
- 564 fulfilled by the lead contact, Melanie Pruvost (<u>melanie.pruvost@u-bordeaux.fr</u>)
- 565 Materials availability:

- 566 Raw sequence data and alignments are available at the European Nucleotide Archive (ENA)
- 567 under accession number ENA PRJEB50940
- 568 Data and code availability:
- 569 Genomic data have been deposited at the European Nucleotide Archive (ENA) and are
- 570 publicly available as of the date of publication. Accession numbers are listed in the key
- 571 resources table. All other previously published genomic data used in this study is available at
- 572 the sources referenced in the QUANTIFICATION AND STATISTICAL ANALYSIS
- 573 section.
- 574 This paper does not report original code.
- 575 Any additional information required to reanalyze the data reported in this paper is available
- 576 from the lead contact upon request.

577 EXPERIMENTAL MODEL AND SUBJECT DETAILS

Nordhouse, lieu-dit "Buerckelmatt" (Bas-Rhin)

578 Archaeological and anthropological information

579

580 Person in charge: S. Plouin, F. Lambach

581 The necropolis of Nordhouse, formed by six tumuli, is located approximately 20 km south of 582 Strasbourg within the alluvial plain of Ill river. These tumuli are mostly dated from the Late 583 Bronze Age IIIb, with cremation materials deposited in the center of a ditched circular 584 enclosure. Accompanied by rich ceramic items, cremated human remains were placed within 585 a wooden architecture. Characteristic potteries from the same phase were found in the eastern 586 sector of each ditch.

587 The necropolis of Nordhouse was then occupied between the 7th and 4th centuries BCE 588 (between Hallstatt C2 and La Tène B1). During the first and early Iron Ages, numerous weed 589 burials were deposited in the tumulus, and each monument hosted between 14 and 27 graves. 590 A total of 101 burials were found. An exceptional female tomb stands out for the abundance 591 and richness of its grave goods, including glass, amber, coral, a large shell from the Red Sea 592 and many gold ornaments.

In the present paper we used the genomic results previously published for four individuals (Brunel *et al.*, 2020), originating from 3 different monuments. Human remains NOR3-15 (an adult female buried with various ornaments) and NOR3-6 (an adult, possible female, buried with an infant and various ornaments) were discovered in tumulus 3, whereas NOR2B6 (an adult male buried with an infant) and NOR4-4 (a young female buried with various ornaments, potentially corresponding to an aristocratic individual) were found in tumulus 2 and 4, respectively.

- 600 Author of entry: S. Plouin and F. Lambach
- 601 References: in prep

602

603 • Sainte Croix en plaine (Haut-Rhin)

604 Person in charge: F. Chenal, Y. Thomas, S. Plouin

On the territory of the commune of Sainte-Croix-en-Plaine, located 11 km south of Colmar (in Alsace, Haut-Rhin), one of the largest funeral complexes discovered in the department extends over more than one hectare. It has been the subject of several preventive excavation campaigns, in 1979-1981, 1997, 1999 and 2005. More than a hundred funerary structures have been unearthed there, mainly within mounds of which only the circular ditches that surrounded them remain today.

- 611 The results of these excavations have provided invaluable information on the knowledge of 612 regional funeral practices between the end of the 2nd and the middle of the 1st millennium 613 BC. The alternation of burial and cremation practices and the occasional presence of wooden 614 containers adapted to the morphology of the deceased could be notably pointed out.
- The funerary structures included a rich material consisting mainly of ceramics and female bronze ornaments dated between the 7th and early 4th centuries BC. Most of them were produced from bivalve stone moulds, in which the metal was cast. The objects were then embellished with a chiselled or engraved decoration that may have completely covered them. The most remarkable bracelets are local products and represent major testimonies of Celtic
- 620 craftsmanship.
- In the present study, we propose genomic results from four individuals from this site. Three of them were discovered in the 'Oberes Holzackerfel' location: Croi1-4 (an adult buried with an exceptional iron razor, S1-4), Croi11 (an adult buried in one of the richest burials on the site, deposited with several grave goods such as an amber bead, S11-2) and Croi12-2 (an adult buried with a lignite bracelet, S12-2). Individual SCPG2 was excavated in the 'Oberholtzackerfeld/Echangeur Gendarmerie' location.
- These individuals were combined to the Jeb8, originating from the same site and previouslypublished in Brunel et al., 2020.
- 629 Author of entry: F. Chenal
- 630 References: in prep
- 631 Colmar "Jardin des Aubépines" (Haut-Rhin)
- 632 Person in charge: M. Roth-Zehner, A. Mauduit.

The settlement of "Jardin des Aubépines" is located in the southwest of the commune of Colmar on a loess layer very favorable for the establishment of pre- and protohistoric deposits. Excavation of the site has established the presence of an imposing ensilage site that begins at Hallstatt B1 and ends at La Tène B1. Nine individuals (2 women, 2 men, 2 immature and 3 undetermined adults; anthropological study: A. Mauduit) were deposited in silos. Some subjects (ST.336, ST.363) were deposited at the bottom of the structures. In all other cases, the burials were deposited when the silo was already beginning to fill in. Some of them were adorned with bronze or iron fibulae attributable to La Tène B1, bracelets and anklet rings. The silo fillings also delivered ceramics from the same period (Landolt *et al.*, 2010, 2012).

The selection of the individuals deposited in these special structures does not appear to be governed by biological criteria such as age or gender. When compared to funerary groups recovered in cemeteries, no special features could be observed, whether at the level of health status (they have no more pathologies or stress markers), of the goods accompanying the deceased, or of the positions and orientations of the individuals.

648 At the proximity of the two silos grouping the human deposits, a silo containing the deposit 649 of approximately ten animals (st. 235), whose skeletons are complete, is noteworthy. The 650 localization of this animal deposit raises the question of its association with the human burials 651 discovered nearby. Among the animals, archaeologists could identify a horse (a small Gallic horse) from which the skull was removed, several dogs, one of which was found in a suit (a 652 653 large dog), at least one piglet and several lambs. The animals discovered in this structure 235 654 were deposited with great care and therefore cannot be considered as usual rejects from habitat context. 655

In the present study, we present genomic data for three individuals: Col239 corresponding to an adult (30-60 years old) male buried with some grave goods, Col330 corresponding to an adult (30-39 years old) male and Col336 corresponding to a young (15-25 years old) female buried with a copper bracelet and presenting a spinal injury that might have been infectious. These individuals were combined to two other individuals, Col153A and Col153i, originating from the same site and previously reported by Brunel et al., 2020.

- 662 Author of entry : M. Roth-Zehner
- 663 Wettolsheim "Ricoh" (Haut-Rhin)

664 Person in charge: C. Jeunesse, M. Roth-Zehner

The Hallstattian Necropolis "Ricoh" (1987-1990) is located on loessic land to the east of the 665 Wettolsheim municipality. It covers an area of approximately 1.2 ha and consists of ten burial 666 667 circles grouping a total of 38 burials and 19 cremations. Half of the tombs are located outside the burial enclosure. The occupation of the necropolis begins at Hallstatt B2/B3-Hallstatt C 668 669 and ends at Hallstatt D1. The cremations belong to the initial phase, while the burials mainly date from Hallstatt C2 and D1. The deceased were found placed in wooden containers into 670 671 large tombs, with a series of vases regularly placed near their feet. Some individuals were 672 adorned with bronze bracelets presenting geometric decorations typical of the Upper Rhine 673 plain, as well as bracelets of lignite, bronze belts, amber and glass beads (Jeunesse, 1988).

674 In the present paper, we present the results for individual Wet429, a young male.

675 Author of entry: M. Roth-Zehner

- 676 Goxwiller (ZAC PAEI, Bas-Rhin)
- 677 Person in charge : S. Goepfert

678 Goxwiller is located approximately 25 km southwest of Strasbourg and 5 km east of the 679 Vosges foothills, on a terrace made up of loessic wind deposits. The excavation, carried out 680 in 2011, covers a total area of 3.8 ha.

681 The first indications of occupation date back to the early Bronze Age and correspond to a 682 well and a pit. After a hiatus of several centuries, a final Bronze Age IIIa complex, consisting 683 of seven widely dispersed structures, was established on the right-of-way. These structures 684 belong to a domestic ensemble whose exact nature cannot be established.

685 The Early Iron Age is the period best represented on the site with 96 structures that can be attributed to the Hallstatt period. Apart from a few miscellaneous excavations (polylobed pits, 686 687 oblong pits, simple pits), the majority of the structures identified correspond to silos that 688 hosted at least 45 individuals. Three of the silos had a particular filling, indicating that they 689 had been reintervened or excavated in their center. One of them, St.287, yielded the skeleton 690 of a child aged between 7 and 11 years old. The skeleton, which was deposited in the original 691 structure, was only superficially affected by the reintervention, which seems to have been 692 quickly filled in. One of the skeletal bones was radiocarbon dated indicating a range covering 693 the entire Hallstattian period (excluding Ha D3): 791-519 BC to 2 σ (Poz-47205, 2510 \pm 35 694 BP).

- Here, we present data for Gox287, a young individual (7-11 years old).
- 696 Author of entry : S. Goepfert
- 697 •

Erstein (Untergasse, Bas-Rhin)

698 Person in charge: F. Abert

In 2016, a survey archaeological excavation at the Erstein "Untergasse" uncovered animportant diachronic site with more than 1,300 archaeological structures.

A first occupation of the Second Iron Age was identified in the western part of the site, encompassing approximately ten burials with exceptional artefacts dated from La Tène B. The burial installation in a rough circle in a restricted space indicates that they were probably originally surmounted by a burial mound. A few nonfuneral structures are also attributable to La Tène, including a silo that provided numerous fragments of ceramics typical of this period and a ditch that crosses the right-of-way from east to west.

The Gallo-Roman period is also represented on the site, particularly in the eastern half of the right-of-way. The structures could only be poorly documented, as most of them have not been excavated. Nevertheless, they have been the subject of a removal of surface material after they had been stripped. 711 The main occupation of the site dates back to the early Middle Ages. It covers the entire 712 stripped surface and is exceptional in terms of size, density and organisation. It also has the 713 particularity of combining settlement structures with funerary areas. Numerous 714 archaeological structures intersect here, bearing witness to a dense and long-lasting human 715 activity. The settlement contains numerous hut bottoms, storage structures (silos and cellars), 716 wells, post hole drawing plans of buildings and numerous pits. Most of these remains are 717 organised around two or three parallel axes, corresponding to communication routes oriented 718 along a north-south axis.

The funerary structures can be divided into two distinct types. In the western part of the site, isolated burials or graves in groups of two to three graves are present among the habitat remains. To the east, along the northern boundary of the excavation, a small cemetery contains numerous burials, the density of which and some overlaps indicate that they were isolated from the habitat in a reserved space which suggests the existence of a religious building nearby.

Here we present genomic results for Ers83-2, a young individual (approximately 10 years old). This individual was combined to three other samples (Ers1164, Ers86 and Ers88) previously published in Brunel et al., 2020.

- 728 Author of entry: F. Abert
- 729

• Buchères « PLA - secteur 1A » (Aube)

730 Person in charge: V. Desmarchelier

731 In 2014, an excavation was carried out in the Aube Logistics Park, in the commune of 732 Buchères, in the south of the Troyes conurbation. This operation was part of the PLA 733 development project, which began with archaeological diagnostics in September 2004. The 734 two stripping operations of 2014 - D41 and D42 - were located to the southeast of this 735 project, in the area known as the "Vignes Neuves" and about 700 meters from the Fontaines 736 de Savoie stream, which crosses the Logistics Park from north to south. They are about 100 737 meters apart and are located on a plateau which also concentrates excavation operations D01 738 (2005), D37 (2011) and D43 (2015). Overall, over the whole of the PLA, the various 739 operations have revealed occupations of domestic or funerary nature, from the early LBK to 740 the modern period. The 2014 excavation has uncovered structures covering approximately 1 741 ha, indicating discontinuous occupation from the ancient Mesolithic to the modern period.

The Second Iron Age is the period best represented. Nearly 20 silos - two with burials and two with dog deposits - associated with pits, post holes, a polylobed pit and a hole containing human skeletons are evidence of domestic occupation in this sector (Desmarchelier, 2020). 745 Almost all of the silos delivered ceramic that permitted anchoring their use as a dump at the end of La Tène A2 and during La Tène B1. Interestingly, this period is poorly represented at 746 747 the local scale despite the start of a peak in the intensity of this type of storage during this 748 period in northern France. There is no dating evidence to establish a proven succession of 749 structures over time, all falling within a broad framework of approximately one hundred 750 years at the beginning of the Second Iron Age. However, as no overlap between structures 751 has been observed, a contemporary or chronologically very close use of the structures can be 752 assumed. Mostly consisting of small domestic waste, the assemblages from the silos do not 753 evoke any particular activity other than conversion into domestic dumps or - in the case of 754 dog dumps or burials - for ritual or funerary purposes.

755 The hole, located to the east of the pickling, was in itself an enigma because of the human skeletons discovered at a considerable depth in its filling. In addition to these deceased, 756 757 deposited respectively at 3.90 and 5 m deep, this structure also revealed numerous remains of 758 fauna at 7 m deep. Certain clues related to decomposition indicated the presence of localised 759 empty spaces inducing a cover of the structure above the human remains. These men did not 760 appear to have suffered from any pathology, traumatic or infection, apart from a sprained 761 right ankle observed for one individual. There is no evidence to indicate the context of their 762 deposition, whether it was an accidental and fatal fall or a burial with a cover.

Since the first archaeological interventions in the Logistic Park in 2005, 23 individuals have therefore been discovered in 14 silos and one pit, most of which were deposited on the dome of the first fill or closer to the bottom of the structure, between Hallstatt C and Tène C. Likewise, like the deceased from the PLA as a whole, the individuals discovered in the silos and the hole are on the whole lacking in stress indicators and pathologies, with signs of senescence being rare and not very intense.

In the absence of more eloquent evidence, the location of the habitat on which these structures depended remains hypothetical. In fact, even if it can be assumed that it was located close to those that delivered most of the furniture, no characteristic structure was found there. It should be pointed out that, with regard to this chronological phase, small, lightly built dwellings have little chance of being preserved, as the batteries of silos, due to their depth, are more easily resistant to erosion.

Here we present the genomic results for two individuals: Buch48-1 and Buch48-2 who aretwo adult males deposited in wells, which is quite rare for the period and the region.

777

778 Author of entry: I. Richard

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780

• Buchères, Moussey, Saint-Léger-près-Troyes « PLA – D37 et D38 » (Aube)

781 Person in charge: C. Paresys

In 2011, Inrap carried out an archaeological excavation in the commune of Buchères, in the "Parc Logistique de l'Aube" (Aube, Champagne Ardenne). This excavation, with a total area of 12,395 m², divided into two separate windows, uncovered several sets of structures covering a vast chronological field from the Neolithic to the contemporary period and different functions (land use, funerary, agricultural; Paresys, 2014).

The main occupation of the site is materialised through eleven funerary enclosures of various shapes, nine circular, one quadrangular and one elliptical. Some ceramic fragments were found in their filling, divided into two main periods, the end of the Neolithic and the end of the first Iron Age. Radiocarbon analyses are consistent with these two periods, and three of the oldest enclosures could be chronologically located between the Neolithic and the end of the Bronze Age. In fact, an enclosure dating from the Early Bronze Age was discovered nearby at the time of the diagnosis in 2005.

Burials dated between Hallstatt C and Tène A were found in three of these enclosures, two in
the area bounded by the ditch, the last of which intersected the ditch of enclosure D37F0062.

The storage of grain is illustrated by five silos distributed over the two picklings. Four of them then housed six deceased, two of them with metal furniture. Of the deceased deposited in the same structure, two were simultaneous and two others deferred in time. These deceased are more recent than those buried in the enclosures between Tène B and Tène C.

In the present study, we present genomic results for individual BUCH82, an adult discoveredin a silo.

802 Author of entry: I. Richard

803

• Champfleury « RN 51 » (Marne)

804 Person in charge: S. Culot

The Champfleury "RN 51" (Marne) site is located south of the city of Reims (less than 6.5 km from its ancient center). It is located on the eastern slopes of the Rouillat valley, which slopes slightly from east to west, at altitudes of 107 m and 100 m respectively. It is also bordered to the east by one of the many dry valleys encountered in the chalk plain. One of the nearest prominences is less than 1 km to the west, rising to 121 m. Further south, the Montagne de Reims, the flagship of this sector, overlooks the plain from a height of 283 m.

The excavation operation uncovered seven sepulchral pits grouping ten individuals, distributed over three distinct groups (Culot, 2012). These burials probably belong to an even larger necropolis, continuing southwards (Champfleury, "A Mi Champs", Bonnabel, 2011). The illustrated funerary practice is characteristic of the early Second Iron Age and classic of the Aisne-Marne archaeological culture as defined by J.-P. Demoule (Demoule, 1999). The material associated with the deceased permitted to specify the chronology, ranging from La Tène A (475 - 400 BC) to La Tène B1 (400 - 325 BC).

818 Here we present the genomic results for individual CHF106, an adult male buried with 819 several grave goods.

820 Author of entry: I. Richard

• Isles-sur-Suippe « Les Sohettes » (Marne)

822 Person in charge: A.-C. Baudry

The Isles-sur-Suippe site is located in the Marne Department, 16 km northeast of Reims.
Excavated in 2014 by Inrap (Baudry, 2021), this 4.8 hectare site consists of four sectors
covering the chronological periods of the end of the Second Iron Age, Antiquity and the First
World War.

The protohistoric occupation consists of an enclosed habitat from the transition between the final La Tène and the beginning of Antiquity. The chronological question is crucial in the case of Isles-sur-Suippe. In fact, approximately fifty architectural units (buildings on posts, palisades) associated with holes, are organised within an enclosure of more than 1.8 ha in surface area. The first elements of dating obtained from the ceramic study and radiocarbon analysis show a relatively short period of occupation of about 150 years, without any apparent chronological hiatus.

834 One of the pits, pit 6950, was discovered on the edge of the settlement, about 50 m east of the enclosure ditch. It is circular and narrow in cross-section, dug into a compact chalk substrate 835 836 at least 6 m deep. In its central part, at a depth of 2.5 m, a deposition zone was discovered, 837 containing animal carcasses and the skeleton of a young man. No perennial furniture was 838 found next to this individual except a large ceramic shard. A second deposit was found at the 839 bottom of the shaft, this time consisting of an isolated millstone. The deposit of the animals 840 and the deceased in the pit, because they were very close in time, strongly link the treatment 841 of cattle and humans. It is hypothesised that these deposits were the result of the same 842 operating chain, the purpose of which remains to be elucidated. These practices, which stand 843 outside of usual funerary practices between the 2nd and 1st centuries BC, raise questions 844 about the purpose of this deposit and the practices that may lead to the association of humans 845 and cattle.

- Here we present the genomic results for individual ISL6950, the young male recovered in thisspecial structure.
- 848 Author of entry: I. Richard
- 849 Urville-Nacqueville (Manche)
- 850 Person in charge: S. Rottier, A. Lefort

The site of Urville-Nacqueville, Normandy, is an Iron Age coastal settlement and funerary site excavated between 2011–14 and again in 2017. This port, located along the Channel, is characterised by the presence of an artisanal sector and a vast cemetery.

The Iron Age activity focuses on the period 120–80 BC and displays significant links with southern Britain, both in terms of the settlement evidence (e.g. the presence of roundhouses, Kimmeridge shale etc) and burial rites (with some adults individuals buried in a position similar to that seen in the Durotigian region of southwest England; Lefort *et al.*, 2015).

The excavations of the Urville-Nacqueville necropolis revealed 112 graves (78 burials and 34 858 859 cremations) containing the remains of at least 127 individuals (of which 41 were cremated). 860 The inhumations are dominated by subadults, and the cremations concern principally adults. The funerary space is organised through the presence of an enclosure in the northeast. Some 861 unusual funerary practices are observed at Urville-Nacqueville, such as deliberate removal of 862 skulls and extra skulls in some burials. This site is also outstanding for the period and the area 863 864 for its size. Indeed, for the Second Iron Age in Normandy were mainly found small 865 cemeteries of less than 30 individuals, usually cremated and lacking evidence for sub-adults (Chanson et al., 2011). 866

Here, we present genomic results for three adult male individuals buried in the so-called'Durotrigian' position: UN 129, UN 19 and UN 85.

- 869 Author of entry: C-E Fischer
- 870 Attichy-Bitry

The La Tène necropolis of Attichy-Bitry " Le Buissonet " is located in the Oise between the 871 towns of Compiègne and Soissons, on the right bank of the Aisne. Partly destroyed by an 872 873 antiquarian settlement, 11 burials are spread over about 1300 m², grouping 12 individuals, 6 874 adults, 5 children and 1 individual of undetermined age. The usual funerary practices 875 discovered in the region consist in individual cremated burials. The deceased wore a panoply 876 of ornaments and clothing accessories made of bronze, iron or lignite, with the men also 877 wearing equipment consisting of weapons. In addition to this, there are also toiletries or tools, chariot parts, deposits of meat and ceramic containers for the presentation and consumption 878 879 of food or liquids. The highest hierarchical rank of this community is expressed in two 880 chariot tombs and a tomb with a circular enclosure where a young child was buried. The 881 funerary occupation of Attichy seems to have extended throughout part of the 3rd century, a 882 period characterised by the abandonment of burial in favor of cremation. The Attichy 883 necropolis can probably be linked to the Aisne-Marne cultural group with a later adoption of 884 cremation for all individuals at the end of the Middle La Tène.

Here we present genomic data for three individuals: Att3, Att27 and Att52-2, that were combined to the individual Att26, previously published in Brunel et al. (2020).

- 887 Author of entry: S. Desenne
- 888 Bucy le Long

889 The necropolis of Bucy-le-Long "la Héronnière - la Fosse Tounise" is located on the right 890 bank of the Aisne, 3 km upstream from Soissons in the Aisne. It is located on a sandy 891 prominence of the alluvial terrace, overhanging the river. It was occupied between the 5th and 4th centuries BC. The necropolis covers an area of 2.5 hectares and originally contained 892 893 around 350 graves, of which 235 have been excavated. Burial is the main mode of deposit 894 and only two cremation graves have been found in the complex. All age groups of adults are 895 present (from 18 to over 80 years old) but the proportion of young adults is important here 896 and the elderly individuals are few. Furthermore, despite the high theoretical infant mortality 897 within this type of population, the bulk of the children are missing. The study of pathologies has not revealed any significant deficiencies or war trauma. The state of health is satisfactory, 898 899 and the perceived traces of arthrosis and rheumatic pathologies are related to the age of the 900 deceased and the repetition of physical tasks. The funeral practices adopted by this population 901 is dressed burial. The women are distinguished by their finery and the men by their 902 weaponry. The rest of the material consists of toiletries, rare tools, ceramic dishes, and 903 foodstuffs, of which only the bones of the meat remain. The elite individuals are 904 distinguished by a monumental tomb known as a "chariot tomb". They are buried on a horse-905 drawn vehicle, a symbol of power.

The necropolis of Bucy-le-Long "Le Fond du Petit Marais", located on the right bank of the Aisne, 5 km west of Soissons, covers 3,200 m2. It comprises 66 burials and 15 monuments organised in a linear fashion along a north/south axis, in two distinct groups separated by at least 30m. Its occupation began at La Tène C1, with the burial ritual, and continued at La Tène C2 and then D1 with the cremation ritual. The deceased are mostly equipped with clothing accessories and food offerings. The most richly endowed tombs are provided with bronze vessels (basins, buckets) and one of them has yielded elements of a chariot.

913

Here, we present genomic data for two individuals: BFT228, from 'La Fosse Tounise' and
BLH447, from 'La Heronniere'. They were added to the individual from 'Le Fond du Petit
Marais', BFM265, previously published in Brunel et al., 2020.

- 917 Author of entry: S. Desenne
- 918 La Piece a Liards
- 919 Person in charge: S. Oudry

920 The Etaples necropolis is located along the Channel coast, near the Canche estuary. It is dated 921 to the Middle/Final Hallstatt (Ha D1-D2) and more specifically to the 6th century BC. One of 922 the main features of this necropolis is a specific funerary ritual corresponding to burial in a 923 lateral bent position. Furthermore, it is the only site in the region dating from this period 924 (Henton et al., n.d.). The pits, which are large and structured, are dug out of chalk. Part of 925 them are arranged inside a quadrangular ditch. Comparisons are to be searched about 200 km further south, in Calvados at Basly and Ifs. The convergence of several funerary features 926 927 concerning the body suggests strong affinities with the funerary systems in use in the 928 communities settled along the Channel coast at the end of the First Iron Age.

- Here we present genomic data for Pal170, an adult buried with a bronze ring.
- 930 Author of entry: S. Oudry
- 931 Vasseny

932 The necropolis of Vasseny "au Dessus du Marais", "Dessus des Groins" is located between 933 the towns of Soissons and Reims, in a meander of the Vesle, a few kilometers from its 934 confluence with the Aisne, on the middle alluvial terrace of the left bank of the river.

935 The necropolis contains 40 tombs spread over a short period of a century, from the second 936 half of the 5th century to the middle of the 4th century BC. The spatial distribution of the 937 burials shows an irregular grid of four concentrations spread over almost one hectare. The 938 ritual of burial is predominant, although at the turn of the 4th and 3rd centuries BC, cremation 939 seems to develop. Only one case of cremation is recognised at Vasseny among 39 burials. 940 The latter correspond, for the most part, to the graves of adults. The deceased present a 941 panoply specific to their sex and rank. The women wear finery (torque, bracelet, pendants, 942 fibula, earrings, etc.) whereas the men are equipped with weapons (dagger, sword, shield, 943 spears and javelins). To these elements are sometimes added toiletries, tools and more 944 frequently food offerings in the form of pieces of meat and ceramic containers intended for 945 the presentation and consumption of food or liquids.

946 The highest hierarchical rank of this community is expressed in three graves of individuals,947 two men and one woman, buried on a chariot.

948 The Vasseny necropolis is part of the Aisne-Marne cultural group as a whole and shows a 949 high degree of homogeneity in the funerary practices of this period. This medium-sized site is 950 part of a geographical network organised on three levels of social integration perceptible 951 within the Aisne-Marne cemeteries.

- Here we present genomic data for two individuals: Vas75 and Vas79-2.
- 953 Author of entry: S. Desenne
- 954

• Barbuise 'Les Grèves de Frécul' and 'La Saulsotte'(Aube)

955 Person in charge: S. Rottier

The site of Barbuise, located in the department of Aube, on the right side of the Seine, is composed of a group of localities discovered as early as the XIX^e century. In 1832, an inventory of the megaliths was carried out by the Société Académique de l'Aube and several menhirs and dolmens at Courtavant and La Saulsotte were surveyed. However, it was not until 1937 that the Latenian cemetery known as "Les Grèves de Frécul" was discovered and partially excavated by Henri Lamarre.

962 The site "Les Grèves de Frécul" was occupied during the Iron Age, between the 5th and the963 3rd centuries BC.

Several excavations were carried out from 1937 to 1975 and revealed 150 burials in five enclosures. The site was then part of rescue excavations during the 1990s and was reexcavated in 2000. During the last excavation, more than 100 burials were counted and almost all of them were associated with a funerary enclosure. However, it is important to note that among all these graves, only 15 are considered to be intact, i.e. not excavated by H. Lamarre in the 1930s and 1940s (Rottier and Piette, 2001).

Here we present genomic results for five individuals from the Iron Age as well as two
samples from the Bronze Age. From the Iron Age period, GDF1231 (enclosure E17),
GDF1264 (enclosure E8) and GDF1341 (enclosure E19) are females whose the age at death
could not be estimated. Two other individuals originating from enclosure E19 were analysed
and correspond to an immature individual (GDF1348), and an adult female (GDF1349-A).
From the Bronze Age period, genomic data were obtained for individuals BPV1445 and
BPV1455.

- 977 Author of entry: C-E Fischer
- 978

• Gurgy 'Les Noisats' (Yonne)

979 Person in charge: S. Rottier

Gurgy's site 'Les Noisats', occupied between 3rd and 1st centuries BC, is located in the
department of Yonne (89), on the right side of the river Yonne. This relatively short period of
occupation represents about 7 generations (one generation corresponding to 28 years;
Moorjani *et al.*, 2016).

This deposit was first investigated in 1997 by S. Collet and F. Müller. The authors 984 985 mentionned a few poorly dated structures of minimal interest, but pointed to the presence of 986 an important funerary site from Early and the Late Iron Age associating a circular enclosure and a quadrangular enclosure, comparable to those discovered at the Gurgy 'La Picardie' site, 987 988 located a few hundred meters away. The funerary complex was excavated by S. Rottier in 989 2004. It consists in a mound of around 700 m² which yielded 40 individuals spread among 35 990 graves. It should be noted that the mound has been levelled and that only the deepest and 991 latest graves remain (Mordant and Rottier, 2004), so the number of individuals does not 992 represent the group as a whole.

Here we present genomic data for four individuals originating from this mound. Sample
GLN29-A corresponds to a male between 7 and 13 years old, GLN32 corresponds to an adult
male with a missing skull, whereas GLN126 and GLN141 correspond to two adult females
buried in the northern part of the tumulus.

997 Author of entry: C-E Fischer

998 • Oppidum du Plan de la Tour (Gailhan, Gard)

999 Person in charge: B. Dedet

1000 The settlement of Plan de la Tour (Gailhan, Gard) is located in eastern Languedoc, in the 1001 foothills of the Cevennes. It was occupied between the 5th and 4th centuries BC. The 1002 excavation delivered the burials of more than twenty subadults. These deceased were not 1003 incinerated, while cremation is the rule in this region for adults admitted to the village 1004 cemetery. They were buried in a small pit of the size of the body inside the houses. The 1005 bodies are not swaddled, as shown by the observation of the position of the limbs.

Here, we present genomic results for one perinatal individual PT7 (sepulture B2, inhumation
W18-23-2). This individual was combined to individual PT2, previously published in Brunel
et al., 2020.

1009

• Oppidum de Pech Maho (Sigean, Aude)

1010 Person in charge: E Gailledrat

Pech Maho (Sigean, Aude) is a small fortified trading post founded at the middle of the 6thcentury BC and abandoned at the end of the 3rd century BC.

1013 The settlement acted as a place of exchange and meeting between native populations and 1014 Mediterranean merchants (Greek, Etruscans, Iberians). Domestic levels yielded some graves

1015 of very young children.

Here we present genomic results for two individuals: sample PECH3 that was found in a deposit (Sep. 71289, obj-71289-1) and corresponds to an adult male, and sample PECH9 that corresponds to a perinatal found on dumping ground.

1019 They were combined to two other individuals, previously published in Brunel et al. (2020): 1020 sample PECH5 originating from an isolated grave (Sep. 46101, obj-46101-2) and 1021 corresponding to a young male (15-18 years old) and sample PECH8 also originating from an 1022 isolated grave (Sep. 47003, obj-47003-1) and corresponding to an adult male.

1023 • La nécropole du Peyrou 2 (Agde, Hérault)

1024 Person in charge: B. Dedet

1025 The Peyrou site at Agde (Hérault), groups an incineration necropolis functioning during the 1026 second half of the 7th century BC (Peyrou 1) and a necropolis hosting 35 burials revealing 1027 very different funerary practices (Peyrou 2) and used from the end of the 5th century to the middle of the 2nd century BC. Among the subadults, 8 perinatals or infants were found 1028 1029 buried in a vase. Adults were buried only with objects relating to the mortuary toilet (perfume 1030 vases) or a symbolic tribute with no difference according to the sex of the deceased. These 1031 practices are identical to the Greeks' rituals, very different from those of the surrounding 1032 region during the Iron Age. Ancient texts attest to the existence of a trade settlement created 1033 by the Greek colonists of Marseilles in this place at this time.

1034

Here we report genomic data for individual PEY73, an adult female buried with a pouring vase. These results were combined to those previously published in Brunel et al. (2020) for two other samples: PEY53, an adult female buried with some grave goods, and PEY163, an adult male buried without any grave goods.

1039

• La Monédière (Bessan, Hérault)

1040 Person in charge: A Beylier

1041 La Monédière (Bessan, Hérault) site yielded a small collection of burials dated from the 2nd1042 century BC.

The site of La Monédière is the place of a Gallic fortified settlement occupied between the 1043 early 6th century and the end of the 5h century BC. Covering an area of nearly 4 ha, this 1044 1045 settlement occupies a slight relief on the right bank of the Hérault river. Its foundation 1046 appears closely linked to very early contacts made in this part of the Gulf of Lyon with the 1047 Mediterranean societies and the establishment, at the mouth of the Herault, of the Agde 1048 littoral counter which is roughly 6 km away. The trading activities, indicated by the 1049 abundance of products imported from the Greek or Etruscan world, are generally at a level 1050 higher than that observed in neighboring establishments. The quantity of amphora reveals the 1051 involvement of this site in trade networks uniting the coast and the interior, as well as its role 1052 in the redistribution of the products transported from the Mediterranean within the framework 1053 of Mediterranean trade, by land or waterways. Benefiting from a favorable geographical 1054 position, La Monédière stands as an essential marketplace and a privileged meeting place 1055 between natives and Greeks, to such an extent that the question of the in situ installation of a 1056 Hellenic community was raised. Its occupation was interrupted towards the end of the 5th 1057 century BC at the time of the foundation of the colony of Agde/Agathè by Marseilles. In the 1058 course of the 2nd century BC, the site was revisited. At this time, a funeral complex was 1059 established, yielding a small collection of burials associated with a very poorly known 1060 settlement, which could be an integral part of the chôra of the Agathe colony.

Here we present the genomic results for two immatures and one adult. Samples BES1096B and BES1154 are dated to the 5th century BC and correspond to two immatures buried in the settlement, a funerary practice common for the area and the period. The last sample, BES1249 corresponds to an adult found in the cemetery dated to the 2nd century BC, whose burial is not representative of the funerary gestures for the area and period, where adults are mostly cremated. These individuals were combined to BES1248, another adult previously published in Brunel et al., 2020.

1068

8 • Le Cailar (Cailar, Gard)

1069 Person in charge: R. Roure

1070 The site of Le Cailar, south of Nîmes, is an important laguna harbour of the Iron Age. It has 1071 been studied since the 2000s and archaeological excavations have shown that the settlement 1072 has been occupied since the 6th century BC and was involved in the exchanges with Greek 1073 Marseille and all of the Mediterranean. The protohistoric and ancient occupation of Le Cailar 1074 lies at the confluence of Vistre and Rhôny. During the whole 3rd century BC, many severed 1075 head and metal weapons were displayed on a large public place near the fortification. About 1076 2700 fragments of human bones were recorded during ten excavation campaigns, almost all 1077 belonging to the skull. Chemical analyses proved that those heads were embalmed (Ghezal et 1078 al., 2019).

Here we present genomic results for five individuals represented by skull deposits: CLR23,
CLR24, CLR31, CLR35 and CLR44. All samples were males and were recovered from the
public place, within the walls.

1082

1083 METHOD DETAILS

1084

• DNA extraction and sequencing

1085 All experiments were performed in the ancient DNA facilities at the PACEA laboratory 1086 (CNRS, University of Bordeaux, France). aDNA was preferentially extracted from petrous 1087 bones but for some individuals, teeth or even intact long bones were selected (see key 1088 resources Table). Bone surface was decontaminated before extraction, ie. scraped, cleaned 1089 with diluted bleach and exposed to ultraviolet (UV) light for each side for 20 min. After soft 1090 surface abrasion with a drill, sampling was performed using a clean drill into the denser 1091 regions around the cochlea of the petrous bone or into the cortical part of the long bones. 1092 Teeth were completely ground to fine powder.

1093 Between 100-250 mg of bone/tooth powder was used for each extraction. aDNA was 1094 extracted using a two-steps procedure adapted from Damgaard *et al.* (2015), and purified by a 1095 silica based method on a MinElute column (QIAGEN) (see Brunel *et al.*, 2020).

1096 For all DNA extract, double-stranded libraries were built from 10 to 25µL of DNA template,

1097 following a protocol proposed by Meyer and Kircher (2010) and using unique index pairs

1098 (Kircher et al., 2012). A partial uracil-DNA-glycosylase (UDG half) treatment was applied to

remove deaminated cytosines except for the final nucleotides at the 5' and 3' reads ends to preserve part of the damage pattern characteristic for ancient DNA (Rohland *et al.*, 2015).

1101 We first screened all indexed libraries via shotgun sequencing targeting around 1 million 1102 reads. Libraries were pooled and sequenced on an Illumina NextSeq 500 (2x75bp reads) at 1103 Institut de Recherches Biomédicales des Armées (Paris, France). Reads were analysed with 1104 EAGER (Peltzer et al., 2016) to process the raw data and to select satisfying libraries for 1105 deeper sequencing. Selection criteria included sufficient endogenous DNA proportion 1106 (>15%), complexity of the library and presence of damage patterns characteristic for aDNA 1107 (see Table S1 for shotgun screening results). Selected librairies were then more deeply 1108 sequenced on the same platform in order to obtain low-coverage genomes of at least 0.1X 1109 (Table S2).

1110

• Read processing, alignment and post-mortem damage

Raw sequence data were processed using EAGER (Peltzer et al., 2016) with the following 1111 1112 steps. Reads were trimmed for adaptor sequences and collapsed into single reads using 1113 ClipandMerge software. Reads were mapped against the Human Reference Genome hs37d5 1114 with BWA (Burrows-Wheeler Aligner) v0.7.12 (Li and Durbin, 2010), and duplicate reads 1115 with the same orientation and start and end positions were removed using DeDup v0.12.1. 1116 Reads with a mapping quality phred score < 30 were excluded. MapDamage v.2.0.6 was used 1117 to observe characteristic aDNA damage patterns, before trimming two bases at the ends of 1118 each read remove residual deaminations with BamUtil to 1119 (https://genome.sph.umich.edu/wiki/BamUtil:_trimBam). A summary of quality statistics is 1120 given in Table S3

1121 **QUANTIFICATION AND STATISTICAL ANALYSIS**

1122

•

Sex Determination

Genetic sex was calculated using the methods described in Skoglund *et al.*, (2013) estimating
the fraction of reads mapping to Y chromosome out of all reads mapping to either X or Y
chromosome (see Table S2).

1126

• Contamination estimates

We used the ANGSD (Analysis of Next Generation Sequencing Data) package to test for heterozygosity of polymorphic sites on the X chromosome in male individuals, applying a contamination threshold of 5% (Table S2). Contamination estimates were extremely low and permitted us to keep all samples for further analyses.

1131 • Uniparen

• Uniparental markers

1132 To process mitochondrial DNA data, reads were mapped to the revised Cambridge Reference 1133 Sequence (rCRS- GenBank Accession Number NC_120920.1). VCF files were built using 1134 bcftools mpileup and then submitted to HaploGrep 2 (Weissensteiner *et al.*, 2016) in order to 1135 determine mitochondrial haplotypes (Table S2). Reliable characterization of maternal lineage 1136 could be conducted for 43 individuals. The combination of our mitochondrial dataset with the 1137 maternal genomes published by Brunel *et al.* (2020) permits to confirm the prominence of

haplogroups H (25,58%), J (20,93%), K and U (both at 15,12%) among French IA groups.
Large chronological groups, from the Palaeolithic to the Bronze Age period, were constituted
to figure out the diachronic evolution of maternal lineages frequencies on the French territory
by combining our dataset with previous published data (Brunel *et al.*, 2020; Fischer *et al.*,
2018, 2019; Fu *et al.*, 2016; Olalde *et al.*, 2018; Rivollat *et al.*, 2020, Figure S2).

Y chromosome haplotypes were called using Yleaf statistical package for each male individual (Ralf *et al.*, 2018). All the 29 male individuals identified in our dataset had sufficient coverage for Y haplotype assessment (see Table S2). Most individuals were found to carry haplogroup R1b1a (69%), other males belonging to haplogroups G2a2 (17,24%), I1 and I2 (both at 6,9%). We compiled our data set with previous published data (Brunel *et al.*, 2020; Fu *et al.*, 2016b; Olalde *et al.*, 2018; Rivollat *et al.*, 2020) to study the evolution of the frequencies of Y chromosome haplogroups from the Palaeolithic to the Iron Age (Figure S3)

• Kinship analyses

We estimated the degree of genetic relatedness between our individuals by applying Relationship Estimation from Ancient DNA (READ; Monroy Kuhn *et al.*, 2018). Of the 61 French Iron Age individuals for which low coverage genomes are available (Figure S4), we identified only three individuals presenting a 2nd degree of relatedness at Attichy-Bitry (North): individual ATT27, individual ATT3 and individual ATT52-2. The other individual from Attichy (ATT26) shares no biological link up to the 3rd degree with the others.

1157

• Inbreeding and diversity estimates

To detect potential inbreeding among the French IA groups and individuals, we calculated length of runs of homozygosity (ROH; Ringbauer *et al.*, 2021) using the software HapROH on individuals carrying more than 300,000 SNPs. We performed hapROH to the pseudo haploid data of 1240k SNPs to detect runs of homozygosity longer than 4 centimorgan for all IA individuals.

1163 Of the individuals providing suitable coverage for this analysis, only individual COL336 1164 from the Iron Age site of Colmar "Jardin des Aubépines" (Haut-Rhin) showed evidence for 1165 long ROH greater than 50 cM. The sum and length distribution of ROH measured for 1166 COL336 suggest their parents were first-degree relatives (Figure S11), i.e., parent-offspring 1167 or full siblings (whose offspring will have a quarter of their genome in ROH). This individual was found deposited in a silo without any particular care. The overall absence of long ROH 1168 1169 for other French IA individuals or groups indicate that the groups considered were 1170 sufficiently large or with controlled union rules to avoid inbreeding (Figure S10).

1171

1172 •

Principal Component Analysis

1173 PCA analysis was run with the Human Origins reference panel for 592,998 autosomal 1174 genotypes in 796 west Eurasian modern individuals using smartpca v10210 (EIGENSOFT) 1175 with the options lsqproject:YES and shrinkmode: YES, using 51 modern populations to 1176 calculate eigenvectors on which aDNA samples were projected. Genotypes were downloaded 1177 from David Reich's website (dataset v44.3.1240K HumanOrigins, available at 1178 <u>https://reich.hms.harvard.edu/allen-ancient-dna-resource-aadr-downloadable-genotypes-</u>

present-day-and-ancient-dna-data) and merged with our dataset. Projections on the first two
 PCs are provided in Figure 1C and S1.

- 1181
- 1182

Genetic clustering and outlier detection

To prepare our dataset for analyses, we divided individuals in six regions and, when possible,
in chronological sub-groups: EIA_Alsace (from 800 BC to 450 BC), LIA_Alsace (from 450
BC to 50 BC), IA_Champagne, IA_Normandy, IA_North, IA_Paris_Basin and IA_South (see
Table S2).

- 1187 We carried a *qpWave* from the ADMIXTOOLS package (https://github.com/DReichLab) 1188 iterated over all individuals in the pool, testing for significant evidence of heterogeneity 1189 relative to a sub-pool of all individuals in the main cluster (except the test individual when it 1190 was part of the main cluster). The right set panel A was composed of: Mbuti.DG, 1191 Ethiopia 4500BP published.SG, CHG, Russia EHG, Russia Ust Ishim HG published.DG, 1192 Russia MA1 HG.SG, Israel Natufian, Jordan PPNB published, Czech Vestonice16, 1193 Iberia_ElMiron, Anatolia_N_published, Morocco_LN.SG, WHG, Iran_GanjDareh_N, and 1194 Russia_EBA_Yamnaya_Samara. We identified outliers from the main cluster individuals
- 1195 when the qpWave p-value was p<0.05 (Fernandes *et al.*, 2020).
- We found six individuals spending as outliers from the chronological and regional group towhich they belong:
- 1198 Bes1248 stands as an outlier from the South_IA group
- 1199 Croi11 stands as an outlier from the Alsace_IA_1 group
- 1200 Col239 stands as an outlier from the Alsace_IA_2 group
- 1201 GDF1341 stands as an outlier from the Paris_Basin_IA group
- 1202 Pech3 stands as an outlier from the South_IA group
- 1203 Pey163 stands as an outlier from the South_IA group
- 1204 Therefore, these individuals were not included in the analyses at the regional level.

We run *qpWave* analyses with the same reference panel comparing BA and IA groups from the French territory and Europe to test for statistically significant differentiation. We created a similarity matrix, which was then used to generate the heatmap using the heatmap.2 function of the R-package gplots (Warnes *et al.*, 2019) (Figure 2).

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• f3-Outgroup and f4-statistics

1211 Outgroup *f3*-statistics were calculated using qp3Pop and *f4*-statistics using *qpDstat* with the 1212 *f4* mode from ADMIXTOOLS (https://github.com/DReichLab). We used the 1240K panel to 1213 optimize the number of SNPs covered by the ancient individuals and get more resolution in 1214 the statistic tests. Standard errors were calculated with the default block jacknife.

To test for specific genomic affinities between IA individuals, we performed a f3-outgroup statistics in the form f3(Mbuti, Ind, Ind). The results were plotted in a heatmap (Figure S5) using the heatmap.2 function of the R-package gplots (Warnes *et al.* 2019). The heatmap shows no specific affinities between individuals from the same site or region (ATT27 and 1219 ATT52-2 were removed from this analysis as they present 2^{nd} -degree genetic relatedness 1220 between them and with ATT 3).

1221 To determine if a specific ancestral legacy could explain the outlier status of the individuals, 1222 we performed f3-outgroup statistic the form f3(Mbuti, X, Outliers/Region) with X being 1223 either one of the three major genetic components of the European population: WHG, Anatolia 1224 Neolithic and Russia Samara EBA Yamnaya. The results show that some individuals 1225 (Bes1248, Col239) seem to have excess in the Yamnaya component compared to their group 1226 of origin (Figure S6). We also performed a f3(Mbuti, Outlier, Region) for each outlier and using 1227 each region. The results were plotted on maps QGis v.3.10 1228 (https://www.qgis.org/en/site/, Figure 4).

- 1229 To test if the Yamnaya component distribution permitted any significant differentiation 1230 between IA groups from UK, French regions (North, Alsace, the Paris Basin, Champagne, the 1231 South) and the Iberian Peninsula, we also performed a f4 statistical analysis, in the form 1232 *f4(Mbuti, Russia_Samara_EBA_Yamnaya ; PopA, PopB)*, where PopA and PopB represented
- 1233 Iron Age groups. The only IA groups found to be genetically differentiated from other groups
- according to the steppe component are the groups from United Kingdom and Normandy (for
- 1235 which this component is the most important) vs. all other IA groups. Interestingly, the f4 test
- 1236 f4(Mbuti, Russia_Samara_EBA_Yamnaya; IA Normandy, IA UK) is not significant, showing
- similar proportions for this component between the UK and Normandy groups (Table S6).
- **• Population modeling**

1239 We used *qpAdm* from the ADMIXTOOLS package (https://github.com/DReichLab) to 1240 estimate admixture proportions for all French IA individuals. To assess the percentage of the 1241 three major components WHG, Anatolia Neolithic and Russia_Samara_EBA_Yamnaya into 1242 each individual, we performed a *qpAdm* analysis with the reference panel B composed of : 1243 Ethiopia_4500BP_published.SG, Mbuti.DG, CHG. Russia EHG, 1244 Russia Ust Ishim HG published.DG, Czech_Vestonice16, Russia MA1 HG.SG, 1245 Israel_Natufian, Jordan_PPNB_published, Iberia_ElMiron). Results are presented in the 1246 Figure 3A and detailed in Figure S9 and in Table S7. In a second model, we performed 1247 *qpAdm* analyses to assess if the various Iron Age groups in France could be modelled with 1248 ancestry represented by Bronze Age groups using different combinations of BA groups from 1249 different regions of France, England, Germany, Italy and Spain with the reference panel A 1250 (Table S4 and S5).

1251 DATA AND SOFTWARE AVAILABILITY

Raw sequence data and alignments are available at the European Nucleotide Archive (ENA)
 under accession number ENA: PRJEB50940

1254 ADDITIONAL RESOURCES

- 1255 Our study has not generated or contributed to a new website/forum and it is not part of a 1256 clinical trial
- 1257
- 1258

1259 **References**

- 1260
- Allentoft, M.E., Sikora, M., Sjögren, K.G., Rasmussen, S., Rasmussen, M., Stenderup, J.,
 Damgaard, P.B., *et al.* (2015), "Population genomics of Bronze Age Eurasia", *Nature*,
 Vol. 522 No. 7555, pp. 167–172.
- Baudry, A.-C. (2021), Occupation Diachronique Dans La Vallée de La Suippe : Isles-SurSuippe, Marne, « Les Sohettes », « Val Des Bois », Rapport de Fouilles, Inrap Grand Est,
 Metz.
- Bonnabel, L. (2011), *Champfleury « A Mi Champs » (Marne), 2003*, Inrap, Châlons-enChampagne.
- Bouffier, S. and Garcia, D. (2012), "Greeks, Celts and Ligurians in South-East Gaul :
 Ethnicity and Archaeology", in Hermary, A. and Tsetskhladze, G.R. (Eds.), *From the Pillars of Hercules to the Footsteps of the Argonauts*, Peeters, Leven-Paris-Walpole, pp.
 21–36.
- Brunel, S., Andrew Bennett, E., Cardin, L., Garraud, D., Emam, H.B., Beylier, A., Boulestin,
 B., et al. (2020), "Ancient genomes from present-day France unveil 7,000 years of its
 demographic history", Proceedings of the National Academy of Sciences of the United
 States of America, National Academy of Sciences, 9 June.
- 1277 Cassidy, L.M., Maoldúin, R., Kador, T., Lynch, A., Jones, C., Woodman, P.C., Murphy, E.,
 1278 *et al.* (2020), "A dynastic elite in monumental Neolithic society", *Nature 2020*1279 582:7812, Nature Publishing Group, Vol. 582 No. 7812, pp. 384–388.
- 1280 Chanson, K., Delalande, A., Jahier, I., Texier, M., Ropars, A., Vauterin, C.-C., Cherel, A.-F.,
 1281 *et al.* (2011), "Les pratiques funéraires à l'Âge du fer en Basse-Normandie : premiers
 1282 éléments de réflexion", L'âge Du Fer En Basse-Normandie. Gestes Funéraires En
 1283 *Gaule Au Second-Âge Du Fer. Volumes I et II*, Presses universitaires de Franche-Comté,
 1284 pp. 51–83.
- 1285 Ciesielski, E., Girard, B. and Roure, R. (2014), "L'exposition d'armes et de têtes coupées au
 1286 Cailar. Pratiques rituelles des Celtes du Midi au iiie siècle avant notre ère",
- 1287 *Http://Journals.Openedition.Org/Archeopages*, Inrap, No. 39, pp. 6–15.
- 1288 Collis, J. (2003), *The Celts: Origins, Myths and Inventions*, Tempus.
- 1289 Culot, S. (2012), *Champfleury « RN 51 » (Marne), 2005*, Inrap, Châlons-en-Champagne.
- Damgaard, P.B., Margaryan, A., Schroeder, H., Orlando, L., Willerslev, E. and Allentoft,
 M.E. (2015), "Improving access to endogenous DNA in ancient bones and teeth",
- Scientific Reports 2015 5:1, Nature Publishing Group, Vol. 5 No. 1, pp. 1–12.
 Dedet, B. (2004), "Variabilité des pratiques funéraires protohistoriques dans le sud de la
- France : défunts incinérés, défunts non brûlés", *Gallia*, [Revue Gallia, CNRS Editions],
 Vol. 61, pp. 193–222.
- 1296 Dedet, B. (2015), "Pratiques funéraires et identité culturelle : Marseille et les indigènes du
 1297 Sud de la Gaule (IVe-IIe s. av. J.-C.)", *Contacts et Acculturations En Méditerranée*1298 Occidentale, pp. 267–283.
- 1299 Demoule, J.-P. (1999), Chronologie et Société Dans Les Nécropoles Celtiques de La Culture
 1300 Aisne-Marne, Du VIe Au IIIe Siècle Avant Notre Ère, RAP.
- 1301 Desmarchelier, V. (2020), *Buchères « PLA Secteur 1A » (Aube), 2014*, Inrap, Châlons-en1302 Champagne.
- Fernandes, D.M., Mittnik, A., Olalde, I., Lazaridis, I., Cheronet, O., Rohland, N., Mallick, S., *et al.* (2020), "The spread of steppe and Iranian-related ancestry in the islands of the
 western Mediterranean", *Nature Ecology and Evolution*, Nat Ecol Evol, Vol. 4 No. 3,
 pp. 334–345.
- Fischer, C.-E., Lefort, A., Pemonge, M.-H., Couture-Veschambre, C., Rottier, S. and
 Deguilloux, M.-F. (2018), "The multiple maternal legacy of the Late Iron Age group of

- 1309 Urville-Nacqueville (France, Normandy) documents a long-standing genetic contact 1310 zone in northwestern France", edited by Calafell, F.PLOS ONE, Vol. 13 No. 12, p. 1311 e0207459. 1312 Fischer, C.-E., Pemonge, M.-H., Santos, F., Houzelot, H., Couture-Veschambre, C., Lefort, A., Rottier, S., et al. (2019), "Multi-scale archaeogenetic study of two French Iron Age 1313 communities: From internal social- to broad-scale population dynamics", Journal of 1314 1315 Archaeological Science: Reports, Vol. 27, p. 101942. Fitzpatrick, A.P. (2011), "Les pratiques funéraires de l'Age du Fer tardif dans le Sud de 1316 1317 l'Angleterre", in Barral, P., Dedet, B., Delrieu, F., Giraud, P., Le Goff, I. and Marion, S. 1318 (Eds.), Gestes Funéraires En Gaule Au Second Age Du Fer. Actes Du XXXIII Colloque International de l'AFEAF. 20-24 Mai 2009, Caen, Presses universitaires de Franche-1319 1320 Comté, Besancon, pp. 15-30. 1321 Fu, Q., Posth, C., Hajdinjak, M., Petr, M., Mallick, S., Fernandes, D., Furtwängler, A., et al. (2016a), "The genetic history of Ice Age Europe", Nature, Nature, Vol. 534 No. 7606, 1322 1323 pp. 200–205. 1324 Fu, Q., Posth, C., Hajdinjak, M., Petr, M., Mallick, S., Fernandes, D., Furtwängler, A., et al. 1325 (2016b), "The genetic history of Ice Age Europe", Nature, NIH Public Access, Vol. 534 1326 No. 7606, p. 200. Furtwängler, A., Rohrlach, A.B., Lamnidis, T.C., Papac, L., Neumann, G.U., Siebke, I., 1327 1328 Reiter, E., et al. (2020), "Ancient genomes reveal social and genetic structure of Late 1329 Neolithic Switzerland", Nature Communications 2020 11:1, Nature Publishing Group, 1330 Vol. 11 No. 1, pp. 1–11. 1331 Gailledrat, E. (1997), Les Ibères de l'Èbre à l'Hérault (VIe-IVe s. Avant J.- C.), Monographi., 1332 Monographies d'Archéologie Méditerranéenne, 1, Lattes, available at: 1333 https://halshs.archives-ouvertes.fr/halshs-00010104 (accessed 1 November 2021). 1334 Gamba, C., Jones, E.R., Teasdale, M.D., McLaughlin, R.L., Gonzalez-Fortes, G., Mattiangeli, V., Domboróczki, L., et al. (2014), "Genome flux and stasis in a five 1335 1336 millennium transect of European prehistory", Nature Communications 2014 5:1, Nature 1337 Publishing Group, Vol. 5 No. 1, pp. 1–9. 1338 Garcia, D. (2006), "Les Celtes de Gaule méditerranéenne. Définition et caractérisation", in 1339 Szabó, M. (Ed.), Celtes et Gaulois. L'Archéologie Face à l'Histoire. Les Civilisés et Les 1340 Barbares Du Ve Au IIe Siècle Avant J.-C., Actes de La Table-Ronde de Budapest, 17-18 1341 Juin 2005, Bibracte, pp. 63–76. 1342 Garcia, D. and Le Bras, H. (2017), Archéologie Des Migrations, edited by Garcia, D. and Le 1343 Bras, H., La Découverte, Paris. Ghezal, S., Ciesielski, E., Girard, B., Creuzieux, A., Gosnell, P., Mathe, C., Vieillescazes, C., 1344 1345 et al. (2019), "Embalmed heads of the Celtic Iron Age in the south of France", Journal 1346 of Archaeological Science, Academic Press, Vol. 101, pp. 181–188. 1347 Guilaine, J. and Garcia, D. (2018), La Protohistoire de La France, edited by Guilaine, J. and 1348 Garcia, D., Hermann., Collection Histoire et Archéologie, Paris. 1349 Haak, W., Lazaridis, I., Patterson, N., Rohland, N., Mallick, S., Llamas, B., Brandt, G., et al. 1350 (2015), "Massive migration from the steppe was a source for Indo-European languages 1351 in Europe", Nature, Vol. 522 No. 7555, pp. 207-211.
- Isoardi, D. (2008), "Tentative d'estimation démographique des populations de l'Âge du Fer
 du versant occidental et méridional des Al pes. De l'archéologie à la démographie", Le *Peuplement de l'arc Alpin*, pp. 225–242.
- Jeunesse, C. (1988), "Wettolsheim-Ricoh, du néolithique à l'ère post-industrielle. Un
 sauvetage archéologique dans la plaine d'Alsace", Roser, Horbourg-Wihr.
- 1357 Joffroy, R. (1954), "La tombe de Vix (Côte-d'Or)", Monuments et Mémoires de La
- 1358 Fondation Eugène Piot, Persée Portail des revues scientifiques en SHS, Vol. 48 No. 1,

- 1359 рр. 1–68.
- Kircher, M., Sawyer, S. and Meyer, M. (2012), "Double indexing overcomes inaccuracies in multiplex sequencing on the Illumina platform", *Nucleic Acids Research*, Nucleic Acids Res, Vol. 40 No. 1, available at:https://doi.org/10.1093/NAR/GKR771.
- Knipper, C., Meyer, C., Jacobi, F., Roth, C., Fecher, M., Stephan, E., Schatz, K., *et al.*(2014), "Social differentiation and land use at an Early Iron Age 'princely seat':
 bioarchaeological investigations at the Glauberg (Germany)", *Journal of Archaeological Science*, Academic Press, Vol. 41, pp. 818–835.
- Lacan, M., Keyser, C., Ricaut, F.X., Brucato, N., Duranthon, F., Guilaine, J., Crubézy, E., et *al.* (2011), "Ancient DNA reveals male diffusion through the Neolithic Mediterranean
 route", Proceedings of the National Academy of Sciences of the United States of
 America, National Academy of Sciences, Vol. 108 No. 24, pp. 9788–9791.
- Landolt, M., Millet, E. and Roth-Zenner, M. (2010), "Pratiques funéraires en Alsace du Ve au
 Ier siècle avant J.-C.", in Barral, P. (Ed.), *Gestes Funéraires En Gaule Au Second Age Du Fer. Actes Du XXXIII Colloque International de l'AFEAF. 20-24 Mai 2009, Caen*,
 Annales littéraires, pp. 207–230.
- Landolt, M., Roth-Zenner, M. and Fleischer, F. (2012), "La chronologie de la céramique de la fin du Hallstatt D3 à La Tène B2 dans le sud de la plaine du Rhin supérieur : l'apport des nouveaux sites alsaciens d'Entzheim (Bas-Rhin), de Geispolsheim (Bas-Rhin) et de Colmar (Haut-Rhin)", in Schonfelder, M. and Sievers, S. (Eds.), *L'âge Du Fer Entre La Champagne et La Vallée Du Rhin, Actes Du Colloque International de l'AFEAF,*Aschaffenburg (D), 13-16 Mai 2010, RGZM, pp. 471–502.
- Lefort, A., Baron, A., Blondel, F., Méniel, P. and Rottier, S. (2015), "Artisanat, commerce et nécropole. Un port de La Tène D1 à Urville-Nacqueville", in Olmer, F. and Roure, R. (Eds.), *Les Gaulois Au Fil de l'eau. Actes Du 37è Colloque International de l'AFEAF*, Ausonius, Bordeaux, pp. 481–514.
- Lejars, T. and Gruel, K. (2015), "Peuples, civitates, pagi", *L'Europe Celtique à l'Age Du Fer*(*VIIIe-Ier Siècles*), Presses Universitaires de France, pp. 349–357.
- Li, H. and Durbin, R. (2010), "Fast and accurate long-read alignment with Burrows-Wheeler transform", *Bioinformatics (Oxford, England)*, Bioinformatics, Vol. 26 No. 5, pp. 589– 595.
- Liu, Y., Mao, X., Krause, J. and Fu, Q. (2021), "Insights into human history from the first decade of ancient human genomics", *Science*, Vol. 373 No. 6562, pp. 1479–1484.
- Marcigny, C., Bourgeois, J. and Talon, M. (2017), "Rythmes et contours de la géographie
 culturelle sur le littoral de la Manche entre le IIIe et le début du Ier millénaire", *Movement, Exchange and Identity in Europe in the 2nd and 1st Millennia BC. Beyond Frontiers*, No. October 2019, pp. 63–78.
- Martiniano, R., Caffell, A., Holst, M., Hunter-Mann, K., Montgomery, J., Müldner, G.,
 McLaughlin, R.L., *et al.* (2016), "Genomic signals of migration and continuity in Britain
 before the Anglo-Saxons", *Nature Communications*, Nature Publishing Group, Vol. 7
 No. 1, pp. 1–8.
- Mathieson, I., Alpaslan-Roodenberg, S., Posth, C., Szécsényi-Nagy, A., Rohland, N.,
 Mallick, S., Olalde, I., *et al.* (2018), "The genomic history of southeastern Europe", *Nature 2018 555:7695*, Nature Publishing Group, Vol. 555 No. 7695, pp. 197–203.
- Mathieson, I., Lazaridis, I., Rohland, N., Mallick, S., Patterson, N., Roodenberg, S.A.,
 Harney, E., *et al.* (2015), "Genome-wide patterns of selection in 230 ancient Eurasians", *Nature 2015 528:7583*, Nature Publishing Group, Vol. 528 No. 7583, pp. 499–503.
- 1406 Meyer, M. and Kircher, M. (2010), "Illumina sequencing library preparation for highly
- multiplexed target capture and sequencing", *Cold Spring Harbor Protocols*, Cold Spring
 Harb Protoc, Vol. 2010 No. 6, available at:https://doi.org/10.1101/PDB.PROT5448.

- 1409 Milcent, P.-Y. (2006), "Premier âge du Fer médio-atlantique et genèse multipolaire des
 1410 cultures matérielles laténiennes", *Pré-Actes, Colloque Du Collège de France*, Vol. 5608,
 1411 pp. 1–25.
- 1412 Milcent, P.-Y. (2009), "Le passage de l'âge du Bronze à l'âge du Fer en Gaule au miroir des
 1413 élites sociale: une crise au VIIIe s. av JC", *De l'âge Du Bronze à l'âge Du Fer En*
- 1414 France et En Europe Occidentale (Xe-VIIe s. Av JC). La Moyenne Vallée Du Rhône Aux
 1415 Âges Du Fer. Actes Du XXXe Colloque International de l'AFEAF, Co-Organisé Par
 1416 l'APRAB (Saint-Romain-En-Gal, 26-28 Mai 2006), Revue Archéologique de l'Est, pp.
 1417 453–476.
- Mittnik, A., Massy, K., Knipper, C., Wittenborn, F., Friedrich, R., Pfrengle, S., Burri, M., *et al.* (2019), "Kinship-based social inequality in Bronze Age Europe", *Science*, Vol. 366
 No. 6466, pp. 731–734.
- Monroy Kuhn, J.M., Jakobsson, M. and Günther, T. (2018), "Estimating genetic kin
 relationships in prehistoric populations", edited by Calafell, F.*PLOS ONE*, Vol. 13 No.
 4, p. e0195491.
- Moorjani, P., Sankararaman, S., Fu, Q., Przeworski, M., Patterson, N. and Reich, D. (2016),
 "A genetic method for dating ancient genomes provides a direct estimate of human
 generation interval in the last 45,000 years", *Proceedings of the National Academy of Sciences of the United States of America*, National Academy of Sciences, Vol. 113 No.
 20, pp. 5652–5657.
- 1429 Mordant, C. and Rottier, S. (2004), Gurgy "Les Noisats" (Yonne), Dijon.
- Mullen, A. (2013), Southern Gaul and the Mediterranean. Multilingualism and Multiple
 Identities in the Iron Age and Roman Periods, Cambridge University Press, Cambridge.
- 1432 Novembre, J., Johnson, T., Bryc, K., Kutalik, Z., Boyko, A.R., Auton, A., Indap, A., *et al.*1433 (2008), "Genes mirror geography within Europe", *Nature*, NIH Public Access, Vol. 456
 1434 No. 7218, p. 98.
- Núñez, C., Baeta, M., Cardoso, S., Palencia-Madrid, L., García-Romero, N., Llanos, A. and
 De Pancorbo Pancorbo, M.M. (2016), "Mitochondrial DNA Reveals the Trace of the
 Ancient Settlers of a Violently Devastated Late Bronze and Iron Ages Village", *PloS One*, PLoS One, Vol. 11 No. 5, available
- 1439 at:https://doi.org/10.1371/JOURNAL.PONE.0155342.
- O'Sullivan, N., Posth, C., Coia, V., Schuenemann, V.J., Douglas Price, T., Wahl, J., Pinhasi,
 R., *et al.* (2018), "Ancient genome-wide analyses infer kinship structure in an Early
 Medieval Alemannic graveyard", *Science Advances*, American Association for the
- Advancement of Science, Vol. 4 No. 9, available
 at:https://doi.org/10.1126/SCIADV.AAO1262/SUPPL_FILE/AAO1262_SM.PDF.
- Olalde, I., Brace, S., Allentoft, M.E., Armit, I., Kristiansen, K., Booth, T., Rohland, N., *et al.*(2018), "The Beaker phenomenon and the genomic transformation of northwest
 Europe", *Nature*, Vol. 555 No. 7695, pp. 190–196.
- Olalde, I., Mallick, S., Patterson, N., Rohland, N., Villalba-Mouco, V., Silva, M., Dulias, K., *et al.* (2019), "The genomic history of the Iberian Peninsula over the past 8000 years", *Science*, Vol. 363 No. 6432, pp. 1230 LP 1234.
- Paresys, C. (2014), Buchères, Moussey, Saint-Léger-Près-Troyes « PLA D37-38 » (Aube),
 Inrap, Châlons-en-Champagne.
- Peltzer, A., Jäger, G., Herbig, A., Seitz, A., Kniep, C., Krause, J. and Nieselt, K. (2016),
 "EAGER: efficient ancient genome reconstruction", *Genome Biology*, BioMed Central,
 Vol. 17 No. 1, p. 60.
- Py, M. (1993), Les Gaulois Du Midi, de La Fin de l'Âge Du Bronze à La Conquête Romaine,
 Hachette, Paris.
- 1458 Ralf, A., Montiel González, D., Zhong, K. and Kayser, M. (2018), "Yleaf: Software for

1459	Human Y-Chromosomal Haplogroup Inference from Next-Generation Sequencing
1460	Data", Molecular Biology and Evolution, Mol Biol Evol, Vol. 35 No. 5, pp. 1291–1294.
1461	Ringbauer, H., Novembre, J. and Steinrücken, M. (2021), "Parental relatedness through time
1462	revealed by runs of homozygosity in ancient DNA", Nature Communications 2021 12:1,
1463	Nature Publishing Group, Vol. 12 No. 1, pp. 1–11.
1464	Rivollat, M., Jeong, C., Schiffels, S., Küçükkalıpçı, İ., Pemonge, M.H., Rohrlach, A.B., Alt,
1465	K.W., et al. (2020), "Ancient genome-wide DNA from France highlights the complexity
1466	of interactions between Mesolithic hunter-gatherers and Neolithic farmers", Science
1467	Advances, American Association for the Advancement of Science, Vol. 6 No. 22, p.
1468	eaaz5344.
1469	Rohland, N., Harney, E., Mallick, S., Nordenfelt, S. and Reich, D. (2015), "Partial uracil-
1470	DNA-glycosylase treatment for screening of ancient DNA", Philosophical Transactions
1471	of the Royal Society of London. Series B, Biological Sciences, Philos Trans R Soc Lond
1472	B Biol Sci, Vol. 370 No. 1660, available at:https://doi.org/10.1098/RSTB.2013.0624.
1473	Rottier, S. and Piette, J. (2001), Barbuise "Les Greves de Frecul" (Aube), Nogent-sur-Seine.
1474	Roure, R. (2020), "Using ritual practices to define the Celtic world and its limits: a matter of
1475	identity", edited by Pierrevelcin, G., Kysela, J. and Fichtl, S. Unité et Diversité Du
1476	Monde Celtique – Unity and Diversity in the Celtic World, Actes Du 42e Colloque
1477	International de l'AFEAF, Prague, 10-13 Mai 2018, AFEAF, Vol. Collection No. 42,
1478	pp. 89–96.
1479	Saag, L., Laneman, M., Varul, L., Malve, M., Valk, H., Razzak, M.A., Shirobokov, I.G., et
1480	al. (2019), "The Arrival of Siberian Ancestry Connecting the Eastern Baltic to Uralic
1481	Speakers further East", Current Biology, Cell Press, Vol. 29 No. 10, pp. 1701-1711.e16.
1482	Schiffels, S., Haak, W., Paajanen, P., Llamas, B., Popescu, E., Loe, L., Clarke, R., et al.
1483	(2016), "Iron Age and Anglo-Saxon genomes from East England reveal British
1484	migration history", <i>Nature Communications</i> , Nature Publishing Group, Vol. 7 No. 1, pp.
1485	
1486	Seguin-Orlando, A., Donat, R., Der Sarkissian, C., Southon, J., Thèves, C., Manen, C.,
1487	Tchérémissinoff, Y., <i>et al.</i> (2021), "Heterogeneous Hunter-Gatherer and Steppe-Related
1488	Ancestries in Late Neolithic and Bell Beaker Genomes from Present-Day France",
1489	Current Biology, Cell Press, Vol. 31 No. 5, pp. 10/2-1083.e10.
1490	Serventi, P., Panicucci, C., Bodega, R., De Fanti, S., Sarno, S., Fondevila Alvarez, M.,
1491	Brisignelli, F., <i>et al.</i> (2018), "Iron Age Italic population genetics: the Piceni from
1492	Novilara (8th-/th century BC) ² , Annals of Human Biology, Ann Hum Biol, Vol. 45 No.
1493	I, pp. 54–45. Skoolund D. Storå I. Cöthorström A. and Iskobsson M. (2012). "A source sou
1494	Skogiund, P., Stora, J., Gotnerstrom, A. and Jakobsson, M. (2013), Accurate sex
1495	Auchago logical Science, Vol. 40 No. 12, pp. 4477, 4482
1490	Archaeological Science, Vol. 40 No. 12, pp. 4477–4482.
1497	Du Far (VIIIa Jan Sidelas). Pressos Universitaires de France
1490	Wornes G.P. Polker, P. Ponobekker, I. Contlemen, P. Liew, W.H.A. Lumley, Meechler
1499	M at al. (2010) "galots: Various P. Programming Tools for Plotting Data version 3.1.1
1500	from CRAN" Https://CRAN R Project Org/Package-gplots_available at:
1501	hom CRAIN, https://CRAIN.R-Flojeci.Org/Fuckage-gpiols, available al.
1502	Meissensteiner H. Pacher D. Kloss-Brandstätter A. Forar I. Spacht C. Bandalt U.I.
1503	Kronenberg F et al (2016) "HanloGren 2. mitochondrial hanlogroup classification in
1505	the era of high-throughput sequencing" Nucleic Acids Research Nucleic Acids Res
1505	Vol 44 No W1 nn W58–W63
1500	тол. тт но. тт 1, pp. тоо-тоо.









Highlights

- 49 low coverage genomes from 27 sites from France, dated to ≈ 1200-80 years cal BCE
- No major migration or population turnover between Bronze and Iron Age in France
- A gradual North/South genetic structuration of IA populations