

# Investigating Neolithic social structures on the basis of unprecedentedly large family trees from the site Gurgy ›les Noisats‹ in France

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## Zusammenfassung

Die Untersuchung von neolithischen sozialen Strukturen auf der Grundlage von großen Stammbäumen von der Fundstelle Gurgy ›les Noisats‹ in Frankreich

Die Aufklärung von Verwandtschaftsstrukturen in vergangenen Gesellschaften steht im Mittelpunkt von gruppeninternen Studien in der Archäologie und Anthropologie. Jedoch war die komplette Rekonstruktion von genetischer Verwandtschaft im archäologischen Kontext kaum realisierbar gewesen. Die Optimierung von Methoden zur Analyse alter DNA macht es nun möglich, genomweite Daten für mehrere Individuen einer einzigen Fundstelle zu erhalten. Diese Daten ermöglichen die Rekonstruktion genetischer Verwandtschaft und erlauben es Rückschlüsse auf die demografische Struktur sowie soziale Organisation prähistorischer Gesellschaften zu ziehen.

Wir stellen hier die Analyse genomweiter Daten von der mittelneolithischen Fundstelle Gurgy ›les Noisats‹, Département Yonne (Frankreich), vor. Auf der Grundlage einer umfassenden Beprobungsstrategie und der gezielten Anreicherung von 1240k SNPs (Einzelnukleotid-Polymorphismen), konnten wir Daten von 94 der insgesamt 128 Individuen gewinnen. Mit Hilfe eines Multi-Proxy-Ansatzes sowie etablierten und neuen Methoden der biologischen Verwandtschaftsbestimmung, war es uns möglich, zwei große Stammbäume zu rekonstruieren: einer, der 63 Individuen über sieben Generationen miteinander verbindet, und ein anderer, der 10 Individuen über vier Generationen verknüpft. Die kombinierten Daten deuten auf eine patrilokal und patrilineal organisierte Gesellschaft hin, welche Exogamie praktizierte. Das weitgehende Fehlen von genetischen Verwandtschaften zwischen nicht-lokalen Frauen und die Analyse der Verwandtschaft im elterlichen Hintergrund der Individuen weist auf ein breiteres regionales Netzwerk hin. Strontiumanalysen bestätigten den nicht-lokalen Ursprung von erwachsenen Frauen, zeigten aber auch nicht-lokale Merkmale der Gründer der Erstgeneration der Fundstelle. Darüber hinaus deuten die osteologischen Sterbealterschätzungen der ersten und letzten Generationen der Stammbäume auf eine viel engere zeitliche Spanne der Besiedlung der Fundstelle hin.

Diese überraschend großen Stammbäume bieten Einblicke, die über die unmittelbare genetische Verwandtschaft hinausgehen und es uns ermöglichen, die Gruppenstruktur, ihre Größe sowie Begräbnis- und Siedlungspraktiken innerhalb eines viel breiteren sozialen und kulturellen Kontextes zu untersuchen.

## Summary

The elucidation of kinship structure in past societies has been at the centre of intra-group studies in archaeology and anthropology. However, the full reconstruction of genetic relatedness in archaeological contexts has rarely been feasible. With the optimization of ancient DNA (aDNA) methods, it is now possible to obtain genome-wide data for multiple individuals from a single site. This data allows the reconstruction of biological relationships and inferences on the demographic structure and social organisation of prehistoric societies.

Here, we present genome-wide data from the French Middle Neolithic site of Gurgy ›les Noisats‹, Yonne Department. On the basis of extensive sampling and the use of the 1240k SNP (Single Nucleotide Polymorphisms) capture array, we obtained data from 94 out of a total of 128 individuals. Using a multi-proxy approach, and following established and novel methods to determine biological relatedness, we were able to reconstruct two large pedigrees: one connecting 63 individuals over seven generations, and another with 10 individuals over four generations. From our combined data, we inferred a patrilocal and patrilineal system, and the practice of female exogamy. The absence of genetic affinities between non-local females and the analysis of parental background relatedness suggest a wider regional network. Strontium analyses confirmed the non-local origin of adult females, but also revealed non-local signatures in the first-generation founders of the site. Moreover, osteological age-at-death estimates from the first and last generations of the pedigrees indicated a much narrower chronological range of the occupation of the site.

These unprecedentedly large genealogies provide insights that go beyond the immediate genetic relatedness and allow us to study the group structure, its size, as well as funerary and settlement practices within a much broader social and cultural context.

## Introduction

The first communities of farmers settled in the northern half of modern-day France at around 5200–5000 cal BC during the early phases of the Neolithic, expanding mainly from central Europe along the Danubian route of diffusion (Allard 2007). Following this early phase, groups then segmented into several smaller cultural entities and in smaller territorial areas, which stabilized during the Middle Neolithic; sometimes this also led to competition (Gallay 2007).

With the transition to the Middle Neolithic, the complexity of the funerary practices increased in the Paris Basin, and more specifically in the Yonne Valley. The Cerny culture (Constantin et al. 1997), partly derived from the Ville-neuve-Saint-Germain culture and representing the final phase of the Linear Pottery culture (LBK), was present in the region from about 4700 cal BC and is known for its associated monumental funerary structures, the so-called *Structures de Type Passy* (STP, ~4700–4300 cal BC). Exogenous influences are, however, also visible in the archaeological record. For example, the southern Chasséen Culture is represented in the artefacts from the graveyard Monéteau ›Macherin‹, Yonne Department (France; Augereau/Chambon 2011), with different grave goods from the Mediterranean sphere being found all over the Paris Basin (Lichardus-Itten 1986; Sidéra 2010), while the Chamblandes-like rigid containers, found in several sites in the southern Paris Basin, point to cultural influences from the Alps and central France (Moinat/Chambon 2007).

Overall, archaeological cultures do not always accord with burial complexes, as different burial types or body positions have been found within the same archaeological cultural groups (Thomas 2011). The spatial boundaries between groups are also not strict, and rather are fluid. Most of the funerary sites ( $n = \sim 20$ ) located in the Paris Basin *sensu stricto* include STP monuments (Chambon/Thomas 2010).

Although contemporary with STP sites, Gurgy ›les Noisats‹, Yonne Department (France; Rottier et al. 2005) is one of the few sites that stand out. The complete excavation of the graveyard of Gurgy ›les Noisats‹ took place between 2004 and 2007 under the direction of S. Rottier (Rottier et al. 2005; Rottier 2007). A total of 134 pits were excavated at the site, uncovering 128 individuals, which makes Gurgy currently the biggest funerary site for the Neolithic in the Paris Basin. Direct radiocarbon dates from human remains range between 5000 and 4000 cal BC, but the most intensive occupation period ranges from 4900 to 4500 cal BC, corresponding to the end of the early Neolithic and the beginning of the Middle Neolithic. A few double, but mainly single burials were uncovered, displaying a wide variety of grave types and cultural influences, including: burials in pits without construction; burials in pits with a cover; burials in rigid containers; and burials in niches (Rottier 2007). Burials in rigid containers echo those found in regions like modern-day Switzerland or the Massif Central and are associated with the Chamblandes phe-

nomenon (Moinat/Chambon 2007). By contrast, burials in niches are common in the Paris Basin during the late LBK phase (Thevenet 2010). Grave goods, notably pottery and flint tools, are scarce and randomly distributed across the cemetery. The elements of adornment are noteworthy for their diversity (Rottier et al. 2005). Overall, there are no diagnostic artefacts that assign Gurgy to a particular Neolithic culture.

Several studies were conducted on the human remains to understand the structure of the Gurgy site<sup>1</sup>. The first population genetics studies explored the mitochondrial genetic diversity<sup>2</sup> and were completed recently by a broader genomic study of western European Neolithic farmers that also included 22 individuals from Gurgy (Rivollat et al. 2020). An integrative study combining mitochondrial data ( $n = 55$ ) with archaeological data was also performed to understand the organisation of the site and to see whether any archaeological feature could be linked to specific maternal lineages (Le Roy et al. 2016). However, no correlation between mitochondrial lineages and archaeological data could be demonstrated.

The optimization of aDNA methods over the last few years has made it possible to obtain genome-wide data (i.e., nuclear and mitochondrial) and to estimate precise genetic relationships between individuals. With these new data, finer-scale local analyses are now feasible, they are increasingly finding use, and they are capable of exploring questions concerning kinship structures and site organisation. This newly gained resolution offers new elements of discussion for the investigation of social structures. Here, we present a summary of the results from our genomic study applied on an extensive sampling of the site of Gurgy ›les Noisats‹. We were able to retrieve genome-wide aDNA data for 94 individuals, allowing us to explore biological relatedness between most of the deceased, and to infer, beyond the biological structure, insights into the social organisation of this Neolithic community. The complete study and associated data are available in Rivollat et al. (2023).

## Data generation and pedigree reconstruction

We attempted to sample Gurgy ›les Noisats‹ as completely as possible. Of the 128 individuals buried at this site, 110 showed skeletal preservation suitable for aDNA analysis. Petrous bones were collected whenever possible ( $n = 94$ ), followed by teeth ( $n = 7$ ), and other bones, such as tibia ( $n = 1$ ), femur ( $n = 1$ ), radius ( $n = 1$ ), scapula ( $n = 1$ ), phalanx ( $n = 1$ ), and unspecified bones ( $n = 4$ ). Samples were processed in the cleanroom facilities of the former Max Planck Institute for the Science of Human History, Jena (now Max Planck Institute for Evolutionary Anthropology, Leipzig), Germany and the Laboratory PACEA, Bordeaux University, France. Each sample was drilled, and bone and/or tooth powder was used to produce DNA extracts from which partial uracil-DNA-glycosylase (UDG) double-stranded DNA libraries with unique

<sup>1</sup> Le Roy 2015; Le Luyer et al. 2016; Rey et al. 2017; Rey et al. 2019; Rey et al. 2021.

<sup>2</sup> Documenting the maternally inherited lineages; Rivollat et al. 2015; Le Roy et al. 2016;

Rivollat et al. 2017.

index pairs were generated. After screening of ~5 million reads by shotgun sequencing, we selected libraries with >0.1% endogenous human DNA (n=105), which were hybridised in-solution to an oligo-nucleotide probe set to enrich for ~1.2 informative nuclear Single Nucleotide Polymorphism (SNP) markers (capture 1240k; Fu et al. 2014; Mathieson et al. 2015). An in-house capture for the complete mitogenome (Maricic et al. 2010; Haak et al. 2015) was applied to all samples. Genetic sex was determined for all individuals (Mittnik et al. 2016) and a capture targeting the entire mappable region of the Y-chromosome was applied to all genetically determined males (n = 57; Rohrlach et al. 2021). We were able to retrieve genome-wide aDNA data for 94 individuals, 22 of which were published previously (Rivollat et al. 2020), as well as mitogenomes from 99 individuals. Individuals who were covered at less than 20000 SNP sites, who were lacking typical patterns of DNA damage at the read ends (4 to 18% of deamination), and/or libraries showing contamination in both nuclear and mitochondrial genomes (<5%; Fu et al. 2014; Korneliussen et al. 2014) were excluded from further analyses.

To determine biological relatedness for first-degree (parent-offspring and siblings) and second-degree relationships (grandparents-grandchildren, uncle/aunt-nephew/niece, and half-siblings), we combined two established methods designed for low-coverage aDNA data. We used *READ* (Monroy Kuhn et al. 2018), which calculates and averages the pairwise mismatch rate and can identify up to first- and second-degree relationships. We then used *IcMLkin* (Lipatov et al. 2015), which estimates the probability of identity-by-descent (IBD) from genotype likelihoods to differentiate between parent-offspring and siblings among first-degree relationships. We combined these estimates with contextual information, such as age-at-death, genetic sex, and uniparentally-inherited markers, to reconstruct pedi-

grees (Fig. 1). Lastly, we estimated genetic links between related individuals by analyzing the inferred shared IBD segments (Ringbauer et al. 2023), which helped us to confirm genetic relatedness up to the tenth degree.

In parallel with the investigation of the genomic data, we explored individual mobility *via* strontium isotope analyses (<sup>87</sup>Sr/<sup>86</sup>Sr) using a laser-ablation technique (Lazzerini et al. 2021) on 57 of the individuals. To contextualise the new genomic data, we commissioned new radiocarbon dates, in addition to the 25 dates that were already available (Rivollat et al. 2015). We used a GIS (Geographic Information System) approach, as applied previously on the mitochondrial data from Gurgy (Le Roy et al. 2016), to investigate the potential correlation between the spatial location of the individuals at the site and genomic and archaeological data. We then applied a Bayesian modelling to the radiocarbon dates using information about the generational succession from the pedigrees to explore the date ranges of the occupation time of the site.

**Inferences on the social and residence patterns**

We reconstructed two large pedigrees (Fig. 1). Pedigree A connects 64 individuals, 20 females and 44 males, spanning seven generations, and Pedigree B connects 12 individuals, seven females and five males, covering five generations. Among the remaining 18 individuals we identified three additional pairs of first-degree relatives. One adult male (GLN311) has two second-degree relatives in Pedigree A, while the 11 remaining individuals are not closely related to any individuals of either pedigree. The two pedigrees are clearly reflected in the spatial layout of the necropolis (Fig. 2). Pedigree A occupies the main space, while Pedigree B is located on the north-eastern side. In both pedigrees we

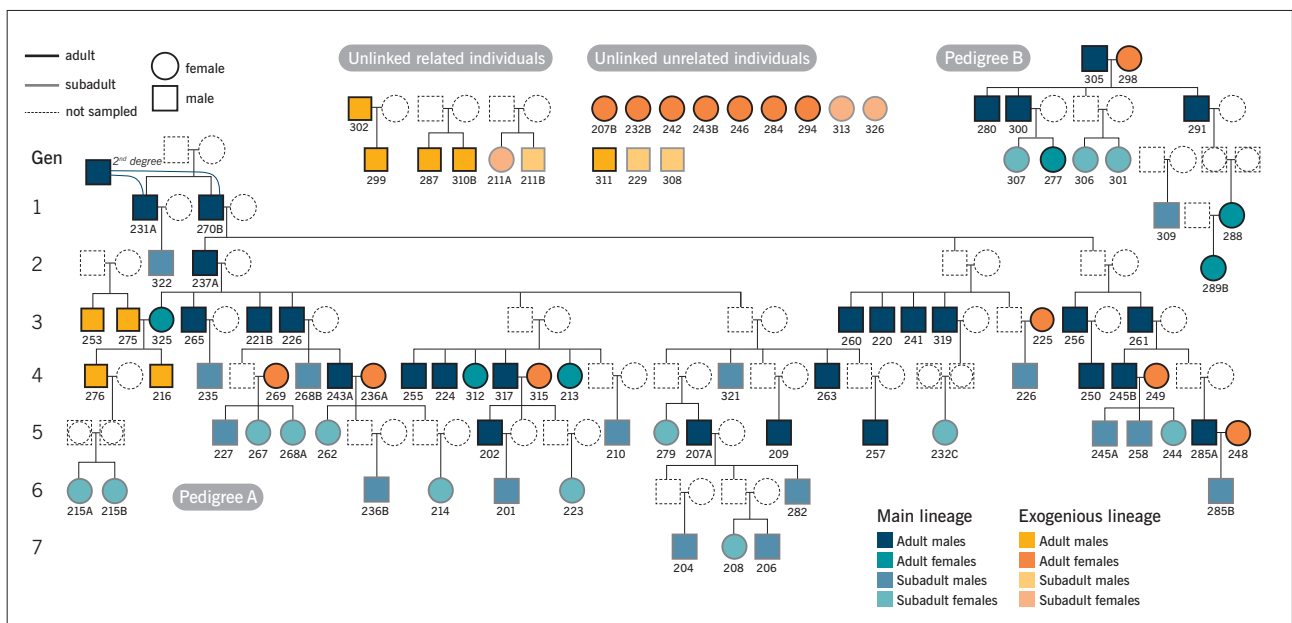


Fig. 1 Reconstructed pedigrees of the Gurgy group coloured by main or exogenous lineages, sex, and age at death.

Abb. 1 Rekonstruierte Stammbäume der Individuen von Gurgy, farblich gekennzeichnet nach Haupt- und Nebenlinien, Geschlecht sowie Alter zum Todeszeitpunkt.

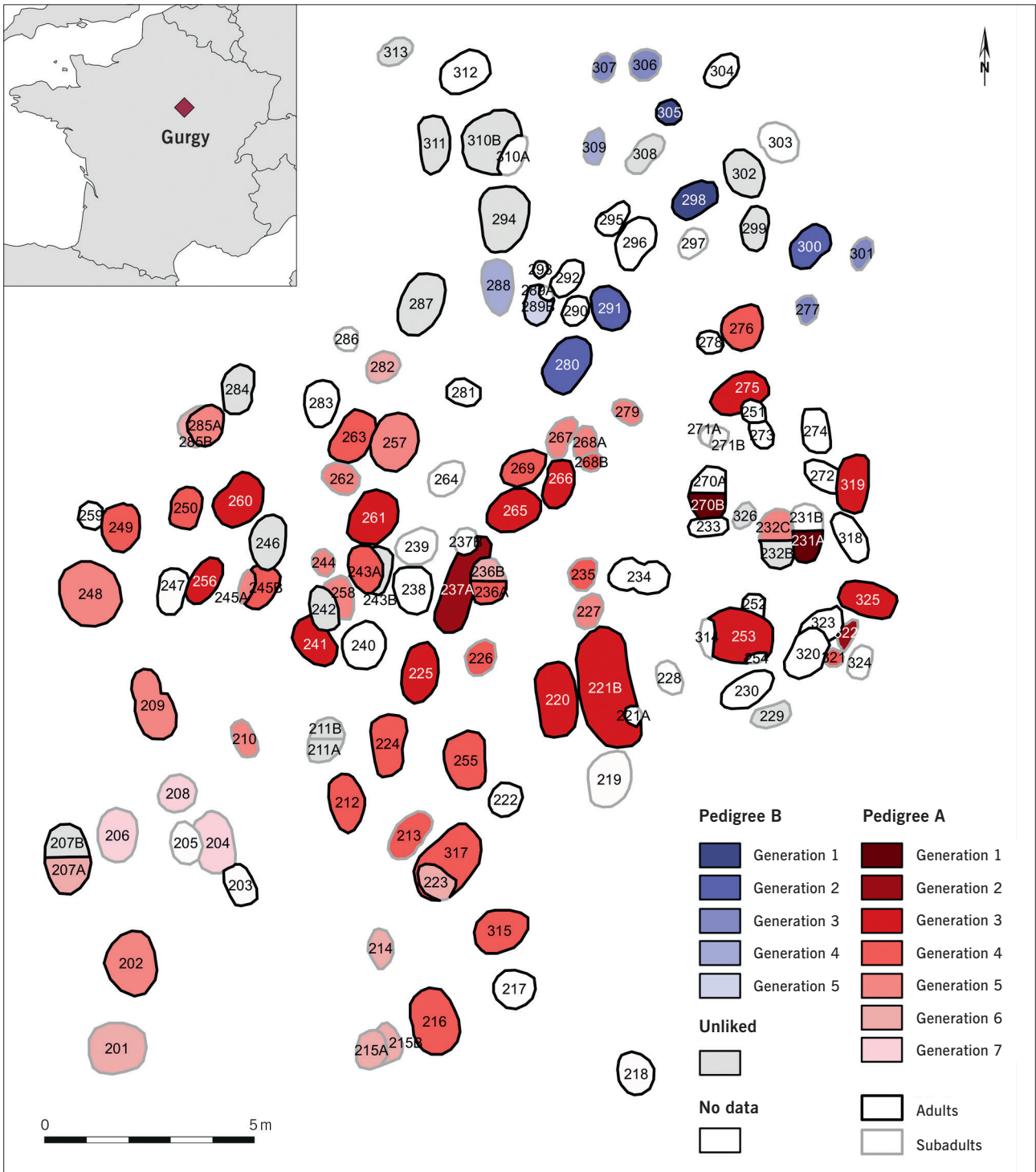


Fig. 2 Geographical location of the Gurgy «les Noisats» site, Yonne Department, in present-day France (inset) and the site layout representing the spatial distribution of the pedigrees and generations.

Abb. 2 Geografische Lage der Fundstelle Gurgy «les Noisats», Département Yonne, im heutigen Frankreich (Markierung) und der Gräberfeldplan, der die räumliche Verteilung der Stammbäume und Generationen widerspiegelt.

observed a spread from the founder generations towards the south-west, by generations through time. Spatial distances are significantly correlated with genetic distances (Mantel test:  $r=0.2$ ,  $p < 0.001$ ), implying that individuals were preferentially buried near their biological family members.

The reconstructed pedigrees A and B are the first of such a large size from a prehistoric site and allow unprecedented insight into the biological structure of the group, and the

social rules that might have led to the observed structure in this particular funerary community.

### Patrilineality

Closer inspection of the pedigrees (Fig. 1) revealed almost exclusively that each generation is linked to the previous

Fig. 3 Gurgy ›les Noisats‹. Photograph of male individuals GLN237A and GLN221B, son and grandson, of GLN270B, Pedigree A's main ancestor, who were buried in the largest pits of the necropolis.



Abb. 3 Gurgy ›les Noisats‹. Befundfoto der männlichen Individuen GLN237A und GLN221B, Sohn und Enkel vom Hauptvorfahr des Stammbaums A (GLN270B), welche in den größten Gruben des Gräberfelds bestattet waren.

generation through the biological father, which connects the whole group of Gurgy ›les Noisats‹ through the paternal line. The paternal lineage is characterised by Y-chromosome haplogroup G2a2b2a1a2, which is carried by 89% of the males in the group. The main paternal line of Pedigree A starts with individual GLN270B and his brother GLN231A. Of the three sons of GLN270B, only one, GLN237A, was buried at the site, and had a large number of children whose descendants were also buried at the site. The importance of the main paternal lineage can be traced in the subsequent generation directly following GLN270B, as the two largest graves of the site were built for his son GLN237A, as well as his grandson GLN221B (Fig. 3). We thus hypothesise that a form of social status was transmitted along the paternal line to his son and grandson.

The patrilineal system as shown by the genetic connections is also visible in some of the archaeological features (Le Roy et al. 2016). Here, the burials of fathers and their subadult male offspring are located significantly closer to each other than any other pairs of individuals, even though we observed a general trend of spatial clusters according to genetically closely related individuals (Fig. 4).

Patrilocality and female exogamy

In parallel with the patrilineal pattern, evidence suggested the practice of patrilocality within the group. Adult females buried at the site, whether they were mothers or not, had no parents buried at the site, which means that they came from

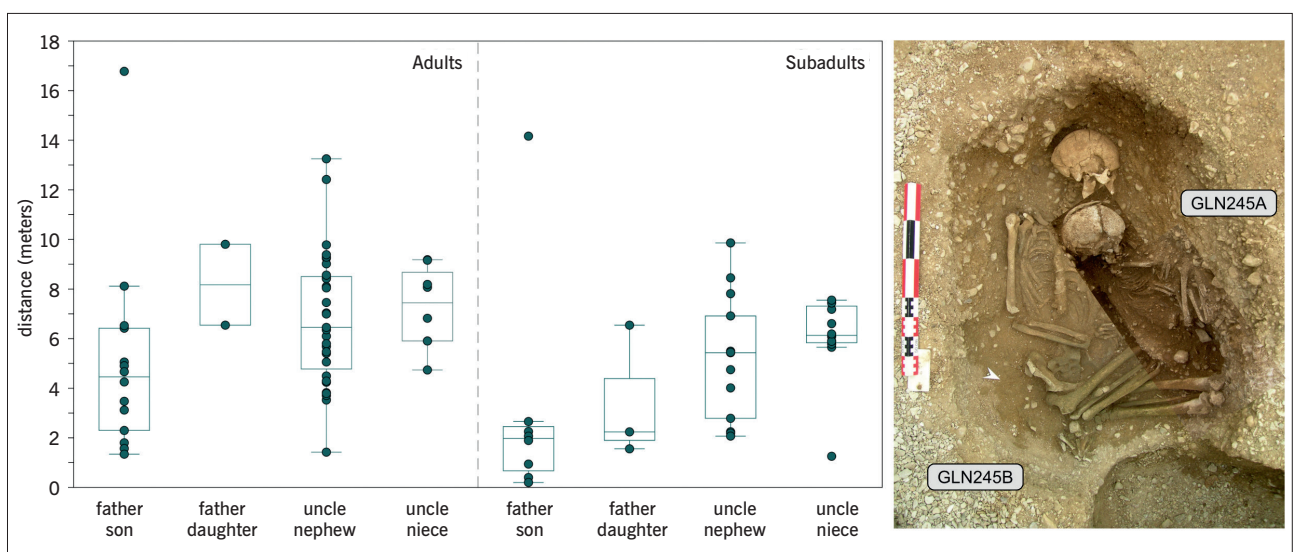


Fig. 4 Gurgy ›les Noisats‹. Spatial distances of father-offspring and uncle-nephew/niece pairs. Fathers and subadult sons are, on average, buried significantly closer to each other than any other pairs. The photograph shows the male individual GLN245B and his son GLN245A buried in the same pit.

Abb. 4 Gurgy ›les Noisats‹. Räumliche Entfernungen von Vater-Kind- und Onkel-Neffe/Nichte-Paaren. Väter und subadulte Söhne sind im Durchschnitt weitaus näher zueinander bestattet, als alle anderen Paare. Das Foto zeigt das männliche Individuum GLN245B und dessen Sohn GLN245A, die in der gleichen Grube begraben wurden.

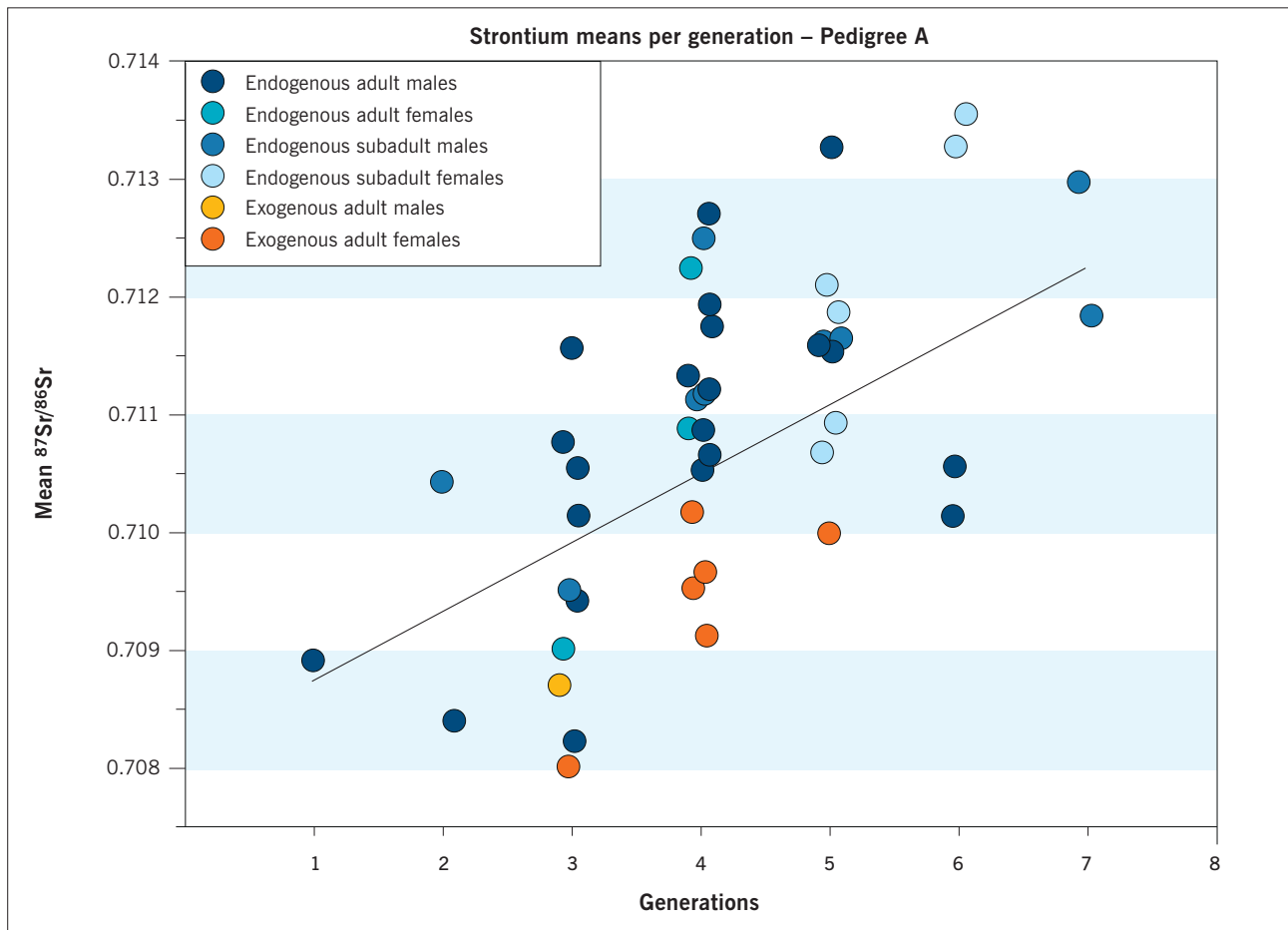


Fig. 5 Gurgy «les Noisats». Mean  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio per age and sex cohort across generations. A significant difference between sex can be observed per generation ( $p=0.01474$ ).

Abb. 5 Gurgy «les Noisats». Mittleres  $^{87}\text{Sr}/^{86}\text{Sr}$ -Verhältnis nach Alter und Geschlechtergruppe über Generationen hinweg. Ein statistisch signifikanter Unterschied zwischen den Geschlechtern kann in jeder Generation beobachtet werden ( $p=0.01474$ ).

a different lineage than those of the main pedigrees (Fig. 1). Six out of 20 of these individuals represent an exception to this rule (GLN325, GLN212, GLN213, GLN277, GLN288 and GLN289B), with only two out of these six having children buried at the site. We note that almost all female descendants from the main lineage who reached an adult age are not present at the site. Indeed, if we consider a natural sex ratio of 1.05:1 males/females at birth (Howell 1976), the ratio of 4.5:1 observed at Gurgy points to a strong imbalance in favour of males among the adult descendants. This can in part be explained by males staying within the group, i.e., suggesting practices of patrilocality akin to the patrilineal structure proposed above in conjunction with female exogamy, in which females move from their birthplace to their reproductive partner's home. Seven adult females were not connected to the pedigrees, and also were not more distantly related as shown by the IBD sharing analysis. Therefore, we speculate that these females could have been the partners of lineage males, but with whom they either did not have any offspring together, or whose common children were not buried at the site, or for whom DNA was not recovered, which would have linked these females through their children to the pedigrees.

Strontium (Sr) isotope analyses provided critical insights into individual mobility. Here, unrelated adult females and

some of those with no parents at the site showed lower  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios than males from the same generation (Fig. 5). While the geological reference map does not allow us to infer a specific geographic origin, this finding provides further evidence that these females grew up in different places before joining the Gurgy community.

The mitochondrial diversity in Gurgy also showcases the female mobility pattern, as the mothers of each generation contributed new mtDNA lineages, but none of these mitochondrial haplogroups was transmitted further than one daughter/son generation. The exception was for the lineage daughter GLN325 who stayed with her biological family and later passed her mitochondrial haplogroup on to her offspring in the next generation.

### Female connections

Based on the observed pattern of a female exogamic residential system practised by the Gurgy group, we explored the specific affinities between these females to gain an understanding of the wider network to which this community is connected. Overall, the heatmap generated from IBD sharing shows only very few connections between females

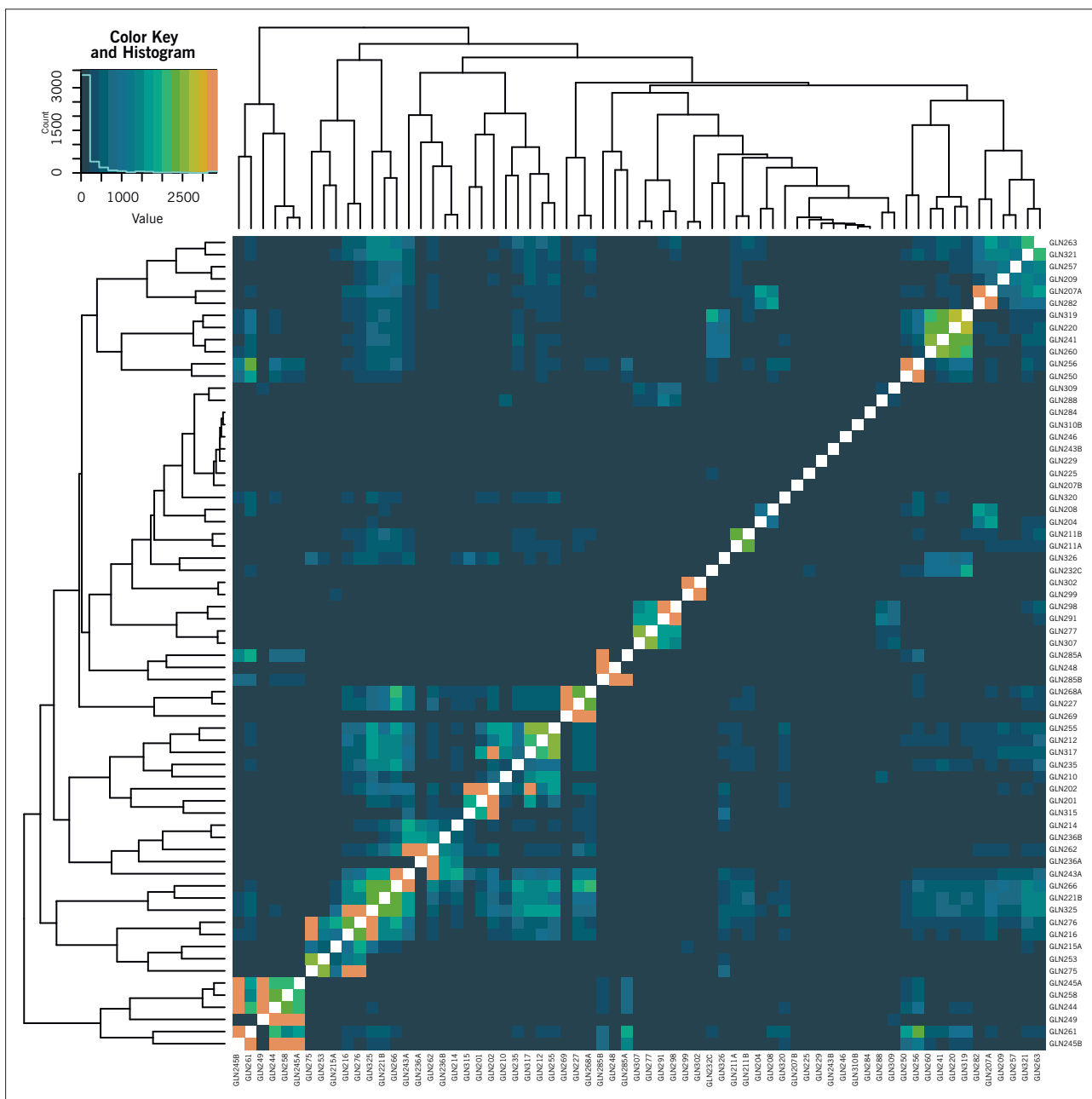


Fig. 6 Gurgy ›les Noisats‹. Heatmap showing pairwise IBD sharing between individuals with more than 500 000 SNPs (n = 72). Different clusters of lighter color reveal the extra-links between the different branches and pedigrees.

Abb. 6 Gurgy ›les Noisats‹. Das Wärmebild zeigt die paarweise IBD-Verteilung zwischen Individuen mit mehr als 500 000 SNPs (n = 72). Verschiedene Cluster in hellerer Farbe zeigen die zusätzlichen Verknüpfungen zwischen den einzelnen Verzweigungen im Stammbaum.

(Fig. 6). We detected three pairs of females who were related in the third or fourth degree, while all other pairs were not genetically related, or too distantly related to be detected. This is consistent with the expected background diversity of the population. The analysis of runs of homozygosity (when an individual carries the same genomic segment inherited from a common ancestor via both parents) also shows no signs of inbreeding within the group (Fig. 7). Only one individual, GLN282, carries long runs of homozygosity, a pattern which suggests that he was the offspring of a second or third cousin relationship. The overall level of background relatedness corresponds to a medium-sized effective population, when compared to, for example, Early Neolithic groups

from central Europe (Ringbauer et al. 2021; Childebayeva et al. 2022).

The results of the IBD sharing analysis are consistent with the inferred mating network from the exogenous connections identified through the reconstructed pedigrees, and revealed additional connections beyond the reconstructed pedigrees, which indicates links through female lines (Fig. 6). Here, we observed several pairs within the pedigrees that, according to the reconstructed pedigrees, appear to share more IBD than expected, but without questioning the robustness of this reconstruction. This includes individuals within Pedigree A, but also between Pedigrees A and B. Intriguingly, all detected links, although relatively

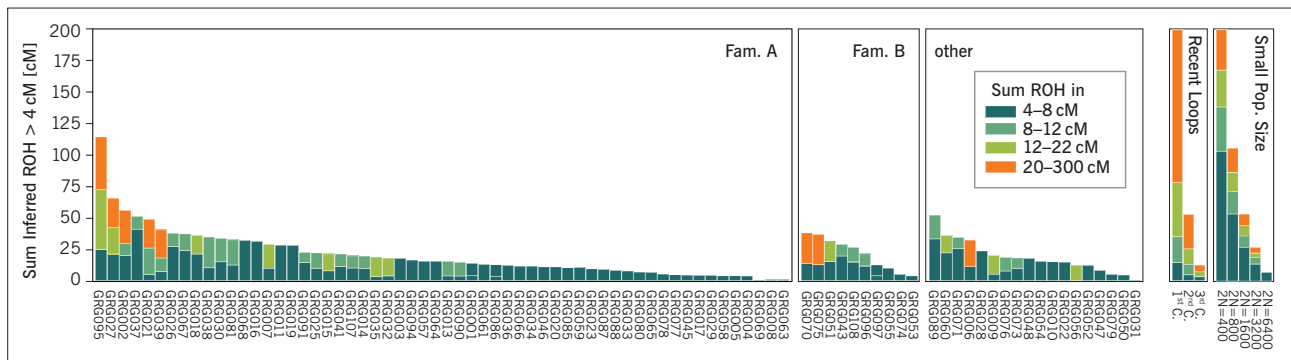


Fig. 7 Gurgy ›les Noisats‹. Runs of homozygosity. Selected individuals with more than 300 000 SNPs ( $n = 86$ ) and simulated data for inbred individuals from parents related at the first- to third-degree, and for individuals from small populations with different sizes for comparison. Individual GLN282 (GRG095) shows an inbreeding signal similar to a first-cousin union, but both carried ROH are 20–22 cM long, therefore this individual is more plausibly the offspring of 2<sup>nd</sup> or 3<sup>rd</sup> cousins.

Abb. 7 Gurgy ›les Noisats‹. Verlauf von Homozygotie. Ausgewählte Individuen mit mehr als 300 000 SNPs ( $n = 86$ ) und zum Vergleich simulierte Daten für inzuchtige Individuen von Eltern, die ersten bis dritten Grades verwandt waren, sowie für Individuen aus kleineren Populationen unterschiedlicher Größe. Das Individuum GLN282 (GRG095) weist ein Inzuchtsmerkmal ähnlich dem einer Verbindung zwischen Cousin und Cousine ersten Grades auf, aber beide ROH sind 20–22 cM lang, daher ist es plausibler, dass dieses Individuum der Nachkomme von Cousin und Cousine zweiten oder dritten Grades ist.

distant, can only be explained through the female lines. A likely explanation is a scenario in which female descendants of those females who had left the Gurgy community returned after a few generations to find a partner in Gurgy upon their return. Alternatively, incoming female partners came from the same community and were maternally related. Both cases would imply that the network of reciprocal mobility within which these movements happened was small enough to retain continuous connections (intentional or unintentional), but at the same time was also sufficiently large to integrate entirely unrelated females. In sum, this lends support to the existence of a relatively wide and fluid exchange network comprising many, potentially smaller, groups, a phenomenon which was described as ›generalised exchange‹ in ethnographic studies (Lévi-Strauss 1971). On the basis of the ROH length distribution, we estimated the effective population size of the communities contributing to the genetic diversity observed at Gurgy to have been ~1835 individuals (1631–2077 95 % CI; Ringbauer et al. 2021). The distribution of runs of homozygosity across Gurgy individuals suggests that most pairs of parents were related to each other *via* co-ancestors within the preceding 5 to 30 generations.

### Occupation of the site

Beyond the kinship structure of the Gurgy group, the pedigrees also contained information about the duration of the site occupation. Individual GLN270B, the male founder of the main paternal line of Pedigree A, has a particular archaeological status as his burial is the only secondary burial of the site deposited inside the grave of the female GLN270A, from whom we could not obtain DNA data (Fig. 8). Only his long bones were placed in the pit, likely in a bundle next to the articulated skeleton of GLN270A, while the rest of his skeleton was missing. This suggests that these remains have been transferred and buried during the early phase of the site, probably because he represented, together with his

brother GLN231A, the main ancestors of the pedigree, and was potentially the senior lineage male. This suggests that this grave was a founding event in the history of the necropolis, even though the relation to the female GLN270A remains unclear. GLN270A could be a close relative (mother, sister, daughter, or further connection?), or a reproductive partner. Alternatively, it could also be the burial of a random person, whose grave-pit was prepared and to whom the remains of GLN270B were added opportunistically. Irrespective of the reasons, the will to translocate the remains of this main ancestor to the site at Gurgy, even if he had potentially died a long time before the secondary burial, marks the importance of him and his lineage to the creation of this new burial place for, and by, his descendants. If GLN270A was indeed the partner in life of GLN270B, then it is also interesting to note that the translocated remains were buried with her and not his brother (GLN231A), or with his potential uncle or half-sibling, GLN320. This would further underpin the significance of this lineage, now represented through her.

The pedigrees reveal an absence of subadults amongst the first four generations in Pedigree A (5 out of 36 individuals), which is rather surprising in light of the estimated mortality patterns in archaic populations (Gage 1989; Wood et al. 2002). However, this pattern is reversed across the last three generations, with 20 out of 25 individuals being subadults. The overall trend is consistent with a scenario in which an entire group of several generations moved near to this new burial site, leaving behind their deceased offspring at a previous funerary site, but transferring the ›ancestor/founder‹ GLN270B. Additionally, the fact that many parents are missing in the last generations suggests that this process was repeated and that the group moved on to settle elsewhere, again leaving behind children who had already passed away at the time. The Sr isotope data provide a further line of evidence in support of these interpretations. Here,  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios are low (~0.709) for the earlier generations, and overall similar to exogenous females, which indicates a non-local origin of the founders (Fig. 5). In contrast,



Sr ratios in males continuously increased with generations, approximating the local Sr signal.

When both pedigrees are compared, overlapping  $^{14}\text{C}$  date ranges and the 3<sup>rd</sup>–4<sup>th</sup> degree connection between GLN263 and GLN298 suggest relative contemporaneity of both. Nevertheless, despite clear evidence for seven consecutive generations in Pedigree A, the occupation time of the site was relatively short. Excluding the founding and outward migrating last generations, the duration of the site's use was likely only 3–4 generations, or 84–112 years (1 generation = 28 years; Fenner 2005). Bayesian modelling of all available radiocarbon dates allowed us to place the interval for Pedigree A to between the late 48<sup>th</sup> and the late 47<sup>th</sup> century BC.

We speculate that the use of the graveyard corresponds to the duration of dwellings. The typical duration of a long-house of the Neolithic Linear Pottery Culture was estimated to be between 20–30 years (Modderman 1968) and up to 75–100 years when maintained (Rück 2007). Experimental archaeology suggested that the lake dwellings in the Jura of the late Neolithic period would have lasted for a period of about ten years without proper maintenance (Pétrequin et al. 2015). However, no settlement was found directly associated with the Gurgy graveyard, precluding the integration of contextual details. An alternative, or complementary, explanation for a limited occupation time could be the depletion of local soils or other natural resources, driven by non-sustainable agricultural practices that could have taken different forms; however, this is still the subject of intense debate (Boserup 1965; Pétrequin et al. 2015).

### Inferences beyond the site: questioning the regional network

The biological structure of the group buried at Gurgy revealed by the two main pedigrees and the unlinked individuals sheds light on some of the rules that potentially governed this community. The patrilineal, patrilocal, and female exogamic pattern we observed requires a population large enough to avoid recurrent close-related females amongst those who came to join the Gurgy group, as was also shown by the background relatedness of the analysis of runs of homozygosity. However, this network of relationships with other groups includes occasional unions with (distantly) related women from the same source group, suggesting preferential links, abiding alliances, or dependencies between some groups.

The independent lines of evidence suggest that the social system at work in the Gurgy community implies a number of external groups presumably bound by reciprocal alliances, which may have been structured by a range of features, such as population size, access to and exchanges of resources, a socio-economic network, or common linguistic and cultural affinities (e.g., shared language[s] and belief systems).

The occupation of the necropolis could be narrowed down to between the late 48<sup>th</sup> and the late 47<sup>th</sup> century BC, based on Bayesian modelling. From an archaeological perspective, the Gurgy site stands in contrast to the regional



**Fig. 8** Gurgy «les Noisats». Photo of female individual GLN270A (no genetic results) with the reburied remains of the main male ancestor GLN270B of Pedigree A.

**Abb. 8** Gurgy «les Noisats». Befundfoto des weiblichen Individuums GLN270A (keine genetischen Ergebnisse) mit den wieder bestatteten Überresten des männlichen Hauptvorfahrens GLN270B von Stammbaum A.

context of contemporaneous monumental sites that are associated with the Cerny Culture, and which were built for selected individuals (Chambon/Thomas 2010). Fleury-sur-Orne, Calvados Department, in Normandy is the only monumental site from the Cerny area that has been genetically investigated to date and it shows a strong social selection of individuals buried in different monuments according to different patrilineal lineages (Rivollat et al. 2022). Given the structural differences between Fleury and Gurgy, but also taking into account the STP sites from the Paris Basin, it remains difficult to draw conclusions by combining information obtained from both studies.

In the case of Gurgy, it is possible that two different communities co-existed in the same region: one that buried their dead at Gurgy and one that had used the STPs, with different funerary practices and attitudes towards social ranking. This hypothesis is reflected in the material culture, as Gurgy does not show a clear attribution to the Cerny Culture, although the site is contemporaneous and Cerny sites are located nearby. Gurgy burials show multiple influences from different cultures, some local, such as alcove burials from LBK-derived groups in the West, while others originated further away, like Chamblandes cists from the Alps, or specific shells from the Mediterranean area. However, if Gurgy was culturally isolated from the surrounding context, this would be inconsistent with the genetic evidence that shows strong links with a wider biological net-

work over several generations, or would instead imply that the network exclusively exceeded the Cerny lacuna.

Given the absence of selection of individuals on the basis of sex, age, economic or social hierarchies at the regional level in Gurgy, an alternative interpretation would be that the site represented the burial practices of the non-elite for a broader society in which the STP-buried individuals were the elite at the regional level. Under this assumption, as the Gurgy site was used by a single group, which was genetically highly related, we would expect contemporaneous graveyards of similar sizes to meet the expectations from the observed genetic diversity estimates, such as mitochondrial haplogroup diversity and runs of homozygosity. However, only three other contemporaneous graveyards without monuments are known from the area, and these are all much smaller: Monéteau ›Macherin‹ located only 3 km from Gurgy and having *Chassen* components, Vignely ›La Porte aux Bergers‹, Seine-et-Marne Department, and Chichery ›sur les Pâturaux‹, Yonne Department, with 15, 17, and 27 buried individuals, respectively<sup>3</sup>. If we consider the total number of individuals buried at these sites as potential non-elite, this number ( $n = 187$ ) is too low compared to the known 120 individuals buried at the monumental STP sites (Chambon 2003; Chambon/Thomas 2010; Thomas 2011). This might suggest a strong bias in the excavation strategy or the preservation of the sites.

Looking at the site level, we observe subtle elements of, if not hierarchy, then at least specific consideration of some individuals, such as the larger sizes of the graves of GLN207B's son (GLN237A) and grandson (GLN221B). However, this example is far from the ostentatious demonstration visible in the STPs, with none of the elements present in STP sites that emphasize a hierarchical structure (monuments, gender-related scenography, grave goods; Chambon/Thomas 2010) are visible at Gurgy. Admittedly, GLN207B, the main ancestor of the largest pedigree, has a very specific

funerary treatment compared to all other individuals buried in Gurgy, but no other sign of power/wealth in the material culture was found. We suggest that it was important for his community/lineage to (re)bury him in the same place where his descendants will be buried for a few generations, but not at the level of supra-regional significance outside the community.

On the basis of combined evidence available at present, we favour the latter hypothesis, suggesting that the different necropolises without monuments in the Paris Basin do in fact represent the non-elite, while many others, which we would assume to have had a similar structure and/or organisation, have not yet been found. This is more in line with the genetic data showing a wide and connected network over several generations. Overall, the lack of comparative data from STP sites and non-monumental sites present in the region imposes a limitation that does not allow us to go beyond a tentative interpretation of our findings.

## Conclusion

These largest pedigrees reconstructed from ancient human DNA data so far represent a major and unprecedented step forward in our understanding of the social organization of a human group from Gurgy ›les Noisats‹, and of Middle Neolithic societies of Western Europe more broadly. What remains to be determined is whether our findings are an exception among the Neolithic societies, where the observed variety of different funerary settings is striking, or whether Gurgy represents the norm of governing social structures and kinship practices during the 5<sup>th</sup> millennium BC. Therefore, our work provides an anchor for further archaeogenetic studies to reach a general consensus on the potentially diverse social organisation(s) of Neolithic societies in Europe.

## Bibliography

### Allard 2007

P. Allard, The Mesolithic – Neolithic transition in the Paris Basin: a review. *Proc. British Acad.* 144, 2007, 211–223, doi:10.5871/bacad/9780197264140.003.0011.

### Augereau/Chambon 2011

A. Augereau/P. Chambon, Les occupations néolithiques de Macherin à Monéteau (Yonne). *Collection Mém.* 53 (Paris 2011).

### Boserup 1965

E. Boserup, The conditions of agricultural growth. The economics of agrarian change under population pressure (London 1965).

### Chambon 2003

P. Chambon, Revoir Passy à la lumière de Balloy: les nécropoles monumentales Cerny du bassin Seine-Yonne. *Bull. Soc. Préhist. Française* 100,3, 2003, 505–515.

### Chambon et al. 2010

P. Chambon/J.-P. Delor/A. Augereau/J. F. G. Bao/

K. Meunier et al., La nécropole du Néolithique moyen de Sur les Pâturaux à Chichery (Yonne). *Gallia Préhist.* 52, 2010, 117–192.

### Chambon/Lanchon 2003

P. Chambon/Y. Lanchon, Les structures sépulcrales de la nécropole de Vignely (Seine-et-Marne). *Mém. Soc. Préhist. Française* 33, 2003, 159–173.

### Chambon/Thomas 2010

P. Chambon/A. Thomas, The first monumental cemeteries of western Europe: the ›Passy type‹ necropolis in the Paris basin around 4500 BC. *Journal Neolithic Arch.* 12,2, 2010, doi:10.12766/jna.2010.37.

### Childebayeva et al. 2022

A. Childebayeva/A. B. Rohrlach/R. Barquera/M. Rivollat/F. Aron et al., Population Genetics and Signatures of Selection in Early Neolithic European Farmers. *Molecular Biol. and Evolution* 39,6, 2022, msac108, doi:10.1093/molbev/msac108.

### Constantin et al. 1997

C. Constantin/D. Mordant/D. Simonin (eds.), La culture de Cerny. Nouvelle économie, nouvelle société au Néolithique. Actes du Colloque International de Nemours 9-10-11 mai 1994. *Mém. Mus. Préhist. d'Île-de-France* 6 (Nemours 1997).

### Fenner 2005

J. N. Fenner, Cross-cultural estimation of the human generation interval for use in genetics-based population divergence studies. *Am. Journal Physical Anthr.* 128,2, 2005, 415–423.

### Fu et al. 2014

Q. Fu/H. Li/P. Moorjani/F. Jay/S. M. Slepchenko et al., Genome sequence of a 45,000-year-old modern human from western Siberia. *Nature* 514, 2014, 445–449, doi:10.1038/nature13810.

### Gage 1989

T. B. Gage, Bio-Mathematical Approaches to the

<sup>3</sup> Chambon/Lanchon 2003; Chambon et al. 2010; Augereau/Chambon 2011; Thomas 2011.

- Study of Human Variation in Mortality. Yearbook Physical Anthr. 32, 1989, 185–214.
- Gallay 2007**  
A. Gallay, Cistes de type Chamblandes: 15 ans de recherches, quels progrès?. In: P. Moinat/P. Chambon (eds.), Les cistes de Chamblandes et la place des coffres dans les pratiques funéraires de Néolithique moyen occidental. Actes du colloque de Lausanne, 12 et 13 mai 2006. Cahiers Arch. romande 110 = Soc. Préhist. Française 43 (Lausanne, Paris 2007) 337–348.
- Haak et al. 2015**  
W. Haak/I. Lazaridis/N. Patterson/N. Rohland/S. Mallick et al., Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature* 552, 2015, 207–211.
- Howell 1976**  
N. Howell, Toward a uniformitarian theory of human paleodemography. *Journal Human Evolution* 5,1, 1976, 25–40, doi:10.1016/0047-2484(76)90097-X.
- Korneliusen et al. 2014**  
T. S. Korneliusen/A. Albrechtsen/R. Nielsen, ANGSD: Analysis of Next Generation Sequencing Data. *BMC Bioinformatics* 15,356, 2014, doi:10.1186/s12859-014-0356-4.
- Lazerzini et al. 2021**  
N. Lazerzini/V. Balter/A. Coulon/T. Tacail/C. Marchina et al., Monthly mobility inferred from isoscapes and laser ablation strontium isotope ratios in caprine tooth enamel. *Scien. Reports* 11, 2277, 2021, doi:10.1038/s41598-021-81923-z.
- Le Luyet et al.**  
M. Le Luyet/M. Coquerelle/S. Rottier/P. Bayle, Internal Tooth Structure and Burial Practices: Insights into the Neolithic Necropolis of Gurgy (France, 5100–4000 cal. BC). *PLOS ONE* 11,7, 2016, e0159688, doi:10.1371/journal.pone.0159688.
- Le Roy 2015**  
M. Le Roy, Les enfants au Néolithique. Du contexte funéraire à l'interprétation socioculturelle en France de 5700 à 2100 ans av. J.-C. Diss. Univ. Bordeaux (Bordeaux 2015).
- Le Roy 2016**  
M. Le Roy/M. Rivollat/F. Mendisco/M.-H. Pemonge/C. Coutelier et al., 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). *Journal Arch. Scien.* 73, 2016, 45–54.
- Lévi-Strauss 1971**  
C. Lévi-Strauss, The elementary structures of kinship (Boston 1971).
- Lichardus-Itten 1986**  
M. Lichardus-Itten, Premières influences méditerranéennes dans le Néolithique du Bassin parisien, contribution au débat. In: J.-P. Demoule/J. Guilaine (eds.), Le Néolithique de la France. Hommage à Gérard Bailloud (Paris 1986) 147–160.
- Lipatov et al. 2015**  
M. Lipatov/K. Sanjeev/R. Patro/K. R. Veeramah, Maximum Likelihood Estimation of Biological Relatedness from Low Coverage Sequencing Data. *bioRxiv* 2015, 023374, doi:10.1101/023374.
- Maricic et al. 2010**  
T. Maricic/M. Whitten/S. Pääbo, Multiplexed DNA Sequence Capture of Mitochondrial Genomes Using PCR Products. *PLOS ONE* 5,11, 2010, e14004, doi:10.1371/journal.pone.0014004.
- Mathieson et al. 2016**  
I. Mathieson/I. Lazaridis/N. Rohland/S. Mallick/N. Patterson et al., Genome-wide patterns of selection in 230 ancient Eurasians. *Nature* 528, 2015, 499–503.
- Mittnik et al. 2016**  
A. Mittnik/C.-C. Wang/J. Svoboda/J. Krause, A Molecular Approach to the Sexing of the Triple Burial at the Upper Paleolithic Site of Dolní Věstonice. *PLOS ONE* 11,10, 2016, e0163019, doi:10.1371/journal.pone.0163019.
- Modderman 1968**  
P. J. R. Modderman, Die Hausbauten und Siedlungen der Linienbandkeramik in ihrem westlichen Bereich. In: H. Schwabedissen (ed.), Die Anfänge des Neolithikums vom Orient bis Nordeuropa. Teil 5. Westliches Europa. *Fundamenta A3* (Köln, Graz 1968) 1–7.
- Moinat/Chambon 2007**  
P. Moinat/P. Chambon, Les cistes de Chamblandes et la place des coffres dans les pratiques funéraires du Néolithique moyen occidental. Actes du colloques de Lausanne, 12 et 13 mai 2006. *Cahier Arch. Romande 110 = Soc. Préhist. Française, Mém.* 43 (Lausanne, Paris 2007).
- Monroy Kuhn et al. 2018**  
J. M. Monroy Kuhn/M. Jakobsson/T. Günther, Estimating genetic kin relationships in prehistoric populations. *PLOS ONE* 13,4, 2018, e0195491, doi:10.1371/journal.pone.0195491.
- Pétrequin et al. 2015**  
P. Pétrequin/A.-M. Pétrequin/C. Schaal, Introduction. Rythme d'occupation des villages et agriculture céréalière. In: P. Pétrequin/A.-M. Pétrequin (eds.), Clairvaux et le »Néolithique Moyen Bourguignon« 2. *Cahiers MSHE Ledoux* (Franche-Comté 2015) 1129–1149.
- Rey et al. 2017**  
L. Rey/G. Goude/S. Rottier, Comportements alimentaires au Néolithique: nouveaux résultats dans le Bassin parisien à partir de l'étude isotopique ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) de la nécropole de Gurgy »Les Noisats« (Yonne, Ve millénaire av. J.-C.). *Bull. Mém. Soc. Anthr. Paris* 29,1–2, 2017, 54–69.
- Rey et al. 2019**  
L. Rey/D. C. Salazar-García/F. Santos/S. Rottier/G. Goude, A multi-isotope analysis of Neolithic human groups in the Yonne valley, Northern France: insights into dietary patterns and social structure. *Arch. and Anthr. Scien.* 11,10, 2019, 5591–5616.
- Rey et al. 2021**  
L. Rey/S. Rottier/F. Santos/G. Goude, Sex and age-related social organization in the Neolithic: A promising survey from the Paris Basin. *Journal Arch. Scien., Reports* 38,103092, 2021, doi:10.1016/j.jasrep.2021.103092.
- Ringbauer et al. 2023**  
H. Ringbauer/Y. Huang/A. Akbari/S. Mallick/N. Patterson et al., ancIBD – Screening for identity by descent segments in human ancient DNA. *bioRxiv* 2023, doi:10.1101/2023.03.08.531671.
- Ringbauer et al. 2021**  
H. Ringbauer/J. Novembre/M. Steinruecken, Parental relatedness through time revealed by runs of homozygosity in ancient DNA. *Nature Commun.* 12,5425, 2021, doi:doi.org/10.1038/s41467-021-25289-w.
- Rivollat et al. 2015**  
M. Rivollat/F. Mendisco/M.-H. Pemonge/A. Safi/D. Saint-Marc et al., When the Waves of European Neolithization Met: First Paleogenetic Evidence from Early Farmers in the Southern Paris Basin. *PLOS ONE* 10,4, 2015, e0125521, doi:10.1371/journal.pone.0125521.
- Rivollat et al. 2017**  
M. Rivollat/S. Rottier/C. Couture/M.-H. Pemonge/F. Mendisco et al., Investigating mitochondrial DNA relationships in Neolithic Western Europe through serial coalescent simulations. *European Journal Human Genetics* 25,3, 2017, 388–392, doi:10.1038/ejhg.2016.180.
- Rivollat et al. 2020**  
M. Rivollat/C. Jeong/S. Schiffels/I. Küçükkalipçi/M.-H. Pemonge et al., Ancient genome-wide DNA from France highlights the complexity of interactions between Mesolithic hunter-gatherers and Neolithic farmers. *Scien. Advances* 6,22, 2020, eaaz5344, doi:10.1126/sciadv.aaz5344.
- Rivollat et al. 2022**  
M. Rivollat/A. Thomas/E. Ghesquière/A. B. Rohrlach/E. Späth et al., Ancient DNA gives new insights into a Norman Neolithic monumental cemetery dedicated to male elites. *Proc. Nat. Acad. Scien. USA* 119,18, 2022, e2120786119, doi:10.1073/pnas.2120786119.
- Rivollat et al. 2023**  
M. Rivollat/A. B. Rohrlach/H. Ringbauer/A. Childebayeva/F. Mendisco et al., Extensive pedigrees reveal the social organization of a Neolithic community. *Nature* 620, 2023, 600–606, doi:10.1038/s41586-023-06350-8.
- Rohrlach et al. 2021**  
A. B. Rohrlach/L. Papac/A. Childebayeva/M. Rivollat/V. Villalba-Mouco et al., Using Y-chromosome capture enrichment to resolve haplogroup H2 shows new evidence for a two-Path Neolithic expansion to Western Europe. *Scien. Reports* 11,15005, 2021, doi:10.1038/s41598-021-94491-z.
- Rottier 2007**  
S. Rottier, L'architecture funéraire des sépultures du Néolithique moyen des Noisats à Gurgy (Yonne, France). In: P. Moinat/P. Chambon (eds.), Les cistes de Chamblandes et la place des coffres dans les pratiques funéraires de Néolithique moyen occidental. Actes du colloque de Lausanne, 12 et 13 mai 2006. *Cahiers Arch. Romande 110 = Soc. Préhist. Française* 43 (Lausanne, Paris 2007) 99–107.
- Rottier et al. 2005**  
S. Rottier/C. Mordant/P. Chambon/C. Thevenet, Découverte de plus d'une centaine de sépultures du Néolithique moyen à Gurgy, les Noisats (Yonne). *Bull. Soc. Préhist. Française* 102,3, 2005, 641–645.
- Rück 2007**  
O. Rück, Neue Aspekte und Modelle in der Siedlungsforschung zur Bandkeramik. Die Siedlung Weisweiler 111 auf der Aldenhovener Platte, Kr. Düren. *Internat. Arch.* 105 (Rahden/Westfalen 2007).
- Sidéra 2010**  
I. Sidéra, De mains méridionales en mains septentrionales. Le long transit des objets et des savoir-faire en Europe occidentale, vers 5100 av. J.-C. *Mél. Casa Velázquez N. S.* 40,1, 2010, 17–32.
- Thevenet 2010**  
C. Thevenet, Des faits aux gestes...des gestes aux sens? Pratiques funéraires et société durant le Néolithique ancien en Bassin parisien. Diss. Univ. Paris 1 Panthéon-Sorbonne (Paris 2010).
- Thomas 2011**  
A. Thomas, Identités funéraires, variants biologiques et facteurs chronologiques. Une nouvelle perception du contexte culturel et social du Cerny (Bassin parisien, 4700–4300 avant J.-C.). Diss. Univ. Bordeaux 1 (Bordeaux 2011).
- Wood et al. 2002**  
J. W. Wood/D. J. Holman/K. A. O'Connor/R. J. Ferrell, Mortality models for paleodemography. In: R. D. Hoppa/J. W. Vaupel (eds.), *Paleodemography. Age distributions from skeletal samples.* Cambridge Stud. Biol. and Evolutionary Anthr. 31 (Cambridge 2002) 129–168, doi:10.1017/CBO9780511542428.

## Sources of figures

|   |                         |   |                         |   |             |
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