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Capturing the fusion of two ancestries and kinship structures in Merovingian Flanders

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The Merovingian period (5th to 8th cc AD) was a time of demographic, socioeconomic, cultural, and political realignment in Western Europe. Here, we report the whole-genome shotgun sequence data of 30 human skeletal remains from a coastal Late Merovingian site of Koksijde (675 to 750 AD), alongside 18 remains from two Early to Late Medieval sites in present-day Flanders, Belgium. We find two distinct ancestries, one shared with Early Medieval England and the Netherlands, while the other, minor component, reflecting likely continental Gaulish ancestry. Kinship analyses identified no large pedigrees characteristic to elite burials revealing instead a high modularity of distant relationships among individuals of the main ancestry group. In contrast, individuals with >90% Gaulish ancestry had no kinship links among sampled individuals. Evidence for population structure and major differences in the extent of Gaulish ancestry in the main group, including in a mother–daughter pair, suggests ongoing admixture in the community at the time of their burial. The isotopic and genetic evidence combined supports a model by which the burials, representing an established coastal nonelite community, had incorporated migrants from inland populations. The main group of burials at Koksijde shows an abundance of >5 cM long shared allelic intervals with the High Medieval site nearby, implying long-term continuity and suggesting that similarly to Britain, the Early Medieval ancestry shifts left a significant and long-lasting impact on the genetic makeup of the Flemish population. We find substantial allele frequency differences between the two ancestry groups in pigmentation and diet-associated variants, including those linked with lactase persistence, likely reflecting ancestry change rather than local adaptation.

Merovingian | kinship | ancestry | ancient DNA

Significance

The extent and impact of Early Medieval population movements on the establishment of trade and cultural networks across the North Sea have been the subject of debate for centuries. Analyzing ancient genomes from the Flemish coast, we find two distinct ancestry groups merging in a Late Merovingian community: the major group with a dense network of distant relationships among individuals and genetic affinity to populations around the North Sea coast and the minor group representing likely continental Gaulish ancestry of unrelated individuals from various inland sources. We also find evidence of local continuity suggesting that similarly to Britain, the Early Medieval population movements had a long-term impact and were integral to the formation of the Flemish population.

Flanders emerged as a pivotal hub of European trade and the birthplace of capitalism by the end of the first millennium, marked by the rise of its coastal and inland waterway-connected cities (1). The name of the region, derived from an old Germanic root *flauma* meaning "inundated land", reflects its nature as flood-prone coastal wetland along the North Sea. Historical and archaeological evidence confirms that the Merovingian period (450 to 750 AD) witnessed expansion of pioneer settlements in salt marshes on the coast and major changes in material culture, socioeconomic, and cultural frameworks and a linguistic transition from Gaulish to Germanic in the North Sea region as a whole (2–5). The terminological and chronological label of the "Merovingian period" is derived from the dynasty of the Merovingians. At the peak of their power, Merovingian kingdoms extended across modern France, Belgium, Netherlands, Luxemburg, and part of Germany. Changes in political power under the rule of these kings may have affected differently population continuity and mobility of upper and lower levels of social hierarchy.

Archaeological research has distinguished two Early Medieval cultural groups in present-day western Flanders, Belgium: 1) communities along the North Sea coast culturally aligned with the "North Sea culture," a complex of shared types of material culture and language dialects (6), and 2) inland river basin communities culturally more aligned with northern France, the Meuse valley, and the Rhineland (7, 8). While these cultural traditions are well established, their interaction and demic relationships as well as the extent to which the movement of people was crucial in establishing trade and cultural networks on the Flemish coast remains uncertain. Ancient DNA analyses of Anglo-Saxon sites in England have provided evidence of a large-scale migration from the continental North Sea zone (cNSz) during the Early Middle Ages that accounted for more than three-quarters

The authors declare no competing interest.

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of the genetic ancestry of individuals buried in these sites (9). Nonetheless, in Flanders, the enduring presence of cremation from the Bronze Age up to the second half of the 7th century AD together with general poor preservation of human remains has restricted so far the use of ancient DNA to illuminate the demographic shifts of this transformative period in this region (10).

The Early Medieval site of Koksijde (675 to 750 AD) is one of the few known Merovingian-period burial grounds from coastal Flanders with detailed burial context descriptions and data from a range of isotopic and osteological methods (11). A previous study of isotope data revealed the cohabitation of two distinct groups of individuals with clear differences in dietary (δ^{15}N, $\delta^{13}C_{col}$), water source (δ^{18}O), and mobility (^{87}Sr/^{86}Sr) isotope profiles (12). In this study, we use whole-genome sequence data from Koksijde and two other medieval sites from present-day Flanders in the context of data available from Early Medieval sites and present-day populations from the North Sea zone to determine the origins of a Late Merovingian community, its genetic relationship to other North Sea communities, their kinship structure, and continuity in time. We will test the hypothesis that the two distinct isotope groups reflect the genetic population structure in the community.

Results

We generated whole-genome shotgun sequence data from 48 human skeletal remains from three Early to Late Medieval sites in present-day Flanders, Belgium, keeping for further genome-scale analyses 44 genomes sequenced to autosomal mean coverage higher than 0.01×, including 34 with coverage >0.12 that were used in imputation-based analyses (Table 1 and *SI Appendix*, Table S1). Four individuals with coverage <0.01× were used only in mtDNA analyses, sex determination, and metagenomic screening. Isotope analyses of 23 individuals originally not included in the study by Spros et al. (12) confirmed the existence of two distinct dietary groups in Koksijde burials by carbon and nitrogen isotope analyses interpretable likely as differences in the abundance of marine and terrestrial sources and revealed additional outliers in strontium isotopes (*SI Appendix*, Table S2). All six individuals from High Medieval Wulpen cemetery had coastal strontium, terrestrial dietary isotope ratios, and oxygen values similar to Koksijde burials.

Analyses of Population Structure. In order to get insights into the genetic ancestry of individuals buried at the Merovingian site at Koksijde, we performed principal component analysis (PCA) on imputed genomes in the context of genomic data from a broader reference dataset of modern and ancient Europeans, including data from a High to Late Medieval (11th to 15th cc) site Wulpen near Koksijde, and burials from Sint-Truiden dating to the Early to Late Medieval periods (Fig. 1*A*). We found that all examined genomes from Medieval Flanders map to a broad regional cluster that covers present-day West and Northwest Europeans (Fig. 1*B*). In contrast to Iron Age French Gaul genomes (13), the majority of which (17/18) cluster with modern French from the UK Biobank, the medieval genomes from Flanders show wider distribution with substantial overlap, particularly in the case of the Koksijde samples, with Scandinavian and Dutch genomes (Fig. 1*C*). A small subset of four Koksijde genomes (KOS001, KOS009, KOS032, and KOS038) map closely to the French Gauls, outside the range of modern Flemish, while the remainder map on modern Flemish, Danish, and Dutch genomes. All five individuals sampled from Wulpen fall within the range of present-day Dutch and Flemish genomes while most of the Sint-Truiden samples lie between the Koksijde and Late Iron Age French Gaul samples.

Genetic distances between the Early Medieval and Late Iron Age populations of the North Sea region, measured by F_{ST}, were greater than they are today (*SI Appendix*, Fig. S1). Genetic distances among Early Medieval sites from the Low Countries, England, and Ireland were comparable to the distances seen today between the Low Countries and Spain. The finding of two distinct subgroups of Koksijde genomes in the PCA could be indicative either of a large randomly mating population maintaining high level of heterogeneity or the presence of a structured population in the Koksijde community at the time of sampling. Under the latter scenario, we would expect to find a deficit of heterozygous genotypes, particularly at variants showing the highest allele frequency difference between the ancestral sources. In an ancestrally diverse population, in contrast, a single generation of random mating would be expected to return genotypes to Hardy–Weinberg equilibrium. To distinguish between these alternatives we applied the Hardy–Weinberg equilibrium test (*SI Appendix*, section SI11) on common variants across the genome and found significant deficit ($P < 0.001$, binomial test) of heterozygous genotypes at variants that failed the HWE test at $P < 0.01$, the effect of which was highest in variants with high F_{ST} values between

Table 1. Ancient genomes analyzed in this study

			Number of individuals		
Archaeological site, province, country	Period, date range	Source	Total	≥0.01×	imputed
Koksijde, W-Flanders, Belgium	Merovingian, 7th to 8th cc	1	30	26	20
Wulpen, W-Flanders, Belgium	High to Late Medieval, 11th to 14th cc	1	6	6	5
Sint-Truiden, Limburg, Belgium	Early to Late Medieval, 8th to 13th cc	1	12	12	9
France	Late Iron Age (LIA), 5th to 1st cc BC	2			18
England	Late Iron Age/Roman	3 to 5			30
England	Early Medieval, 5th to 9th cc	6			152
Ireland	Early to Late Medieval, 7th to 13th cc	6			21
Netherlands	Early Medieval, 4th to 11th cc	6			22
Alt-Inden, N-Rhine, Germany	Merovingian, 5th to 8th cc	6			9
Lower Saxony, Germany	Early Medieval, 5th to 10th cc	6			26
Rathausmarkt, Schleswig, Germany	High Medieval, 11th to 12th cc	6			11
Denmark	High Medieval, 11th to 13th cc	6			7

Note: ≥0.01×—number of genomes sequenced to coverage ≥0.01×, imputed—number of genomes imputed in this study; all date ranges except for the Late Iron Age France are AD. Sources: 1—this study, 2—Fischer et al. (13), 3—Scheib et al. (14), 4—Schiffels et al. 2016, 5—Martiniano et al. (15), and 6—Gretzinger et al. (9).

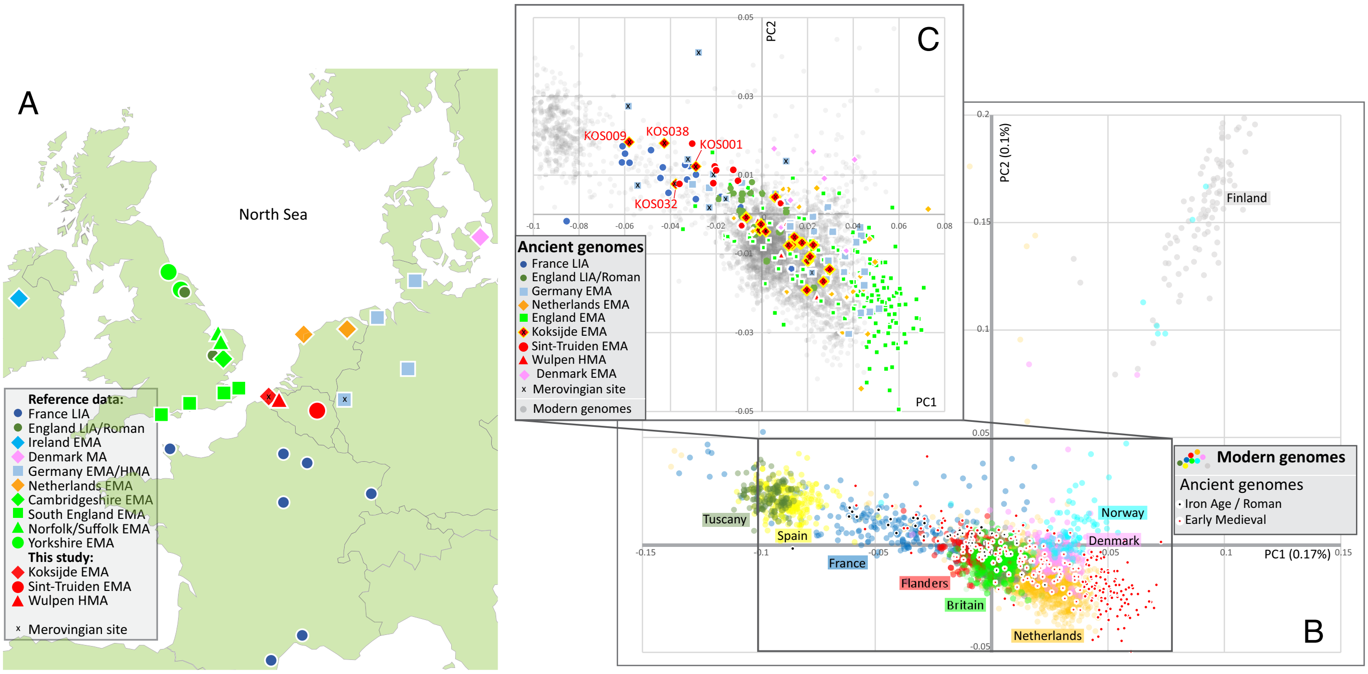


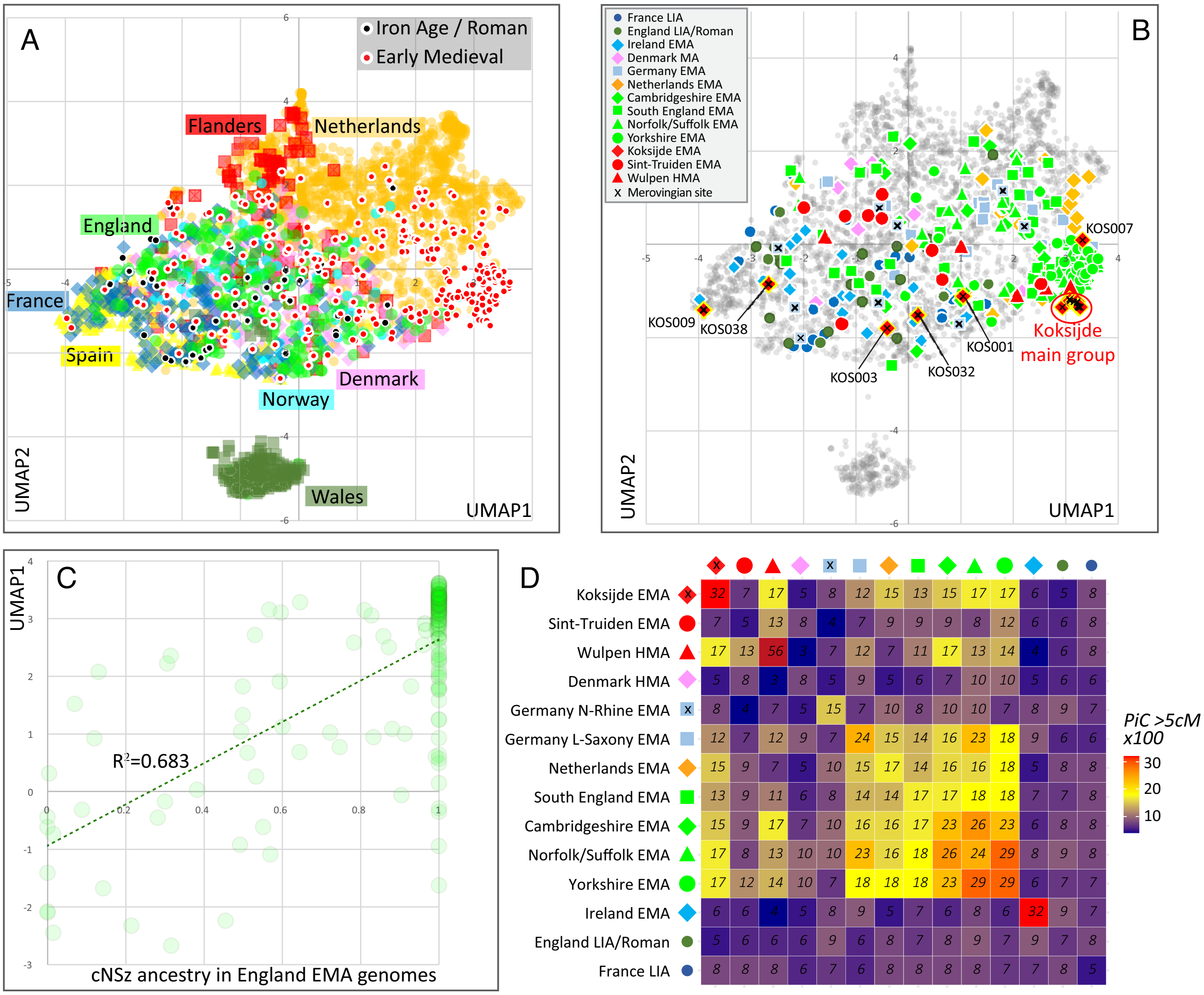
Fig. 1. Sampling locations and genetic ancestry of the examined Early/Later Medieval genomes from present-day Flanders, Belgium. (*A*) Map of the North Sea region with Early (EMA) and High (HMA) Medieval, Roman, and Late Iron Age (LIA) archaeological site locations used in data analyses, including genomes reported in this study (red) and available reference data. (*B*) Principal component analysis (PCA) of medieval genomes from present-day Flanders, Belgium, and selected modern and ancient genomes from Europe. Modern population sources: 99 FIN—Finnish, 107 IBS—Iberian, 107 TSI—Toscan genomes from the 1000 Genomes Project; 97 DEN—Danish, 98 NOR—Norwegian, 93 FRA—French individuals from the UK Biobank; 126 FLA—Flemish and 115 NED—Dutch from the MinE consortium data. (*C*) Ancient imputed genomes with coverage >0.1× were included in the PCA after removal of 1st and 2nd-degree-related individuals from modern and ancient cohorts. PCA was run with FlashPCA2 without projection and included 20 Koksijde, 9 Sint-Truiden, 6 Wulpen individuals from this study, 18 Iron Age French Gaul samples from Fischer et al. (13), and 248 Early medieval genomes from Gretzinger et al. (9). Individual identifiers are shown for the four Koksijde outliers.

Late Iron Age genomes from France and Early Medieval genomes from England. The deficit of heterozygous genotypes was significantly ($P < 0.001$, Chi-square test) reduced after removal of the four outliers suggesting that the Koksijde community was indeed genetically structured.

We next applied outgroup f3 analyses on imputed Koksijde, Sint-Truiden, and Wulpen genomes to search at group and individual levels the closest ancestral populations. We found (*SI Appendix*, Table S4) that the three medieval sites in present-day Flanders, Belgium, share most genetic drift with Early Medieval genomes from England (9) and Langobard genomes from Hungary and Italy, the ancestry of which is best modeled with a source in Britain or Germany (16). Notably, between the two Merovingian sites, Koksijde from Flanders and Alt-Inden from North Rhine-Westphalia (9), drift sharing appears to be low (*SI Appendix*, Table S4). Compared to the Koksijde main group, the group of four outliers showed lower (Z > 4) affinity to Early Medieval North Sea coast populations as well as Viking Age groups from Scandinavia and the North Sea coast (*SI Appendix*, Table S5). Further f4 tests of imputed ancient genomes from Flanders showed higher allele frequency sharing with Early Medieval England than with continental Iron Age sources (*SI Appendix*, Fig. S2). Similarly, Koksijde, as well as Wulpen and Sint-Truiden, genomes showed higher affinity to Early Medieval genomes from England than to genomes from the other Merovingian site, Alt-Inden (*SI Appendix*, Fig. S3).

To further test the hypothesis that the Koksijde community was genetically structured, we used long shared allelic intervals (LSAI) in combination with unsupervised clustering methods to study the ancestry sources of Koksijde genomes and their connectedness with ancient and modern genomes of the North Sea region. Using IBIS (17) we detected 401,202 individual pairs sharing LSAIs longer than 5 cM in a pooled data of 322 ancient imputed genomes and 3,295 modern North and West European individuals from the UK Biobank (18), MinE consortium data (19, 20), GoNL (21), and 1000 Genomes Project Phase 3 data (22). With the Leiden algorithm (23) applied on the IBIS output with two-level search range, we extracted 32 communities with 15 or more individuals, the geographic distribution of the majority of which was region-specific (*SI Appendix*, Table S6). Applying UMAP (24) on the probability of individual connectedness (PiC) scores (25) estimated for the 32 extracted communities revealed the separation of modern West European genomes by broad geographic regions and the clustering of the majority of Early Medieval genomes with present-day Dutch, Danish, and English genomes (Fig. 2*A*).

The majority of Koksijde genomes cluster with contemporary Early Medieval genomes from England and the Netherlands, separately from the Iron Age/Roman genomes from France and Britain (Fig. 2*B*). Individuals from Early Medieval England that cluster close to the Koksijde genomes have the majority of their ancestry in cNSz according to the qpAdm estimates of (9). We find high correlation ($r^2 = 0.68$) between the cNSz ancestry in Early Medieval English genomes from Anglo-Saxon cemeteries as estimated by Gretzinger et al. (9) and the UMAP1 values (Fig. 2*C*). This is further reflected in the positioning of the Koksijde outliers (Fig. 2*B*) among genomes with low cNSz ancestry. Notably, four of the five outliers with low UMAP1 values (KOS001, KOS003, KOS009, KOS032, and KOS038) were also outliers in the allele frequency–based PC analyses (Fig. 1). In contrast, Koksijde's main group, clustering together with Early Medieval English genomes with high cNSz ancestry (Fig. 2*B*), shows the highest connectedness with the Early Medieval genomes from England and the Netherlands while having low connectedness with High Medieval genomes from Denmark as well as the genomes from the Merovingian site Alt-Inden from Gretzinger et al. (9) study (Fig. 2*D*). Notably, among the genomes with high UMAP1 values,



	◆	●	▲	◆	■	■	◆	■	◆	▲	●	◆	●	●
Koksijde EMA ◆	32	7	17	5	8	12	15	13	15	17	17	6	5	8
Sint-Truiden EMA ●	7	5	13	8	4	7	9	9	9	8	12	6	6	8
Wulpen HMA ▲	17	13	56	3	7	12	7	11	17	13	14	4	6	8
Denmark HMA ◆	5	8	3	8	5	9	5	6	7	10	10	5	6	6
Germany N-Rhine EMA ■	8	4	7	5	15	7	10	8	10	10	7	8	9	7
Germany L-Saxony EMA ■	12	7	12	9	7	24	15	14	16	23	18	9	6	6
Netherlands EMA ◆	15	9	7	5	10	15	17	14	16	16	18	5	8	8
South England EMA ■	13	9	11	6	8	14	14	17	17	18	18	7	7	8
Cambridgeshire EMA ◆	15	9	17	7	10	16	16	17	23	26	23	6	8	8
Norfolk/Suffolk EMA ▲	17	8	13	10	10	23	16	18	26	24	29	8	9	8
Yorkshire EMA ●	17	12	14	10	7	18	18	18	23	29	29	6	7	7
Ireland EMA ◆	6	6	4	5	8	9	5	7	6	8	6	32	9	7
England LIA/Roman ●	5	6	6	6	9	6	8	7	8	9	7	9	7	8
France LIA ●	8	8	8	6	7	6	8	8	8	8	7	7	8	5

Fig. 2. Genetic ancestry analyses based on LSAI sharing and community extraction. (*A*) UMAP plot of 27 PiC vectors estimated for communities extracted with the Leiden method from LSAI sharing (>5 cM threshold) data for 322 ancient and 3,295 modern genomes. Geographic origin of modern populations is highlighted with different colors. (*B*) The same plot as *A* but with geographic sources of the ancient individuals indicated by color. (*C*) Correlation between the UMAP1 and continental North Sea zone (cNSz) ancestry reported for English Anglo-Saxon and Roman context burials by Gretzinger et al. (9). (*D*) Heatmap of mean LSAI sharing PiC scores estimated for 14 ancient groups of individuals directly without community extraction.

one individual, KOS007, mapped separately from the others in the main group. As a whole, Koksijde genomes show higher ($P = 0.048$, *t* test) LSAI sharing locally with High Medieval Wulpen genomes (mean PiC = 0.17) than with contemporary Sint-Truiden genomes from Limburg (PiC = 0.07; *SI Appendix*, Table S7). While the Wulpen genomes show the highest affinity locally with present-day genomes from the Belgian provinces of East and West Flanders, we do not find similar regional patterns for Koksijde or Sint-Truiden, suggesting that the regional differences between Belgian and Dutch provinces emerged after the Early Middle Ages.

As our PCA, f4 tests and analyses of individual connectedness pointed to at least two different ancestry sources in Koksijde, one related to Early Medieval North Sea communities and the other likely to local Gaulish populations, we further explored the sources of ancestry of Koksijde individuals with qpAdm (26) using data from Late Iron Age France (13) as the proxy for Gaulish ancestry, and Early Medieval genomes with >99% cNSz ancestry from England (9) as proxies for coastal North Sea ancestry. Analyses comparing the results obtained with imputed and haploid-called data (*SI Appendix*, Tables S8–S13) showed consistency in identification of the major contributor, with differences of the assigned ancestry proportions between imputed and haploid-called targets spanning from 0.023 to 0.359, with an average of 0.139 (*SI Appendix*, Table S13). We also tested the performance of four different proxies of the coastal North Sea ancestry (*SI Appendix*, Table S9). Consistent with PCA, f4 tests, and IBD analyses, the qpAdm results show that the Koksijde samples can be generally clustered in two groups: one with a high England EMA-like ancestry and one with a high French Gaul-like ancestry. Five individuals (KOS001, KOS009, KOS010, KOS032, and KOS038), including four PCA outliers (Fig. 1), showed the highest proportion (>90%) of Gaulish ancestry (Fig. 3) in tests specifying either two (*SI Appendix*, Tables S9 and S10) or one ancestral source (*SI Appendix*, Tables S11 and S12). Notably, in the main ancestry group by PCA (Fig. 1), we find a high level of variability in individual ancestry proportions, with a range of 0 to 68% of Gaulish ancestry.

Kinship Analysis. Apart from genetic ancestry, kinship analyses can be used to study community structure in cemeteries of multiple burials like Koksijde. To test whether the burials belonged to one or a few family groups, we first examined uniparentally inherited

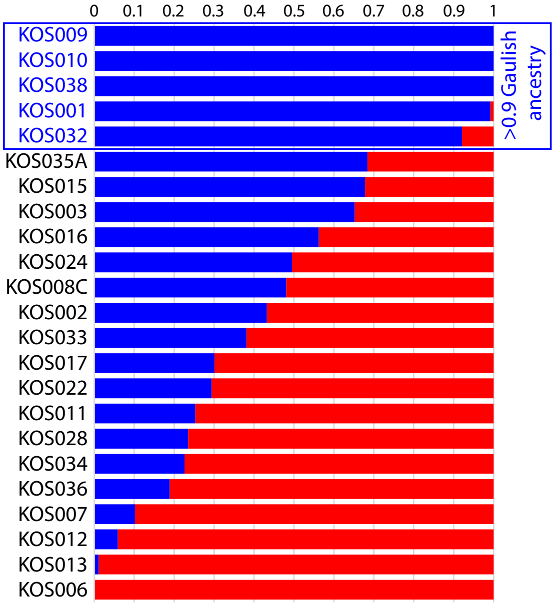


Fig. 3. qpAdm-based Gaulish and North Sea zone ancestry estimates in Koksijde burials. Presented Gaulish (blue) and North Sea zone (red) ancestry proportions represent the best fit qpAdm model (*SI Appendix*, Table S13) for each individual tested.

mitochondrial DNA (mtDNA) and Y chromosome markers for matches between individuals. Our finding of 23 distinct mtDNA haplotypes among 30 individuals examined (*SI Appendix*, section SI6 and Tables S1 and S14), and similarly high diversity of Y chromosome lineages (*SI Appendix*, section SI7) argues against the scenario that the burials could have been arranged around one or few elite families.

To uncover kinship ties beyond those detectable with uniparental markers and to test whether the two distinct ancestry groups we had detected were linked by kinship, we utilized first pairwise mismatch estimation on the pseudohaploid data with READ (27). The analyses revealed (Fig. 4) three pairs of 1st-degree and one pair of 2nd-degree relationships. Among the 1st-degree relatives, KOS022 and KOS024, confirmed by mtDNA haplotype match and shared IBD2 segments (*SI Appendix*, Table S1) to be a brother and sister pair, were buried close to other two individuals (KOS004 and KOS027) who shared the same mtDNA U4c1a lineage, but had too low coverage to be included in autosomal kinship analyses. KOS022 and KOS024 had mixed ancestry profiles (*SI Appendix*, Table S11) and isotope values indicating terrestrial diet (*SI Appendix*, Table S1). Other 1st-degree cases include a pair of brothers (KOS005 and KOS011) and a mother–daughter pair (KOS034 and KOS035A, *SI Appendix*, Table S1). Interestingly, the older woman (KOS035A), possibly the mother, had predominantly (0.68) Gaulish ancestry (*SI Appendix*, Table S11) and isotope signature of terrestrial diet (*SI Appendix*, Table S1) while the younger woman (KOS034) had only minor (0.23) Gaulish ancestry, six 3rd- to 7th-degree relationships with members of the main ancestry group (Table 2), and isotope signature of marine diet (*SI Appendix*, Table S1). The two brothers, KOS005 and KOS011, also with marine diet, carry Y chromosome haplogroup E2, which, according to available ancient DNA evidence, appears earliest in Europe in the context of Visigoth burials in Spain (28). We also detected one 2nd- and two 3rd-degree related pairs that were further confirmed by IBD analyses (Table 2). These included the 2nd-degree relationship between KOS012 and KOS034, which could reflect, for example, an uncle–niece relationship. KOS012 shares mtDNA identity with another male individual KOS018 who could potentially be his brother and the father of KOS034. The father–daughter relationship would be supported by the proximity of KOS034 and KOS018 burials, with the former buried between KOS018 and KOS035A. Due to low sequence coverage of KOS018, we could not genetically confirm this relationship.

We further used IBIS to assess the extent of sharing of long (>7 cM) IBD segments among the 23 imputed Koksijde genomes and detected 33 relationships in the main ancestry group in contrast to their complete absence in four outliers in the PCA (Fig. 1) with >90% Gaulish ancestry as well as KOS003, an outlier (Fig. 2) with 65% Gaulish ancestry (Table 2). The individual with the highest connectedness, KOS006, is a male individual, with no detectable Gaulish ancestry and perimortem weapon-related trauma on his left maxilla and parietal bone indicating a likely violent death. We detect, however, no prevalence of male individuals among the individuals with the highest number of relationships as among the eight individuals with most relationships, five are female. Another male with weapon-related trauma (KOS010) is an outlier with no relationships with other burials. Two of the third-degree relationships involve KOS033, an elderly female with a marine-influenced diet signature and predominantly North Sea zone ancestry, with two other main ancestry group individuals with marine-influenced diet. She is also distantly (7th degree) connected to KOS013 with whom she shared mtDNA J1c7a haplotype identity.

An exception to the pattern of main ancestry group individuals having extensive distant kinship ties with each other is KOS007, an individual with no detectable Gaulish ancestry and no apparent kinship ties with the rest of the sample which explains his distance from the main group in LSAI-based analyses (Fig. 2*B*). However, KOS007, one of the three males with Y chromosome haplogroup I1, shares multiple >7 cM IBD segments with three Anglo-Saxon

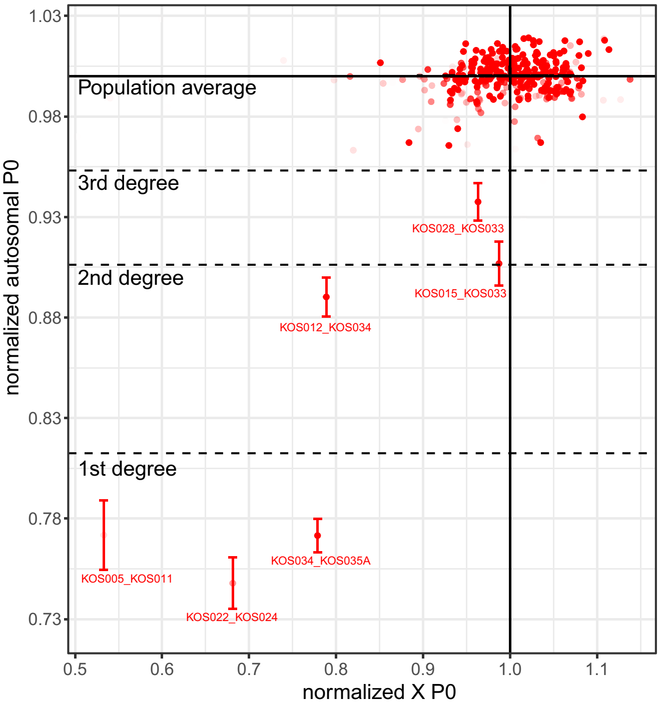


Fig. 4. Cases of 1-3rd-degree relatedness among Koksijde burials. Each individual data point (filled circle) represents a normalized pairwise difference value (P0) of a pair of Koksijde genomes estimated with READ (27). In total, 26 individuals with >0.01× were included. The aggregate coverage of each pair is reflected by the opacity of the color of the filled circle. Dashed lines indicate the cutoffs estimated as in ref. 27. Error bars with two SEM are shown for the pairs of 1st to 3rd degree of relatedness only. Considering more complex inheritance, X chromosome P0 estimates are shown only for illustrative purposes.

Table 2. Sharing of IBD segments longer than 7 cM among imputed Koksijde genomes

	KOS001*	KOS009*	KOS032*	KOS038*	KOS003	KOS007†	KOS022	KOS008C	KOS002	KOS016	KOS017	KOS015	KOS011	KOS013	KOS036	KOS012	KOS033	KOS034	KOS028	KOS006	No_rel	Sex	Gaulish_a
KOS001*																					0	XX	0.88
KOS009*																					0	XY	1
KOS032*																					0	XY	0.8
KOS038*																					0	XX	1
KOS003																					0	XX	0.63
KOS007†																					0	XY	0
KOS022												**6**			**8**						2	XX	0.37
KOS008C											**8**								**7**	**7**	3	XX	0.52
KOS002											**6**	**4**					**5**				3	XY	0.49
KOS016											**6**							**7**	**8**		3	XY	0.51
KOS017								**2**	**7**	**4**											3	XY	0.26
KOS015							**6**		**19**						**4**		**3**				4	XY	0.66
KOS011														**6**		**4**		**5**	**6**	**5**	5	XY	0.2
KOS013													**5**		**8**	**8**	**7**			**7**	5	XX	0
KOS036							**3**					**16**		**2**		**7**				**4**	5	XX	0.03
KOS012													**14**	**3**	**3**			**2**	**8**	**7**	6	XY	0.02
KOS033									**14**			**39**		**2**				**6**	**3**	**5**	6	XX	0.39
KOS034										**4**			**10**			**55**	**6**		**6**	**6**	6	XX	0.22
KOS028								**3**		**2**			**6**			**2**	**31**	**6**		**5**	7	XX	0.19
KOS006								**3**					**7**	**3**	**22**	**5**	**9**	**5**	**9**		8	XY	0

Note that numbers of shared >7 cM IBD segments are shown below the diagonal and the degree of relatedness inferred with IBIS (17) above the diagonal.
No_rel—total number of related individuals who share at least 2 IBD segments (>7 cM) in the sample.
Gaulish_a—proportion of Gaulish ancestry inferred with qpAdm (*SI Appendix*, Table S6, model using French Gaul and Early Medieval Netherlands as sources).
*Genetic outliers in PCA (Fig. 1).
†KOS007 shared only a single >7 cM segment internally within the Koksijde sample (with KOS015) while sharing multiple segments externally with three English (ELY001, ELY002, and I16508) and one German (IND017) Early Medieval individuals. No other Koksijde individual shared multiple >7 cM segments externally.

context burials from England (ELY001, ELY002, and I16508) and one individual (IND017) from the German Merovingian site. No other Koksijde individual shared multiple >7 cM segments outside their community.

To test whether the abundance of distant relationships we detected with the IBD analyses could be affected by extensive inbreeding and background IBD sharing we applied hapROH (49) on the imputed genomes of 23 Koksijde and six Wulpen individuals. We identified no cases of inbreeding and no long (>8 cM) segments in the Koksijde individuals (*SI Appendix*, Table S15) while among the six later medieval Wulpen individuals we detected one individual (WPK001A) with an 18 cM run of homozygosity which could indicate distant (~3rd/4th cousin) relationship between the parents. These results suggest that the abundance and complexity of distant relationships among the Koksijde main ancestry group of individuals is not a reflection of extensive background IBD sharing due to small effective population size or inbreeding.

Analyses of Health and Phenotype-Informative Variants. We compared the frequencies of 116 selected SNVs associated with diet, immunity response, resistance to pathogens and pigmentation phenotypes (*SI Appendix*, Table S16) in Koksijde genomes pair-wise to reference data from 35 imputed genomes of French Iron Age (13), 248 Early Medieval genomes from the North Sea region (9) and modern Dutch and Belgian genomes from the GoNL and MinE data (19, 21). After multiple test corrections, a total of ten variants retained significance, including two lactase-persistence variants, one associated with leprosy, one with celiac disease risk, and six pigmentation-related variants involved in lighter eye, hair, and skin pigmentation (*SI Appendix*, Tables S16–S18). None of the examined variants showed significant differences between Koksijde main group and present-day Low Countries. Eight variants, including all pigmentation and lactase persistence SNVs, showed higher frequency ($P < 0.00001$) in Early Medieval English, Koksijde, and modern genomes from the Netherlands and Belgium, compared to Iron Age France. Five Koksijde outliers (KOS001, KOS009, KOS010, KOS032, and KOS038) with the highest (>0.9) Gaulish ancestry by qpAdm tests showed allele frequencies similar to Iron Age France. Notably, in the case of the leprosy (rs3135388) and celiac disease (rs2395182) associated SNVs, Early Medieval English genomes with high cNSz ancestry had higher frequencies of the risk alleles than modern and ancient genomes from the Low Countries.

Discussion

Major genetic changes unfolded along the coasts and across the North Sea during and after the transformation of the Western Roman Empire. Gretzinger et al. (9) showed that more than three-quarters of ancestry in Anglo-Saxon Period burials from England had continental genetic ancestry. Similarly, our genome-scale analyses of Merovingian-period Koksijde burials in present-day Flanders, Belgium, revealed the main ancestry component shared with Early Medieval genomes from England and the Netherlands and a smaller fraction potentially traceable to earlier Gaulish ancestry. The clustering of the majority of Koksijde individuals with contemporary English and Dutch genomes suggests that a substantial shift to the NSz ancestry in the Early Medieval North

Sea zone was not only restricted to the British Isles but also characteristic to the southern coast of the North Sea.

The majority of Koksijde burials cluster together with Early Medieval genomes from East England and the Netherlands, including one male individual (KOS012; S23 in ref. 11) buried with a Frisian sceatta coin in his mouth (likely as a Charon token). Sceatta coinage reflects the late 7th-century intensification of long-distance networks connecting major trading settlements around the North Sea coasts (29). Interestingly, among the outlier group of predominantly Gaulish ancestry, we find one individual (KOS009; S9 in ref. 11) with a fibula most commonly found in northern France. These two individual examples suggest that grave gifts may have been related to the genetic ancestry and identity of the deceased. Notably, individuals of these two ancestries are buried together and our finding of a mother–daughter pair (KOS034 and KOS035A) illustrates ongoing admixture between them. In the local context of the Flemish coastal region in the 7th century, the arrival of groups and individuals with different backgrounds can specifically be understood in the pioneering context of post-Roman expansion into the almost completely empty saltmarshes that were gradually silting up in this period (30).

Among the Early Medieval sites from present-day Flanders, Belgium, we see a clear difference between the coastal Koksijde and the inland Sint-Truiden cemetery, the latter showing less affinity to the NSz cluster (Fig. 2*D*). Due to the prevalence of cremation practice during the Iron Age and Roman periods, lack of genetic evidence from earlier time periods, and scarcity of Early Medieval burial evidence in the Flemish coastal region, our analyses of the Merovingian burials cannot answer directly when the NSz ancestry was introduced to the Flemish coast. The archaeological analyses of the patterns of change in the North Sea Zone material culture suggest that the foundations of the shared cultural phenomena between East England, Friesland, and the Flemish coast can be traced back to the 3rd to 5th centuries (31, 32). By the 6th century, this diversity had crystallized into distinct regional traditions. We find support for this notion by observing differences between the EMA groups in the intensities of LSAI sharing (Fig. 2*D*, *SI Appendix*, Table S7), but we also find that these differences would have been temporary and subject to further change in High and Late Medieval periods as they are not reflected in the patterns of regional differences among modern populations.

Our analyses revealed a network of distant kinship ties among Koksijde burials but we were unable to find close kinship between Koksijde individuals and other contemporary NSz communities examined so far. The ability to detect 1st-generation migrants via kinship ties relies on extensive sampling and thus their absence does not constitute evidence of a lack of mobility in this Merovingian-period community during the life span of its individuals. Multi-isotopic study of the Koksijde burials (12) highlighted the challenges of the inference of mobility from stable isotope data as strontium values of the majority of burials matched with those from a wide range of coastal sources while oxygen values suggested either 1) mobility of Koksijde individuals after their childhood from a source outside Belgium, possibly from the Atlantic coastline regions of Portugal, Wales, or Ireland, or 2) that their difference from the baseline reflected diversity of local oxygen values. Our additional oxygen data from Wulpen, where we know the individuals were locals, show much higher δ^{18}O values than the baseline as well ($\sim$+3‰$_{dw}$). The isotope data in which Koksijde and Wulpen are temporally and spatially apart, yet, both reflect higher δ^{18}O values than expected. Combined with the genetic evidence, this supports the explanation that an area within the southern North Sea basin, size and extent unknown, is characterized by high δ^{18}O values. As similarly high δ^{18}O values can be observed across a wide geographic range, these are therefore not necessarily incompatible with the mobility of Koksijde individuals from coastal North Sea regions on one hand. On the other, our genetic results rule out ancestry from the Atlantic coast regions with δ^{18}O values similar to Koksijde. Thus, with the combined evidence from isotope and genetic data, long-distance migration scenarios can be ruled out while local mobility scenarios can not.

The combined evidence of high levels of mtDNA and Y chromosome diversity, relatively small number of 1st- to 3rd-degree relationships in autosomal kinship analyses, the presence of two ancestry groups and admixed individuals suggest that the Koksijde burials are representative of a bigger community rather than a small isolated familial group or selected elite. The lack of long runs of homozygosity (*SI Appendix*, Table S15) argues against scenarios of extremely small population size in either ancestry groups and against inbreeding being common in the community. Although limited by the power of our small sample size to detect weak or modest differences, our analyses can rule out extreme sex-specific biases and patterns in ancestry and kinship relationships among the burials. Other than a weak (19/30, $P = 0.049$, binomial test) overrepresentation of male individuals, we do not find biases in individual clustering to ancestry groups by sex and despite extensive kinship ties we do not find pedigrees characteristic to elite burials (e.g., ref. 33) signaled by the dominance of a single patri- or matriline in the burials. KOS006, a male individual with perimortem weapon-related trauma to the head, had no detectable Gaulish ancestry and the highest number of kinship ties in the group, with eight other sampled individuals. Yet, his kinship ties to other burials are defined solely through autosomally inherited markers: his mtDNA haplogroup H39b is unique in the cemetery and his closest Y chromosomal "relative," the outlier KOS032 with >90% Gaulish ancestry, shared with him a common Y chromosome ancestor in haplogroup R1b8-Z372 likely more than 50 generations before their birth (https://www.yfull.com/tree/R-Z372/).

Our finding that Koksijde genomes showed high LSAI sharing locally with Wulpen genomes suggests local genetic continuity from the Merovingian to High Medieval period. This evidence argues against scenarios by which the Koksijde community could be viewed as an unsuccessful immigrant group. While LSAI sharing between Koksijde and modern populations was similarly high with modern populations from different Belgian, Dutch provinces and England (*SI Appendix*, Table S7), we found a signal of local peak of LSAI sharing for Wulpen in present-day provinces of East and West Flanders suggesting that patterns of local population structure have changed relatively less since the High Medieval period. Both Koksijde and Wulpen showed, however, relatively low LSAI sharing with Early Medieval Sint-Truiden, which highlights the existence of local heterogeneity of the gene pool of Early Medieval Belgium even though these differences may not mirror exactly those in the present-day populations.

Both genetic and strontium isotope data identified heterogeneity within the Koksijde site, with a notable overlap of outliers including KOS009, KOS032, and KOS001 (*SI Appendix*, Table S1). These outliers have strontium isotope values suggesting mobility from diverse inland sources. Their genetic modeling with qpAdm points to >90% Gaulish ancestry (*SI Appendix*, Tables S9–S13). KOS001 is also an outlier in terms of burial orientation, being the only individual not facing east. Individuals with high Gaulish ancestry, with the exception of KOS001, had isotope signatures of terrestrial diet while the main ancestry group had predominantly marine-influenced diet (*SI Appendix*, Table S1 and Fig. S4). Ancestry could, thus, explain the dietary groups identified by the δ^{13}C and δ^{15}N values, an explanation that could not be given with the isotope results alone. It is interesting, however, that while the community may have been mixed, their diets were not assimilated significantly enough to be observable in their isotopes. Notably, four of the five outliers with >90% Gaulish ancestry and terrestrial diet—KOS009, KOS010, KOS032, and KOS038—had also been highlighted by osteological analyses as individuals with high levels of mechanical stress and trauma, including indications of disease in KOS009, and, evidence of nonspecific stress during growth (in form of *cribra orbitalia* and enamel hypoplasia) in KOS010 and KOS038 (11). On the other hand, and in contrast to findings from a Merovingian site from present-day Germany (34), our metagenomic screens did not detect the large-scale presence of infectious agents in Koksijde, nor signs of coinfections (*SI Appendix*, section SI13). However, it is hard to determine whether this is due to less pathogens, or to preservation issues, sampled tissue, or pathogen type.

The results of genetic, isotope, and osteological analyses combined point to the possibility that the Koksijde community was socially structured, being at its core dominated by individuals with North Sea zone ancestry, while being at the same time open to migration from local inland sources. This is in line with current archaeological and historiographical understandings of Early Medieval communities (e.g., refs. 31 and 35). In the analyses of phenotype-informative markers, we observed substantial allele frequency differences between Koksijde main group and French Iron Age genomes in six pigmentation and two lactase persistence variants. Five Koksijde outliers with >90% Gaulish ancestry showed allele frequencies similar to the French Iron Age group, which combines individuals from across France, being used here as a proxy for Gaulish in a wider sense, while the main ancestry group of Koksijde showed frequencies similar to the present-day North Sea region, including the Low Countries. Although these variants include the strongest targets of positive selection in Europe (36), our results suggest that these allele frequency differences between the Koksijde main group, on one hand, and the outliers and French Iron Age genomes on the other, were likely driven by ancestry shift rather than local adaptation. Given the presence of individuals representing the full range of ancestry proportions and a mother-daughter pair with substantial ancestry differences, it is likely that the Koksijde burials represent a snapshot of the time when this ancestry fusion was taking place. Allele frequency shifts of functional variants during episodes of massive gene flow have been reported before, with variants associated with lighter eye and hair pigmentation showing opposite trend in Scandinavia during the Viking Age to the one observed here (37). It is also notable that the Koksijde main ancestry group with high lactase persistence allele frequency had a predominantly marine rather than terrestrial diet.

Materials and Methods

Archaeological background of the three studied sites is presented in *SI Appendix*, section SI1, and details of the 48 individual samples analyzed in this study are reported in Table 1 and *SI Appendix*, Table S1.

Ancient DNA extraction, library preparation, and sequencing (*SI Appendix*, section SI2). DNA was extracted from bones and teeth following protocols described elsewhere (38). All samples were processed in dedicated ancient DNA facilities at the University of Tartu. The double-stranded libraries were sequenced on the Illumina NextSeq 500 platform.

Isotope analyses (SI3) were carried out at the Vrije Universiteit Brussel (VUB), Belgium, at the Archaeology, Environmental Changes and Geo-Chemistry (AMGC) laboratory.

Data Processing and Authentication (*SI Appendix*, section SI4). Overlapping paired-end reads were trimmed and merged (39), and the fragments were mapped to the human reference genome (40). ContamMix 1.0-10 (41) was used to estimate mtDNA contamination rate. For male individuals, contamination was also estimated on the basis of chromosome X heterozygosity using the two contamination estimation methods implemented in ANGSD (42). mapDamage2.0 (48) was used to estimate the frequency of C to T transitions in the 5′ end of the DNA fragments.

Uniparental Haplogroups (*SI Appendix*, sections SI6 and SI7). Mitochondrial DNA haplogroup assignments made with HaploGrep2 were manually checked for consistency with PhyloTree (43). Y chromosomal haplogroups were assigned by investigating informative sites 256,463 binary Y chromosome SNPs and confirmed with pathPhynder (15).

Imputation (*SI Appendix*, section SI8). Individuals with mean autosomal coverage >0.1× were imputed using QUILT 1.0.2 (44) with HRC reference panel (45). The results were filtered to remove the low-quality variants. For imputation accuracy estimation, the highest coverage (10×) genome (KOS028) was downsampled to 0.1×, 0.2×, 0.3×, 0.5×, and 3× coverage. Downsampled replicas were imputed with QUILT and assessed for heterozygote sensitivity as a measure of imputation accuracy.

Detecting IBD and LSAI segments (*SI Appendix*, section SI10). IBD/LSAI segments (25) and kinship coefficients were estimated from merged plink files of 61 imputed ancient genomes. In genetic ancestry analyses (Fig. 2), we used >5 cM and for kinship analyses >7 cM threshold. The PiC score (25) for individual x in group Z was estimated as the proportion of individuals from group Z with whom individual x shared IBD above the given threshold. Unsupervised community extraction analyses on IBIS .coef files were performed using the Leiden algorithm (23).

qpWave and qpADM analyses (*SI Appendix*, section SI11). All analyses were performed sample-wise, considering each Koksijde sample as the target. Modeling of two-way admixture events was performed with a custom list of left populations: Gauls, and England early Medieval (EMA) samples from Kent, York (Yrk), Cambridge (Cam) and Norfolk (Nor). As right groups, a list of ancient groups, either temporary or geographically unrelated to the putative admixture event, was used. Only qpAdm results that showed significance in qpWave (P-value < 0.001) are reported. qpWave and qpAdm were applied on both imputed (prefix i) and nonimputed data (prefix ni), adjusting the left and right populations accordingly, so that the imputed data are modeled with imputed groups (when available) and nonimputed data are modeled with nonimputed data.

Phenotypes (*SI Appendix*, section SI12). From the imputed data, we extracted the genotype information at 116 SNPs (46, 47) associated with diet, disease, and pigmentation phenotypes.

Metagenomic analysis (*SI Appendix*, section SI13). Sequencing data were quality checked using FASTQC and MultiQC at multiple points during the analysis. Outputs were filtered for the presence of 256 selected microbial taxa and high-quality viral hits. The presence of taxa was validated by mapping reads to appropriate reference sequences ((48), (49), (50)).

Data, Materials, and Software Availability. Sequencing data can be found in the European Nucleotide Archive (ENA) at EMBL-EBI under Accession No. PRJEB70768 (51).

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