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Distinct ancestries for similar funerary practices? A GIS analysis comparing funerary, osteological and aDNA data from the Middle Neolithic necropolis Gurgy "Les Noisats" (Yonne, France)

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ABSTRACT

The French Paris Basin is well known as a complex cultural area of the Early/Middle Neolithic, particularly with respect to funerary practices. Gurgy "Les Noisats", which is an important necropolis in the southern Paris basin, is a burial site (N = 128) associated with the first Neolithic groups established in that area. The understanding of the necropolis composition and organization is complicated given the substantial homogeneity of the site's spatial organization in relation to a great diversity of characterized funerary traits. The unprecedented quantity of genetic (mitochondrial DNA), osteological (sex, age), and archaeological (funerary) data obtained for the Gurgy necropolis facilitates the search for potential correlations between cultural and biological (i.e. genetic and osteological) diversity at the site level. Despite the application of the powerful geographic information system, no correlation could be detected (i) between individual maternal lineages and specific bioarchaeological profiles (ii) or between maternal lineages and spatially identified bio-archaeological clusters. Therefore, analyses were performed to test for a correlation between the maternal ancestries of the individuals (i.e., hunter-gatherer/Central European farmer and Southern European farmer ancestries) and specific funerary traits. Again, the homogeneity of the funerary treatment of all of the individuals regardless of their potential maternal ancestries is striking. Taken together, our results regarding the way in which the Gurgy necropolis functioned provide strong evidence for the acculturation of all maternal ancestries groups, at least in terms of funerary practice. In addition, the demonstration of a recurrent association of adult men and immature individuals suggests a patrilocal system, which could be consistent with the detected acculturation of women who present a hunter-gatherer ancestry.

1. Introduction

The Middle Neolithic period in France starts around 4900 cal. BC and ends around 3600 cal. BC (Allard et al., 2006; Sénépart et al., 2014; Voruz et al., 1995) and is characterized by an important multiplication of cultures compared to the previous culturally homogeneous LBK culture (Whittle and Cummings, 2007). In the Paris Basin, this cultural wealth can be observed particularly well in the funerary world (Chambon and Leclerc, 2003; Chambon et al., 2013), with contemporaneous sites including either single burials which can be grouped or are isolated next to domestic structures, or collective graves, the first funerary monuments and necropolises of various sizes. The beginning of the Middle Neolithic, the Villeneuve-Saint-Germain culture (around 4900 cal. BC), appears as a mix of cultural influences from Danubian and Mediterranean Neolithic spheres with some Mesolithic components (Augereau, 2004; Lichardus-Itten, 1986; van Berg, 1990). Subsequently, the main culture of the Middle Neolithic in the Paris Basin is the Cerny

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culture (Fig. 1), spanning approximately from 4700 to 4000 cal. BC, and described in detail by Constantin et al. (1997). The Cerny culture is characterized by three types of funerary sites. The long and linear monuments known as the Passy Structures (Duhamel and Presteau, 1997; SI_1) constitute the most impressive type encountered amongst these funerary sites. They generally contain only one or a small number of single burials, and archaeo-anthropological studies have presented persuasive arguments in favor of funerary selection of the individuals buried in these structures (Thomas et al., 2011). The second type of funerary sites corresponds to the Malesherbes tombs which are also common in the region and consist of simple pits covered with large stone slabs (Verjux et al., 1998; SI_1). Numerous small necropolises are the third Cerny funerary type (Chambon and Leclerc, 2003).

Our study focuses on the Middle Neolithic necropolis of Gurgy "Les Noisats", which was excavated from 2004 to 2007 and is located in the department of Yonne in the southern Paris Basin (Fig. 1A–B). The cultural attribution of the necropolis is still in question since the dates for the site clearly overlap with the Cerny culture but no characteristic funerary practice from this culture could be identified. Within a Middle Neolithic context, the Gurgy site is particularly interesting because (i) it is associated with the first farmer groups established in the southern Paris Basin and can therefore provide important information concerning the processes involved in the regional Neolithization and (ii) it represents one of the most important, expansive necropolises excavated in the Paris Basin region (together with the necropolis of Monéteau; Augereau and Chambon, 2011), as it is a grouping of 134 pits with 128 buried individuals. The exceptional size of the Gurgy necropolis is linked to its long period of use, which ranges between 5000 and 4000 cal. BC, with the most intensive occupation level ranging between 4900 and 4500 cal. BC (Rottier et al., 2005). Based on the special character of the Gurgy necropolis, a multidisciplinary study was developed to better understand the necropolis organization and to clarify its functioning. The study initially focused on archaeological and osteological data and enabled us to note an interesting diversity of funerary practices e.g. body position, body orientation and grave goods (Fig. 1C–G) despite a highly homogeneous spatial organization (Le Roy, 2015; Rottier et al., 2005).

In the Neolithic context, the integration of archaeological, osteological and genetic data has been primarily used to investigate potential kinship relationships between individuals deposited in multiple or collective burials (Haak et al., 2008; Keller et al., 2015; Lacan et al., 2011a; Lee et al., 2012). For example, the

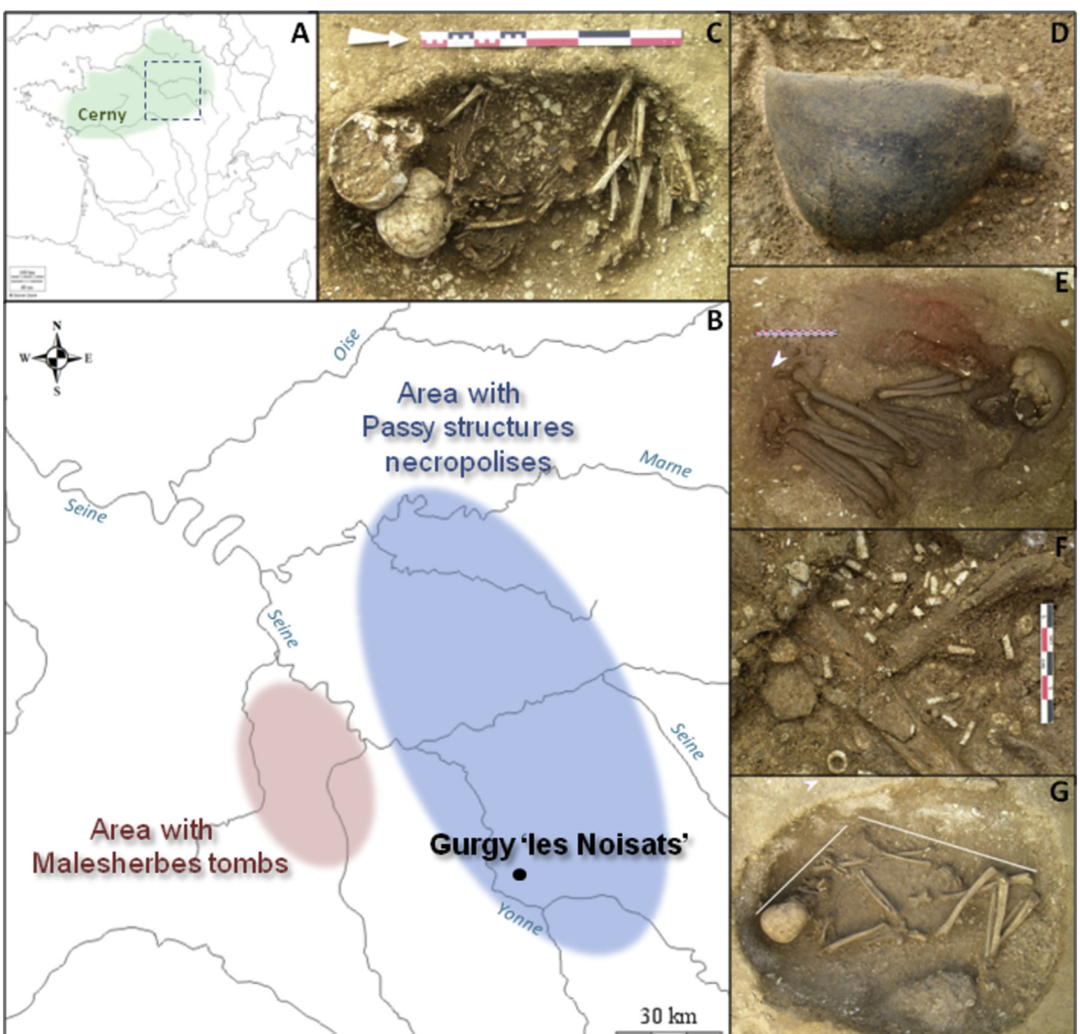


Fig. 1. Paris Basin localization in France (**A**), the Gurgy necropolis location and the schematic repartition of distinct funerary practices encountered in the Paris Basin (after Thomas et al., 2011) (**B**). Illustration of the funerary variability encountered in the Gurgy necropolis: double burial st_211 (**C**), ceramic cup discovered in burial st_249 (**D**), ochre in burial st_298 (**E**), a large number of beads in burial st_294 (**F**) and evidence of a wall effect in burial st_249 (**G**).

multidisciplinary analysis of the Corded Ware Culture site of Eulau (Germany; Haak et al., 2008) provided the oldest molecular genetic evidence of a nuclear family deposited in a multiple burial. Paleogenetic data obtained a few years later for the Late Neolithic collective burial of Les Treilles (France; Lacan et al., 2011a) provided a persuasive argument regarding the patrilocality of a farmer group and highlighted the importance of funerary practices through the identification of the grouping of paternally-linked individuals. To our knowledge, only one multidisciplinary approach including aDNA data addressed the correlation between funerary diversity and individual identities and origins in the Neolithic. The study on the Neolithic site of Vedrovice (Czech Republic) used the combination of archaeological arguments with aDNA, stable isotopes and dental micro-wear evidence to provide unprecedented insight into the life history of the LBK farmers including diet, migrations, ancestry, personal identity, social position and life experience (Zvelebil and Pettitt, 2013). However, only sixteen mitochondrial profiles could be obtained for the Vedrovice burials (Bramanti, 2008), and the important characterized genetic diversity did not facilitate conclusions regarding the organization of the necropolis.

Recently, a paleogenetic study conducted on Gurgy obtained the largest mitochondrial (mtDNA) gene pool from a single archaeological site for the Early/Middle Neolithic period, with 39 HVS-I (hyper-variable sequence I) mitochondrial sequences and haplogroups for 55 individuals (Rivollat et al., 2015). The phylogeographic analyses performed on the Gurgy gene pool suggested a mixture of maternal lineages associated with farmers linked to the Danubian and the Mediterranean Neolithic migration routes. The agreement of these genetic arguments with archaeological data indicating material exchange between northern and southern French Neolithic groups during this period may represent the most ancient evidence of admixture between farmers from the Danubian and Mediterranean spheres during the European Neolithization. A hunter-gatherer (descendants') participation in the Gurgy gene pool was also put forward as an explanation for the identified lower genetic differentiation between ancient hunter-gatherers and the Gurgy group, the lowest ever observed compared with other Early Neolithic populations (Rivollat et al., 2015).

The size and importance of the Gurgy necropolis within the Paris Basin during the Middle Neolithic together with the large mitochondrial gene pool obtained for this farmer group allowed us to develop a general approach that aims to test for statistical links between archaeological, osteological and genetic data. The use of a geographic information system (GIS) is particularly suited for this type of global study because it allows rapid, effective comparisons of a large variety of data. The relevance of the GIS approach to prehistoric sites is well known, and GIS is generally applied to the analysis of artifact distribution in discussions on the organization of settlements and to identify potential specialized areas (Allen et al., 1990). In France, the first application of GIS analysis to a funerary context was performed by Guillot and Guy (1996) for the collective grave of Saint-Sauveur (Late Neolithic; France), who clearly noted the time efficiency and the completeness of such an approach. To date, the rare GIS studies focusing at the scale of a necropolis (including Gurgy) have only considered osteological and archaeological data (Lacombe et al., 2014; Le Roy, 2015; Le Roy et al., 2014). Therefore our analysis is innovative in the way it seeks potential correlations between funerary traits (e.g., pit shape, individual positions, grave goods, and chronological data), osteological data (e.g., sex, age-at-death) and maternal lineages (mtDNA). The approach enables us to test for evidence of maternal kinship or maternal ancestry implication in the necropolis organization or specific funerary practices by looking for potential clusters inside the necropolis, based on different types of data.

2. Materials and methods

2.1. Osteological data

The osteological data considered in the GIS analysis includes sex assessment and age-at-death. The primary sexual diagnosis was performed using two methods: probabilistic sexual diagnosis (Murail et al., 2005) and a morphological method (Bruzek, 2002). Due to the poor preservation of certain skeletal remains, a secondary sexual diagnosis (Murail et al., 1999) was conducted whenever possible. Sex assessment of the youngest individuals was not performed due to the non-reliability of the methods (Bruzek and Murail, 2006). Age assessment of immature individuals was performed according to maturational stages of deciduous or/and permanent teeth (Moorrees et al., 1963a, 1963b). In several cases, bone maturation was also used because of bone fragmentation (Scheuer and Black, 2000). Individuals with immature state of osseous or dental maturation are considered as immature. For adult individuals, the method of age at death estimation provides reliable results (Schmitt, 2005).

Among the 128 individuals uncovered in the Gurgy necropolis, we identified 57 immature skeletons with mixed age ranges from 0 to 19 years old, which indicates that there was no strict exclusion of a specific age class. Among the adults ($N = 53$) and individuals aged 15 years and older ($N = 18$), sex was assessed for 34 males and 20 females. The sex of a total of 74 individuals (including immature individuals) remains unidentified (Table 1; Le Roy, 2015).

2.2. Funerary data

Data concerning funerary practices of the Gurgy group include burial type, pit type, deposit position, grave goods and radiocarbon dating. Most of the burials were single ($N = 114$), but a small number of possibly double or voluntarily associated burials occurred ($N = 6$). The pit inhumations assumed different forms and exhibited two types: simple ($N = 110$) and complex ($N = 12$). The complex pits were represented by either fitting walls (wattling) or a lateral over digging (alcove; SI_1). The majority of the corpses were buried in perishable coffins ($N = 86$), whereas a small number of other corpses were directly deposited into the pit. However, all archaeo-anthropological evidence supports a decay in a void for all of the individuals (Le Roy, 2015). The deposits were primary, as defined by H. Duday (2009). Immature and adult individuals exhibited approximately the same burial position, lying on the left side with limbs flexed at an angle higher than 90° (hyperflexed) or between 20 and 90° (flexed), but a number of atypical cases also occurred, for example, two female individuals were in a ventral position (Table 1). However, all encountered body positions fit into the known Cerny diversity.

Grave goods were found associated with 82 buried individuals, whereas other graves were empty of such goods ($N = 48$). The most frequently occurring goods were ochre, fauna remains and flint stones. Rare goods were also found, such as a ceramic cup, a green stone pendant and a large number of beads ($N = 10$).

Radiocarbon dating was performed on 39 individuals chosen from across the necropolis and provided 30 reliable dates that ranged between 5100 and 3980 cal. BC. We provide the dates for the genotyped individuals ($N = 13$), calibrated according to the INTCAL 2004 curve (SI_2).

2.3. Paleogenetic data

We added the mitochondrial data obtained for 55 individuals from the necropolis and published in a previous paper (Rivollat et al., 2015) to the GIS analysis. As a reminder, we were able to

Table 1
Summary of the primary data concerning osteological (age-at-death and sex assessment) data and individual deposit positions from Gurgy "Les Noisats".

	Number	Body position			Upper limbs			Lower limbs		
		Left side	Dorsal	Other	Flexed	Hyperflexed	Other	Flexed	Hyperflexed	Other
Male	34	19	14	1	2	17	15	10	23	1
Female	20	11	5	4	3	6	11	9	10	1
Undefined	74	50	9	15	9	24	41	29	26	19
Adults	53	34	16	3	5	24	24	17	32	4
Individuals aged >15 y	18	9	4	5	0	5	13	6	9	3
Immature individuals	57	37	8	12	9	13	35	25	18	14
Total	128	80	28	20	14	42	72	48	59	21

characterize 55 mitochondrial haplogroups (using SNPs typing) and among these, 39 individuals provided HVS-I sequences (Table 2). The dataset is accessible at the Genbank database (accession numbers KP863031-KP863069). In the first parts of the GIS analyses, the funerary and osteological data were compared to the individuals' mitochondrial haplogroups and haplotypes to establish the presence of specific links between funerary traits and maternal lineage, i.e., more or less close maternal relatives.

In the second part of our analyses, the funerary and osteological data were compared with the potential maternal ancestry of the individuals (in term of descendants of ancient groups) to detect ancestry-specific funerary practices. In fact, the large existing mtDNA dataset on ancient populations facilitated a clear association of specific mitochondrial haplogroups with either hunter-gatherer or farmer maternal ancestry, as proposed by Brandt and colleagues in 2013. The associations of specific mtDNA haplogroups with European hunter-gatherers, farmers from central Europe or farmers from southern Europe (SI_3) could be confirmed through the principal component or multidimensional scaling analyses conducted by Rivollat et al. (2015). Therefore, we proposed three distinct ancestry groups: (i) a group with hunter-gatherer (HG) ancestry characterized by haplogroups U4 and U5; (ii) a group that derives from central European farmers (Central_F) characterized by HV, V, T, J, N1a; and (iii) a group that descends from southern European farmers (South_F), who present haplogroups H, X, and other U. Individuals who present the haplogroup K could not be linked with any specific ancestry and were classed in the "Undetermined" group.

Based on this classification scheme, we grouped 8 individuals in the HG ancestry group (14.5%), 13 individuals in the Central_F ancestry group (23.6%) and 23 individuals in the South_F group (41.8%). The frequencies of mitochondrial lineage U4 and U5 (1.8% and 12.7%, respectively) associated with the proposed HG ancestry are significantly higher in the Gurgy group than in previously studied groups from the Early and Middle Neolithic (Brandt et al., 2013).

We used Arlequin software (version 3.5.1.2; Excoffier et al., 2005) to calculate the genetic diversity of the entire group and of specific groups based on archaeological data or maternal ancestry (SI_4). An exact test of differentiation based on haplotype frequencies (Raymond and Rousset, 1995) was used to check for any group's genetic distinction.

2.4. GIS

A spatial analysis was performed using ArcGIS software. This approach facilitated the rapid performance of a high number of cartographic and statistic analyses and the subsequent simultaneous testing of numerous hypotheses. Potential statistically significant spatial associations between each specific and combined funerary/osteological data and each maternal haplogroup/haplotype/ancestry group were checked.

To analyze the dispersion of the burial pits inside the necropolis of Gurgy "Les Noisats", a centroid (or geographical center of the feature) that represents each individual average x- and y-coordinate was calculated. The global characteristics of the site were defined according to the mean center and the standard deviational ellipse and used to compare the distributions of selected data. Then, the standard deviation ellipse of each funerary, osteological and genetic data was measured. The orientation and size of the ellipse indicated where the studied data were distributed, at one standard deviation. Next, spatial distance analysis was used to highlight clusters within the entire necropolis area using CrimeStat software. The nearest neighbor index was measured to identify the difference of the mean distance from the expected distance compared with the mean distance for a hypothetical random distribution. This index is calculated using the ratio between the two mean distances. According to the results, the distribution can be clustered, random,

Table 2
Details of the mitochondrial haplogroups (identified through SNPs genotyping) and/or HVS-I haplotypes and their potential ancestry (see 2.3. for ancestry attribution) characterized on Gurgy individuals (for details, see Rivollat et al., 2015).

	Number of haplogroups	Number of HVS-I haplotypes	Potential ancestry
H	**20**	**13**	**South_F**
H1	10	7	
H3	4	3	
U	**9**	**6**	**South_F** **HG**
U4	1	0	HG
U5	7	5	HG
K	**11**	**7**	**Undetermined**
T	**2**	**1**	**Central_F**
J	**6**	**5**	**Central_F**
X	**2**	**2**	**South_F**
N1a	**3**	**3**	**Central_F**
V	**2**	**2**	**Central_F**
Total	**55**	**39**	

Macro-haplogroups are represented in bold.

or dispersed (Zaninetti, 2005). In order to identify these aggregates, we used the K Ripley's and Hotspot Analysis using Nearest Neighbor Hierarchical spatial clustering (Zaninetti, 2005). These statistics allowed us to only consider the geographical coordinates of chosen data and were used only on osteological and archaeological data. Several clusters have been identified previously (Le Roy et al., 2014). Among these, only three spatial clusters (adult, male and immature individual clusters) included individuals sharing a common funerary trait, e.g., same position of the body or same type of pit. All other identified clusters always exhibited only one shared trait, e.g. the same position of the upper limb, the same type of pit … (Le Roy, 2015). In the present study, we examined correlations between the detected osteological/archaeological clusters (SI_5) and the maternal haplogroups/haplotypes/ancestry groups (SI_3).

Following Zvelebil and Pettitt (2013) we tested the combination of archaeological data with aDNA through this innovative GIS approach.

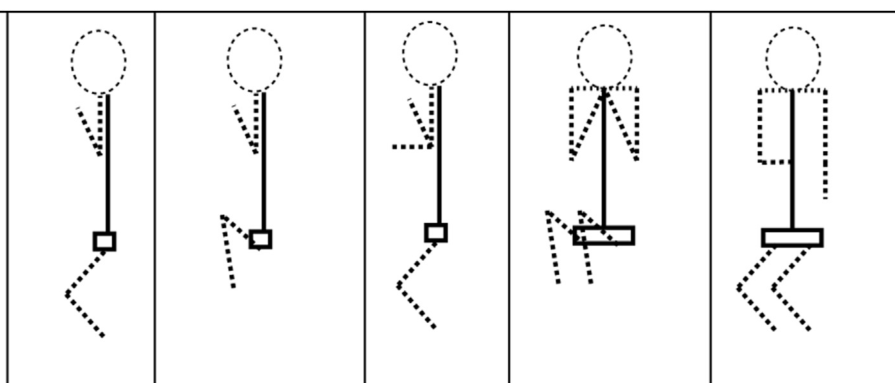
3. Results

3.1. Test for correlation between funerary/osteological data and individual maternal lineages

First, we tested if each identified mitochondrial haplogroup/haplotype, that could be a potential indicator of kinship or origins of the individuals, was statistically associated with a specific funerary trait and/or osteological data. No statistical association could be established in this first set of analyses, which revealed the absence of links between funerary traits, osteological data and specific maternal lineage (all p-values >0.05; SI_6).

No statistically significant correlation between body position and mitochondrial lineage could be identified (SI_6). Five main body positions were noted across the entire necropolis but no single position appeared to be specifically associated with a maternal lineage (Fig. 2). Interestingly, no correlation could be found between any specific funerary trait and the mitochondrial haplogroup H. This is the most common haplogroup among the necropolis (36,4%) and has been recognized from the Mesolithic period in Western Europe onwards (de la Rua et al., 2015; Di Benedetto et al., 2000; Hervella et al., 2012). Also, no correlation between funerary traits and haplogroup N1a was found, haplogroup N1a being considered as a maternal marker of the Early Neolithic of Central Europe, i.e. LBK groups (Haak et al., 2005, 2010).

We then looked into each sample of individuals sharing the same haplogroup to test for potential significant spatial grouping of burials according to maternal lineage. Only one spatial cluster could be characterized for burials belonging to haplogroup K (Fig. 2, SI_7). This cluster includes three individuals sharing the same haplotype K_16224C: one male adult and two immature individuals aged between 1 and 6 years. The identification of the same HVS-I sequence for these three individuals could point out towards more or less close maternal relatives. Although the association of these three individuals appears to be clearly intentional since two of the burials are superposed, no significant sharing of other funerary traits could be noted. Unfortunately, no radiocarbon dating was available for these samples, which hinders a more detailed discussion concerning the structure's chronology. Other direct associations between burials were also observed, i.e., either double burials or superposed structures. However, none of these burials shared a common mitochondrial lineage (Fig. 3). In addition, a high proportion of male adult - immature associations was observed. Indeed, among the 36 detected associations, 22 included male adults, whose burial pits were either directly connected with or closer than 1 m to an immature individual's pit. In contrast, only eight associations involved women and only six associations involved individuals for whom sex is still undefined. Additionally, no funerary selection according to age-at-death could be detected because all of the immature age classes were included. Except for the previously discussed group that shares the same haplotype



Body positions					
Total of individuals	n=6	n=26	n=3	n=5	n=3
Haplogroups (Concerned Individuals)	H (x2)	H (x7); J(x2); K (x2); N1a (x1); U (x3)	H (x2)	J (x2); H (x1); X (x1); K (x1)	N1a (x1); H (x1)
Potential maternal ancestries	South_F	Central_F ; South_F ; HG	South_F	Central_F ; South_F	Central_F ; South_F

Fig. 2. Representations of the five main body positions observed in the necropolis of Gurgy "Les Noisats" and the mtDNA haplogroups/potential maternal ancestries characterized for each group.

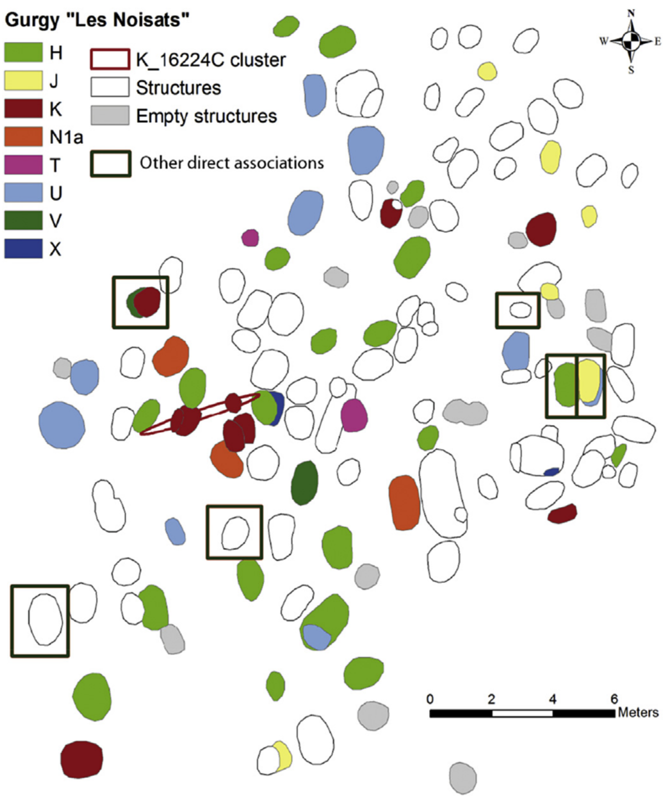


Fig. 3. Localization of the spatial cluster of individuals who share the K_16224 haplotype (brown ellipse) and of the double burials or superposed structures (black squares).

K_16224C, all other adult male - immature groups for which aDNA data were available presented distinct mitochondrial haplogroups/ haplotypes.

3.2. Test for correlation between funerary/osteological clusters and mitochondrial lineages

Although no spatial hot spot could be identified for the different mitochondrial lineages characterized in Gurgy, several specific spatially defined clusters based on funerary and/or osteological data have been detected in the necropolis previously (SI_5; Le Roy et al., 2014). We checked for correlations between these identified clusters and specific maternal groups.

First, a spatially defined cluster based on the "adult" category was detected (SI_7). This grouped 11 individuals: six males, two females and three with sex unidentified (Fig. 4A, Cl.1). No shared trait could be identified as strictly linked to this group (SI_8). Another spatial cluster could also be defined according to the "male" category that overlapped with the adult cluster (Fig. 4A, Cl.2, SI_7). This second cluster included five adult individuals. Again no specific trait could be identified as strictly linked to this group. Interestingly, the concentration of these two clusters is not linked to a specific maternal lineage either (Fig. 4A).

Considering the "immature" data, a spatial cluster was highlighted in the southwest section of the necropolis. The cluster included four individuals. Two belonged to the [1–4] age class, the two others belonged to the [1–9] age group. Whereas the burials included in this "immature" cluster present quite homogenous funerary patterns, they do not share a specific mitochondrial haplogroup (Fig. 4B, Cl.3, SI_7).

Therefore, it clearly appears that all of the spatial clusters identified through osteological and archaeological data do not reflect a specific maternal link between individuals.

Using the available aDNA data (SI_4), we checked for potential genetic differentiation between the groups associated with these funerary/osteological clusters and the remainder of the Gurgy group. Despite the small number of individuals, the maternal diversities measured for the groups inside the clusters were systematically higher than those measured outside the clusters, which indicates that no intentional association according to maternal lineage guided the spatial groupings. However, when we limit the analysis to the defined cluster based on the feature "individuals with the head orientated to the south" ($N = 9$), we find a statistically significant differentiation between this group and the remainder of the Gurgy population (exact test of population differentiation: $p = 0.03 \pm 0.005$). This outcome indicates that the genetic composition of this archaeologically defined cluster may be intentional. However, burials with the individuals' head orientated to the south is the most common orientation encountered in the necropolis and thus may not be culturally informative.

3.3. Test for correlation between funerary/osteological data and maternal ancestries

Previous studies have proposed the association of different mtDNA haplogroups with potential distinct ancestries, i.e. HG vs. farmer ancestries (Brandt et al., 2013; Rivollat et al., 2015). In addition, summary statistics obtained for the Gurgy gene pool suggested the admixture of maternal lineages with distinct farmer ancestries linked to the Danubian and the Mediterranean Neolithization routes (Central_F vs. South_F; Rivollat et al., 2015). Even though this classification is not exclusive, we checked for a potential correlation between cultural/osteological data and proposed maternal ancestries.

No single specific funerary trait was statistically correlated with any ancestry group (SI_6). For example, the five main body positions encountered in the Gurgy necropolis did not appear specifically linked to any ancestry (Fig. 2).

The spatial distribution of the ancestry groups appears homogenous, with no specific area dedicated to one particular ancestral group (Fig. 5). However, the individuals potentially attributed to HG ancestry appear to be slightly marginalized. This suggests a specific distribution of individuals with HG ancestry on the periphery of the necropolis, whereas other ancestry groups show a narrower distribution with an axe oriented North-East/ South-West (Fig. 5, SI_9). The results indicate that these individuals sharing HG ancestry were excluded from the center of the necropolis. Because most of the defined clusters based on osteological data were detected in this central area, this could indicate that individuals with proposed HG ancestry were not included in the archaeologically or osteologically defined clusters.

Finally, despite the low frequency of grave goods encountered in the Gurgy burials, several grave goods were considered to be rare and exceptional based on their scarce presence in the necropolis and in a regional context, e.g., green stone pendants, a ceramic cup, a beaver-tooth set, etc. Concerning individuals with such rare grave goods ($N = 10$), we could point out that four present a potential HG ancestry, corresponding to 50% of HG ancestry group. In comparison, only 17.4% of the South_F ancestry and 7.9% of the Central_F ancestry groups are associated with these rare goods. Subsequently, two observations can be proposed concerning the group defined on the category "association with rare grave goods": (i) its genetic diversity (0.93 ± 0.12) was not significantly different from the group without rare goods (0.95 ± 0.03), and (ii) these two groups could not be genetically differentiated using the exact test of differentiation ($p = 0.59 \pm 0.01$), which indicates no clear maternal

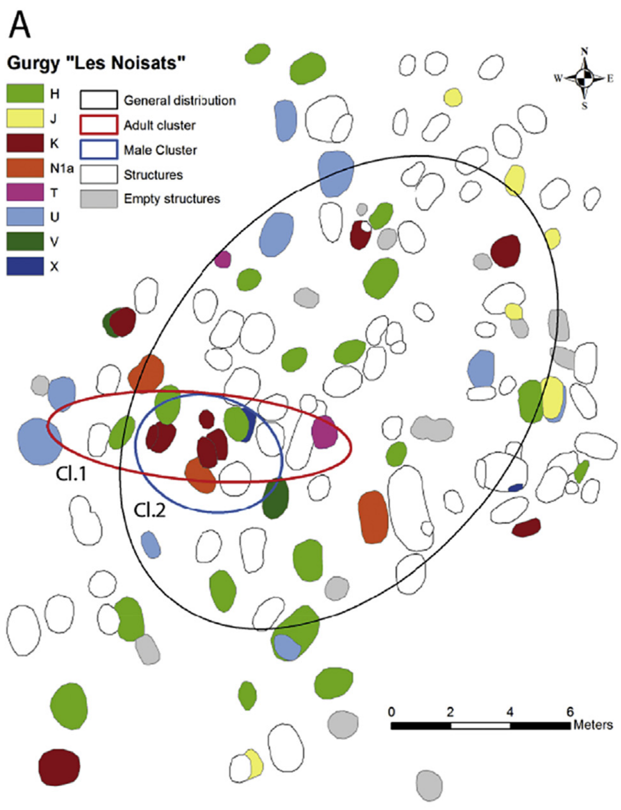


Fig. 4. Localization of spatially defined clusters based on osteological data and distribution of mitochondrial lineages. **A**) Defined clusters based on the data “adult” (Cl.1) and “male” (Cl.2). **B**) Defined clusters based on the data “immature” (Cl.3).

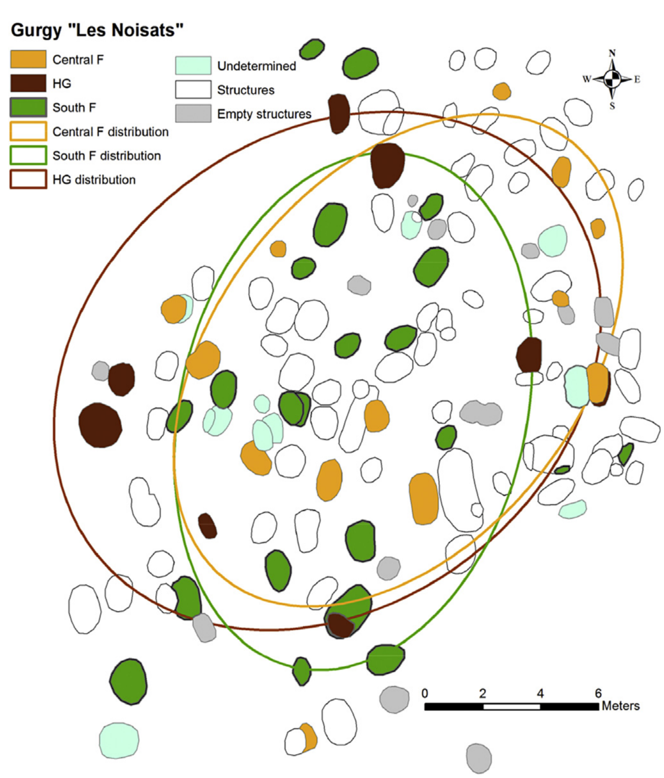


Fig. 5. Spatial distribution of the groups defined according to their potential ancestry: HG/Central_F/South_F.

specificities for the group “association with rare grave goods” (SI_4).

4. Discussion

The necropolis of Gurgy “Les Noisats” is characterized by apparent homogeneity in funerary practices but exhibits variable funerary traits in terms of body position, orientation, and grave goods (Le Roy, 2015). The analyses conducted in this study demonstrate that none of these variable funerary traits was significantly associated with a specific maternal lineage. This result was systematically confirmed based on the analyses carried out on an individual scale or on an archaeological/osteological clusters scale. Only one case of a small cluster of burials, which grouped three possibly maternally related individuals sharing haplotype K_16224, could be highlighted. Thus, despite (i) the use of an effective, powerful GIS approach and (ii) the application of this approach to an unprecedented number of archaeological/osteological and genetic data collected for one archaeological site, no clear indications of the influence of maternal relationships on the functioning of the Gurgy necropolis could be established. Because no data have been yet obtained on the Y-chromosome variability of the Gurgy group, the question of an influence of paternal relationships in the necropolis organization remains open. The picture that clearly emerges from our analyses is of a genetically diverse group presenting substantial maternal genetic diversity (0.95 ± 0.03) but which is culturally homogeneous. The measured maternal diversity is comparable to those previously described for LBK groups (Derenburg is 0.96, Halberstadt is 0.95 and Karsdorf is 0.9; Brandt et al., 2013, Haak et al., 2005, 2010). It is interesting to note that the cultural and biological (considering genetic and osteological data together) uniformity of the Gurgy group has been recently similarly demonstrated in connection with diet. Indeed, preliminary isotope results obtained for the group indicated a surprisingly low variability of $\delta^{13}C$ and $\delta^{15}N$ levels, revealing a dietary homogeneity rarely observed for a single ancient population (Rey et al., 2014).

Some associations between particular funerary traits and specific genetic groups could be found when the potential maternal ancestries of the individuals were analyzed. For example, the individuals who share HG ancestry, i.e., who present U4 and U5 haplogroups are significantly more frequently associated with goods that rarely occur in the region and the period (e.g., a ceramic cup or green stone pendants). Added to this, we demonstrated that the spatial dispersion of the HG ancestry group is preferentially located on the site's periphery, whereas individuals associated with farmer ancestries appear randomly distributed across the entire necropolis. The potential exclusion of the individuals with HG ancestry from the center of the necropolis and their association with uncommon grave goods suggests a slightly different status, although this could not be distinguished using other funerary or osteological data. Except for these rare observations, we could not detect any other funerary specificity for the groups distinguished through potential HG or farmer ancestries. Such an important uniformity of treatment of the population suggests the complete acculturation in Gurgy of individuals who originated in diverse source populations, *i.e.,* hunter-gatherers and farmers who derived from the Danubian and Mediterranean diffusion routes.

A clear genetic discontinuity between the mitochondrial gene pools of hunter-gatherers and early farmers has been consistently observed at the advent of farming in Central Europe and in the Iberian Peninsula (Bramanti et al., 2009; Brandt et al., 2013; Haak et al., 2010; Hervella et al., 2012). aDNA evidence obtained for the Middle and Late Neolithic in Germany suggests a slow but steady increase in hunter-gatherer assimilation following an initial period of cohabitation (Brandt et al., 2014). The possible funerary distinction of the individuals who share HG ancestry can be linked to the apparently important HG heritage in Gurgy. The maternal haplogroups traditionally associated with hunter-gatherer groups (U4 and U5) were found in a significantly higher proportion in the Gurgy group than in Neolithic groups further east or south, more ancient than or contemporaneous with Gurgy, i.e., groups that date from 5500 to 4000 cal. BC. According to the data compiled in a previous study (Rivollat et al., 2015), Gurgy's U4 and U5 frequencies reached 1.8% and 12.7%, respectively, whereas lower frequencies for these haplogroups were measured in farmer groups from Central Europe (0% and 4.1% respectively; Bramanti, 2008; Brandt et al., 2013; Brotherton et al., 2013; Burger et al., 2007; Haak et al., 2005, 2010; Lee et al., 2013) or from Southern Europe (0% and 5.3% respectively; Gamba et al., 2012; Hervella et al., 2012; Lacan et al., 2011b). Because the Gurgy necropolis included the burials of one of the most ancient farmer groups established in the region, these observations support a more significant hunter-gatherer/farmer admixture at the advent of farming in the southern Paris Basin than previously found in Central or Southern European regions. The aDNA data obtained for the Gurgy necropolis, which demonstrate a significant hunter-gatherer contribution to the group genetic make-up, strongly support a scenario of increasing hunter-gatherer admixture with increasing geographic distance from the Near East. This scenario finds particular resonance in the conclusions of the model-based studies conducted by Rasteiro and Chikhi (2013).

Patrilocality has been regularly proposed to explain the progressive assimilation of the hunter-gatherer maternal lineages in farmer gene pools. For example, Bollongino et al. (2013) observed the co-existence of an agriculturalist and a fisher-hunter-gatherer group in the Blätterhöhle site (4th millennium cal. BC, Hagen, Germany) 2000 years after the arrival of farmers in Central Europe. The progressive contribution of maternal hunter-gatherer lineages to the farmer gene pool was explained by potential patrilocality, which implies the progressive integration of hunter-gatherer women in the group. Indeed, Brown (2014) proposes patrilocality for Neolithic groups as the “most parsimonious explanation” for the important mitochondrial diversity measured in ancient farmers groups from Spain, France and central Europe. She also suggests that individuals with maternal HG ancestry and found in Neolithic groups might represent direct contribution from hunter-gatherer groups to farmer ones. The patrilocal pattern was already suggested by more ancient archaeological studies proposing that the exchanges of ceramics, stone tools and livestock between hunter-gatherer and farmer communities may have occurred in parallel with individual exchanges through marriages (Gronenborn, 1999). In addition, strontium isotope analyses conducted in the Neolithic context which regularly reveal an allochthonous origin for the farmer group women also provided substantial evidence of a patrilocality system (Bentley et al., 2003, 2012). In these cases, a correlation between funerary treatments and individual origins could be established based on ground stone adzes reserved for local individuals.

The question of a patrilocal system was also raised in the Gurgy region by archaeological evidence (Le Roy, 2015; Thomas et al., 2011). The preferential grouping of males and immature individuals encountered in the Gurgy necropolis has also been noted in the Passy monumental structures. Although the sex of the immature individuals could not be identified in these cases, the grouping of immature individuals with men suggests the strong social power of male adults in the human group, as expected for groups that present the patrilocal system. Moreover, the high genetic diversity of the group strongly supports this matrimonial mode. In summary, the archaeological and genetic data compiled for the Gurgy necropolis is consistent with the proposed patrilocal pattern, including the assimilation of allochthonous hunter-gatherer and farmer women in the group. This patrilocal system may have permitted exchanges of women between more or less distant groups, permitting the maintenance of villages too small to employ an endogamic system (Passard, 1983). The funerary homogeneity observed in the Gurgy necropolis supports a complete acculturation of all of the individuals who present potentially distinct maternal ancestries.

5. Conclusion

The unprecedented number of archaeological, osteological and aDNA data available for the necropolis of Gurgy “Les Noisats” represents a unique opportunity to use an innovative GIS approach to test for special correlations between cultural and osteological data. We studied the spatial distribution of the individuals from this new perspective to confirm or identify hypotheses presented in traditional studies. This multidisciplinary approach could also include stable isotopes and dental micro-architecture to complete the understanding of the functioning of the Gurgy necropolis.

The Gurgy necropolis gathered the burials of individuals who present distinct maternal origins or ancestries but share the same funerary practices, even with a long use that ranges from 5000 to 4000 cal. BC. Individuals with hunter-gatherer, Central European farmer or South European farmer maternal ancestries seem to have benefited from a common treatment in death. This funerary homogeneity, observed since the establishment of the necropolis, could represent early evidence of a complete admixture and acculturation of groups which encountered one another in Gurgy. The complete integration of individuals who shared a hunter-gatherer ancestry into the Gurgy farmer group is noteworthy, and these results could illustrate an increasing hunter-gatherer admixture with farmer groups that were migrating in Western Europe. However, because comparable datasets are not available for the regional and cultural context, the results obtained for the Gurgy group could represent a special case in the Paris Basin context. Nevertheless, these observations should initiate a discussion concerning the processes involved in the Paris Basin Neolithization and encourage similar analyses for the first farmer groups to reach different regions of French territory. Currently, model-based analyses are being conducted to test the continuity between the Gurgy group and the different hunter-gatherer/farmer ancestries groups proposed in this study. Finally, the paleogenomic analysis of the Gurgy group may provide important evidence of the specific ancestry of each Gurgy individual and quantify the contribution of each hunter-gatherer/farmer population to the Gurgy group make-up. Of course, the significant acculturation proposed for the Gurgy site may not be considered to represent a norm for the Neolithic period in the Paris Basin given the diversity of funerary practices observed for the period in this area. To advance the understanding of the hunter-gatherers/farmers relationships at the advent of farming in Europe, additional multidisciplinary studies appear necessary. We believe that the large diversity of funerary structures encountered in the Paris Basin provides a wide playground to test various practices of cultural and genetic admixture between human groups.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jas.2016.07.003.

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