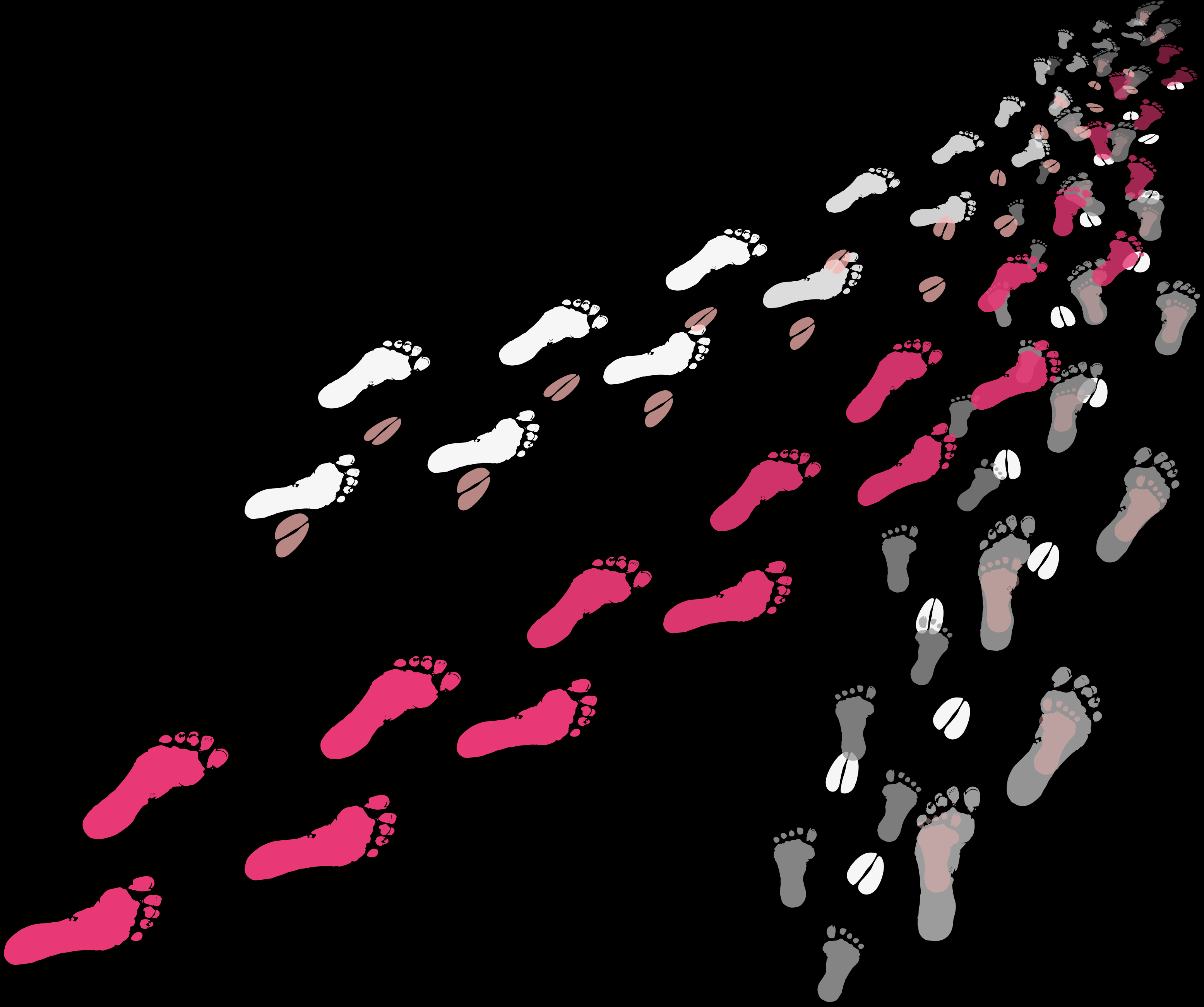

Migration und Integration von der Urgeschichte bis zum Mittelalter

Migration and Integration from Prehistory to the Middle Ages

9. Mitteldeutscher Archäologentag vom 20. bis 22. Oktober 2016 in Halle (Saale)

Herausgeber Harald Meller, Falko Daim, Johannes Krause und Roberto Risch

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Harald Meller,
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Johannes Krause und
Roberto Risch

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Sektion Fallstudien/ Section Case Studies

Investigating Anglo-Saxon migration history with ancient and modern DNA

Stephan Schiffels and Duncan Sayer

Zusammenfassung

Die angelsächsische Migrationsgeschichte anhand alter und moderner DNA

Die britische Bevölkerungsgeschichte ist geprägt von einer Reihe von Einwanderungswellen, unter anderem während der römischen Besetzung ab 43 n. Chr. und der frühangelsächsischen Migrationsperiode nach 410 n. Chr. Bis vor kurzem war der Einfluss dieser Ereignisse auf die genetische Bevölkerungsstruktur in Britannien unklar. Zwei neuere genetische Untersuchungen von 19 britischen Proben des 1. Jh. v. Chr. bis zum 8. Jh. n. Chr. haben nun neue Erkenntnisse in dieser Hinsicht erbracht. Dieser Beitrag stellt beide Untersuchungen vor, präsentiert eine neue gemeinsame Analyse aller 19 Proben und stellt die Resultate in den größeren archäologischen Zusammenhang. Als einige der wichtigsten Resultate sind zu nennen: 1. der Nachweis einer starken genetischen Kontinuität von der späten Eisenzeit bis zur römisch-britischen Zeit; 2. eine klare Zunahme der Verwandtschaft zwischen der modernen holländischen und der angelsächsischen Bevölkerung, die auf die Einwanderung zahlreicher Menschen in dieser Zeit hinweisen; 3. die Einschätzung der angelsächsischen Herkunft in der modernen englischen Bevölkerung auf durchschnittlich 38 %; 4. Hinweise auf eine frühe Vermischung von angelsächsischen Einwanderern mit der einheimischen britischen Bevölkerung.

Summary

British population history has been shaped by a series of immigration periods, including the Roman occupation from AD 43 and Early Anglo-Saxon migrations after AD 410. Until recently, the extent to which these events changed the genetic population structure in Britain was an open question. Two recent genetic studies have provided new insight by analysing the genome sequences from 19 ancient British samples, dating from between the 1st century BC and the 8th century AD. Here we will review these two recent studies, present a joint analysis of all 19 available samples, and put the results into a wider archaeological context. Key results reviewed here include: 1. high levels of genetic continuity between the Late Iron Age and the Romano-British period; 2. a clear increase in ancestry related to the modern Dutch population during the Anglo-Saxon period, suggesting a substantial arrival of new people during this time; 3. an estimated 38 % average Anglo-Saxon ancestry in the modern English population; 4. evidence for early admixture of Anglo-Saxon immigrants and indigenous British inhabitants.

Introduction

Great Britain has undergone substantial cultural changes during the last 2000 years, as documented in the archaeological record, in historical sources, and through linguistic evidence. One of the most significant changes occurred in the period between the end of Roman rule (AD 410) and around AD 700. We refer to this time period as the Anglo-Saxon migration period (or Early Anglo-Saxon period), although our genetic evidence suggests continuous migration into the Middle Saxon period (AD 700–900), an observation supported by recent archaeological finds from Stoke Quay, Buttermarket, and Boss Hall in Ipswich (county Suffolk) (Scull 2009). During this time, changes in archaeological material culture are well documented, with links to the archaeological record from the North Sea coast and northern Germany (Lower Saxony) (Hamerow 2004; Härke 2011). At the same time, later historical sources, for example Bede's *Ecclesiastical History of the English People* (Bede, Historia Ecclesiastica), report an influx of continental migrants (Angles, Saxons, Frisians, Jutes), who settle in Britain and substantially influence society and culture. Moreover, Bede also infers that significant mobility continues into the 8th century, the period when he is writing; for example: »Their metropolis is the city of London, which is situated on the bank of the aforesaid river, and is the mart of many nations resorting to it by sea and land« (Bede, Historia Ecclesiastica, 89). One of the most obvious cultural consequences of these migrations was linguistic replacement in England. This is most observable in the place name evidence, the east of England having names derived from a Germanic language, while western England shows a greater survival of Romano-British place names (Fig. 1).

Background

Archaeological background

Within archaeology, the nature of these »Anglo-Saxon migrations« is the subject of an evolving debate. In the 20th century, archaeologists drew conclusions which paral-

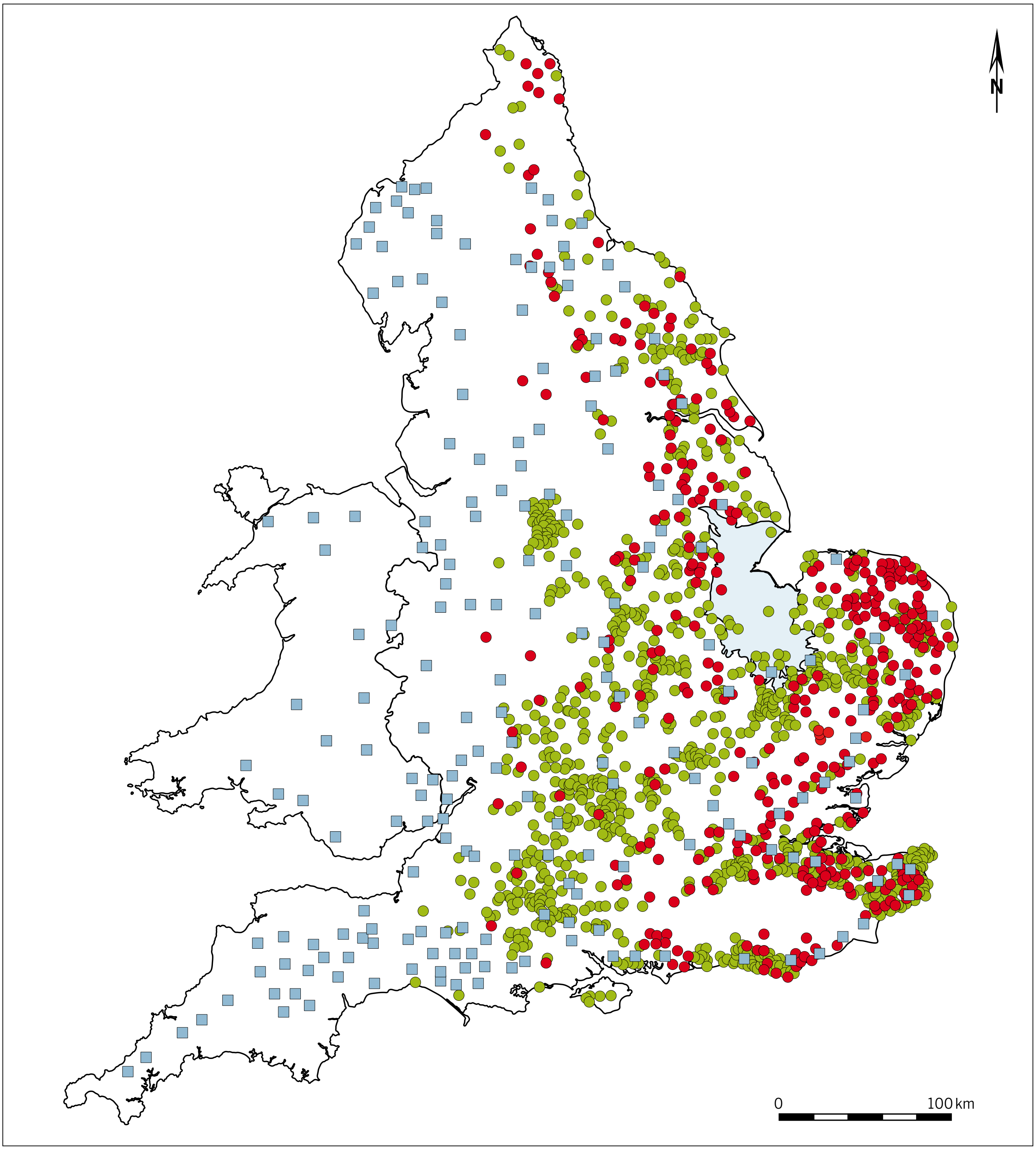

Fig. 1 Schematic linking of Early Anglo-Saxon cemeteries with place names. In green spots: Anglo-Saxon cemeteries. In red spots: place names ending in -ing or -ingas probably from Old English and dating to around the 7th century AD. In blue squares: place names which are probably of Romano British origin. The light blue area marks the Fens, a marshy landscape feature which influenced the location of settlements.

Abb. 1 *Schematische Verbindungen zwischen frühangelsächsischen Gräberfeldern und Ortsnamen. Grün: angelsächsische Gräberfelder. Rot: Ortsnamen mit der Endung -ing oder -ingas, wohl aus dem Altenglischen übernommen und ins 7. Jh. n. Chr. datierend. Blau: Ortsnamen wahrscheinlich römisch-britischer Herkunft. Hellblau markiert sind die Fens, eine Moorlandschaft, die die Standortwahl der Siedlungen beeinflusste.*

leled the dominant historical narrative inferred from the writing of Bede and the Anglo-Saxon Chronicle. According to this narrative, the Angles, Saxons, and Jutes overwhelmed the established population who in the 5th and 6th centuries AD had just emerged from Roman administration, and were left vulnerable by the withdrawal of the mobile Roman army. Writers like E. Leeds, J. Myers and, to a lesser extent, V. I. Evison tended to take a historically derived approach and assumed that brooches and other dress artefacts found in graves could be used to identify these distinct migrant groups (Leeds 1913; Myres 1937; Evison 1987).

In the later decades of the 20th century this narrative changed to include a cultural transition brought about by a smaller, mobile elite who assimilated the autochthonous peoples following post-imperial malady. These same brooches were now understood to have been part of a multistaged and mutable process of ethnogenesis and as possible evidence, not of ethnicity, but rather of the emergent regional identities which later developed into the Anglo-Saxon kingdoms of East Anglia, Essex, Kent, Mercia, Northumbria, Sussex, and Wessex around the 7th century. It has been assumed that these fewer immigrants would have been mostly warriors, with only small numbers of women or families involved (Härke 2011).

Archaeological evidence for ethnic distinctions is often ambiguous. For example, Early Anglo-Saxon buildings included two basic domestic types, firstly sunken feature buildings (SFB) and secondly posthole buildings. While SFBs are recognised as an imported technology, other continental building types, such as long houses, are nearly absent (Hamerow 2004). The conspicuous near-absence of long houses indicates that modes of habitation in early medieval England were influenced asymmetrically by Romano British and northern-European buildings and ways of using these spaces.

It has also been noted that the early medieval enamelling of metalwork was an insular practice, absent on the continent. Interestingly, however, »Celtic« hanging bowls and their decorated enamelled escutcheons are found in wealthy 7th-century »Anglo-Saxon« burials, and in association with elite sites including Sutton Hoo and Rendelsham, both near Woodbridge, county Suffolk (Scull et al. 2016). This has been interpreted as evidence of trade with, and the survival of, Celtic metal smiths (Scull 1985). Yet in the 6th century, »Anglo-Saxon« objects that were also enamelled were deposited in Early Anglo-Saxon cemeteries around the eastern Fen, implying that this technology need not have been restricted to people with a »Celtic« background (Fig. 2).

Burial practices have been used to infer ethnic differences (Faull 1977) and suggested that crouched burials were employed by an indigenous population, drawing on an Iron Age burial tradition, to contrast with immigrant Anglo-Saxon graves within a single cemetery. However, this idea has been largely rejected (Devlin 2007). Indeed, the integration of British and Anglo-Saxon peoples in the 6th century is itself a controversial concept. H. Härke (2011) prefers to see separate enclaves of British and Anglo-Saxon people who gradually assimilated over time. This argument is partly based on skeletal height data which he suggests shows greater divergence between sites or samples in the early period than in the middle and later periods. This is certainly thought-provoking, but must be considered carefully, as the small differences in height described (around 15 mm) could also result from nutritional rather than ethnic differences, for example caused by changes in farming and milling technologies (Thomas et al. 2016).

Wasperton, a cemetery in the Avon Valley (county Warwickshire), included some burials with Roman style hobnails, and others with Anglo-Saxon objects (Carver et al. 2009). These differences are chronologically disparate, but the presence of both indicates a degree of continuity in burial practice despite a change from Roman to Anglo-Saxon material culture within burials. In the past this continuity had been implied, inferred from the location of some early Anglo-Saxon cemeteries adjacent to Roman buildings or settlements, for example Caistor by Norwich (Norfolk county) or Swaffham (district Lincolnshire) (Myers/Green 1975; Hills/Wade-Martins 1976). Interestingly, both regional and local differences in the number of weapons and other Anglo-Saxon objects indicate considerable differentiation between 5th- and 6th-century burial practice. From this we might suggest that there were different modes of British and Anglo-Saxon integration, both between regions and within particular local communities. Oakington, in many ways a typical Cambridgeshire cemetery, was sampled as part of this DNA study. The dress artefacts from Oakington included applied disc, saucer, and cruciform brooches, objects which have been used previously by archaeologists to differentiate Angles from Saxons because of their regional distributions, but are found together at this site (Mortimer et al. 2017). In this place, and in other contemporary communities, these objects may not have embodied biological heritage at all but perhaps conveyed more nuanced expressions of identity which carried meaning in the 6th century AD as regional kingdoms began to emerge (Fig. 3).

Genetic Background

Prior to the two studies from 2016 presented here, genetic analyses were scarce[1]. The nature and impact of the Anglo-Saxon migration period, in particular, was discussed using analyses of data on mitochondrial DNA and Y chromosome diversity in the contemporary British population, which has very limited resolution. More recently, a major study based on genome-wide data from several thousand modern British samples estimated the fraction of Anglo-Saxon ancestry in modern British people at 10 %–40 % (Leslie et al. 2015). While this estimate is interesting for understanding the impact of the migrations on today's population, analysing modern DNA alone cannot provide detailed insight into the immigration process itself.

In 2016, two studies presented the first ancient genomes from Great Britain, which provided a number of novel results on the subject (Martiniano et al. 2016; Schiffels et al. 2016). In this article, we will present results from these two studies, focusing on the article by S. Schiffels et al. (2016), which was co-authored by the authors of this article. We will also present a joint analysis of the two genetic data sets, and put the results into a broader archaeological context.

Studied Samples

The 19 samples studied here come from six different sites in England (Tab. 1; Fig. 4).

R. Martiniano et al. (2016) generated complete genomes for seven Roman soldiers from York. No radiocarbon date is

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[1] Weale et al. 2002; Capelli et al. 2003; Thomas et al. 2006; Töpf et al. 2006.

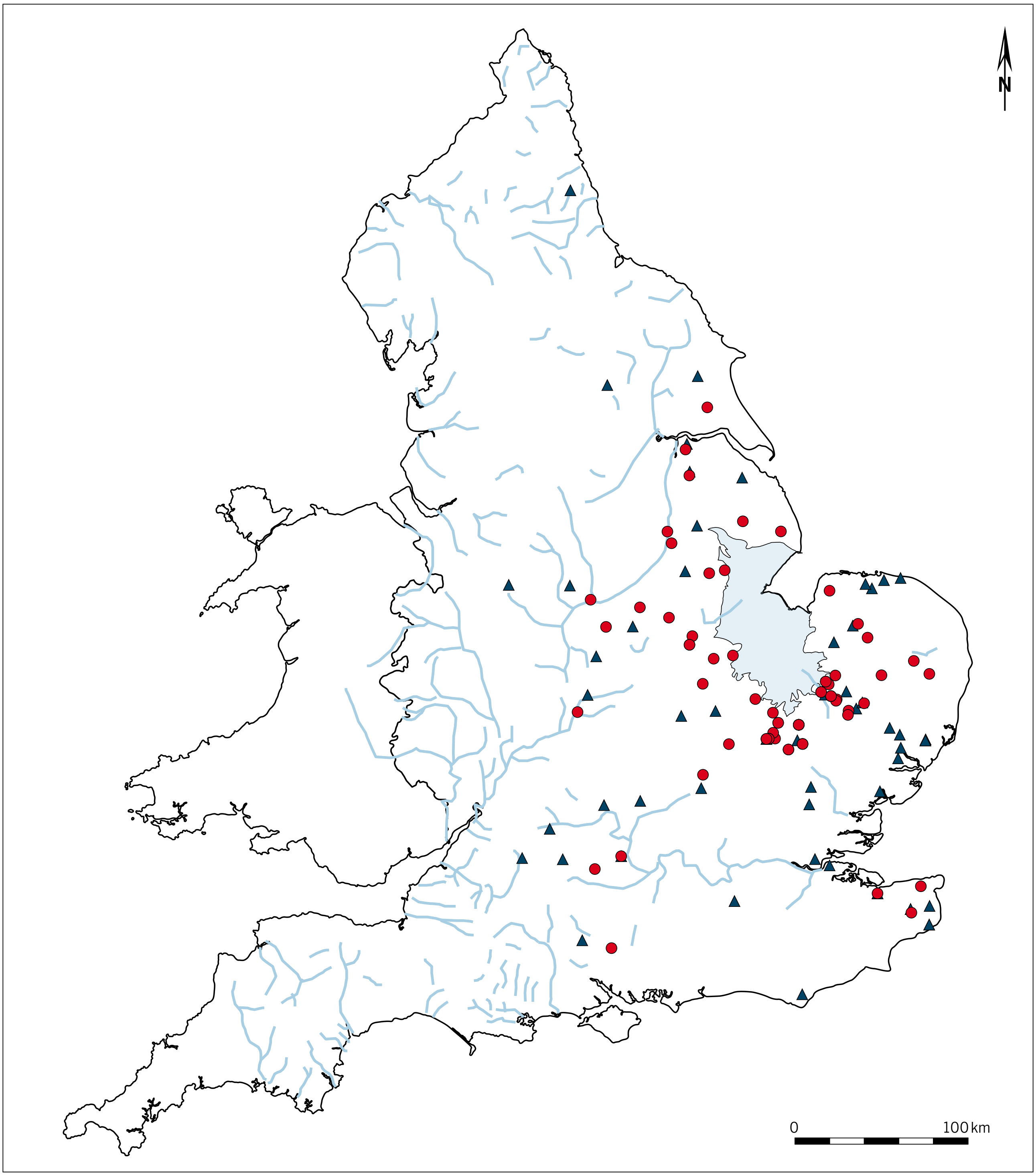

Fig. 2 Distribution of Celtic river names and enamelled objects. Illustration highlighting the survival of Celtic river names (blue lines) and the distribution of 6th- and 7th-century enamelled escutcheons from hanging bowls (in dark blue) and predominantly 6th-century Anglo-Saxon enamelled objects (in red). A group of Anglo-Saxon objects can be found next to the eastern Fen, marked by the light blue area.

Abb. 2 *Verteilung der keltischen Flussnamen und emaillierten Objekte. Die Abbildung zeigt die erhaltenen keltischen Flussnamen (blaue Linien) und die Verteilung von emaillierten Zierscheiben von Hängeschalen des 6. und 7. Jhs. n. Chr. (dunkelblau) einerseits sowie von angelsächsischen emaillierten Objekten vor allem des 6. Jhs. n. Chr. andererseits (rot). Auffällig ist eine Konzentration angelsächsischer Objekte in der Nähe des östlichen Fen-Gebietes (hellblaue Fläche).*

available, but York was founded in AD 71 and became a regional capital in AD 200. The age of these samples can be historically bounded to between the 2nd and late 3rd or possibly the 4th century, as also supported by the onsite dating evidence (Martiniano et al. 2016, supplementary note 1,1.1). Two further samples from northern England were sequenced, one from Melton (East Yorkshire) dated to the late Iron Age, and one Middle Anglo-Saxon sample from Norton (county Durham). In Schiffels et al. (2016), 10 complete genomes were obtained from three sites, with coverages of up to 12 x. The three Iron Age samples for the study were taken from graves excavated at cemeteries near Cam-

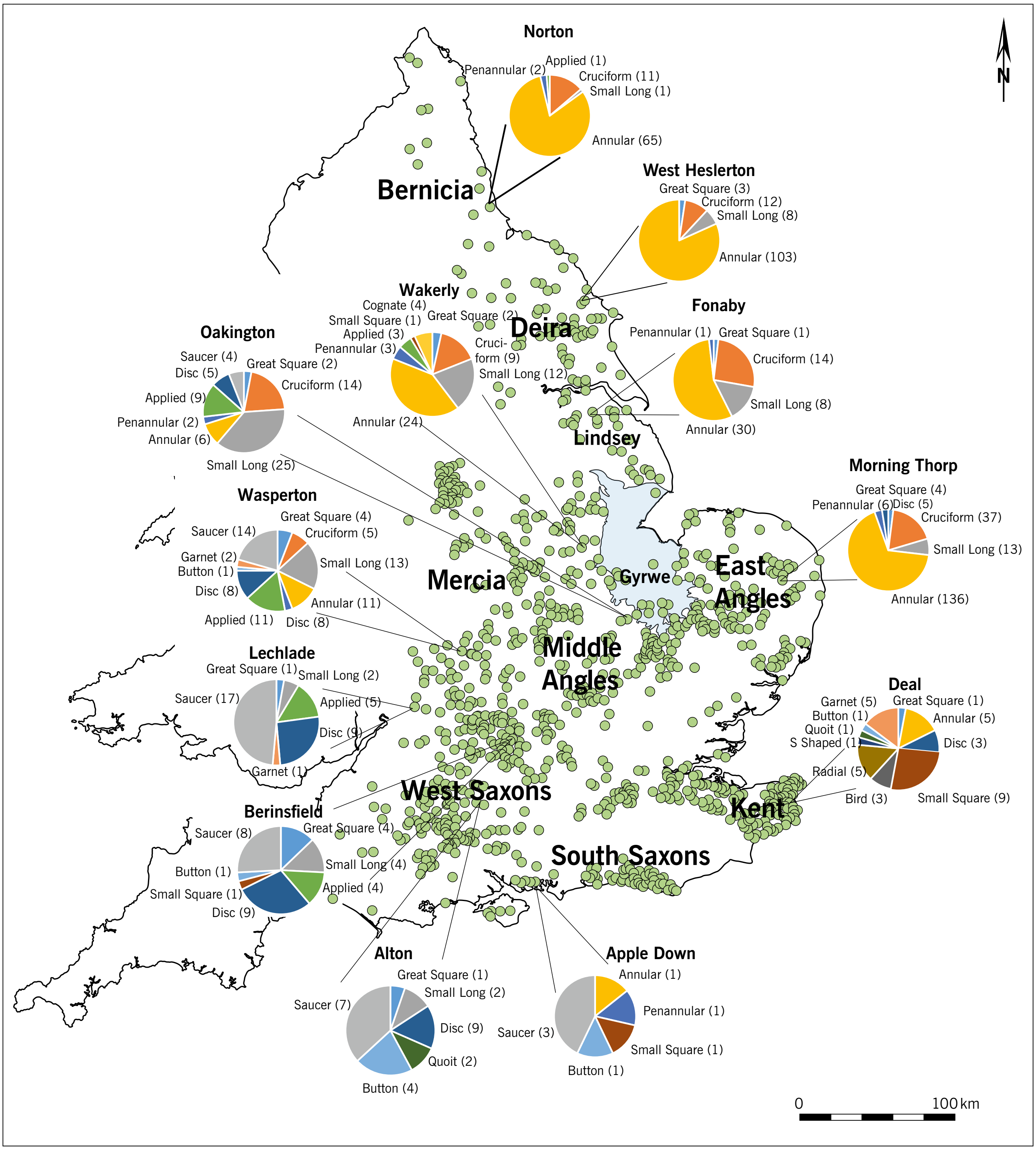

Fig. 3 Distribution of Early Anglo-Saxon cemeteries and grave goods. The distribution of Early Anglo-Saxon cemeteries is depicted in green. The pie charts illustrate the different proportions of female dress accessories in twelve cemetery sites. In the North East and East Anglia, annular and cruciform brooches predominate, in the West, saucer and disc brooches are more common, while Wasperton, Wakerly, and Oakington have all of these brooches in different proportions. The brooches found in Kent are often more varied and many have Frankish parallels. The locations of the Anglo-Saxon kingdoms around AD 600 are also indicated. The light blue area marks the East Anglian Fens.

Abb. 3 *Verteilung der frühangelsächsischen Gräberfelder und Grabbeigaben. Die frühangelsächsischen Gräberfelder sind grün markiert. Die Kreisdiagramme illustrieren die verschiedenen Anteile von Frauentrachtbestandteilen aus zwölf Gräberfeldern. In Nord-Ost-Anglien und Ost-Anglien überwiegen Ring- und Kreuzfibeln, in West-Anglien sind Schalen- und Scheibenfibeln stärker vertreten, während in Wasperton, Wakerly und Oakington alle Fibeltypen in unterschiedlichen Anteilen vorliegen. Die Fibeltypen in Kent variieren oft mehr und viele weisen fränkische Parallelen auf. Die Ausdehnung der angelsächsischen Königreiche um 600 n. Chr. ist ebenfalls eingezeichnet. Die hellblaue Region bezeichnet das Fen-Gebiet in Ost-Anglien.*

bridge, one at Linton and two at Hinxton (both district Cambridgeshire). The third site, Oakington, produced four samples from a large Early Anglo-Saxon cemetery with over a hundred burials from the 5th and 6th centuries AD. Three further Anglo-Saxon samples were found at Hinxton. The Hinxton site today also hosts the Wellcome Trust Sanger Institute, at which the genomes of these ten samples were produced.

Sample	Publication	Site	Age	Mapped Reads	Genomic Coverage (X)	Sex	Y haplogroup	MT haplogroup
3DRIF-16	Martiniano et al. 2016	York	2nd–4th century AD*	28,683,678	0.7	Male	R1b1a2a1a1-M405	H6a1a
3DRIF-26	Martiniano et al. 2016	York	2nd–4th century AD*	50,652,260	1.1	Male	J2-L228	H5
6DRIF-18	Martiniano et al. 2016	York	2nd–4th century AD*	41,157,853	1.1	Male	R1b1a2a1a-L52/L11	H1bs
6DRIF-21	Martiniano et al. 2016	York	2nd–4th century AD*	48,712,821	1.2	Male	R1b1a2a1a2c2-DF63	J1c3e2
6DRIF-22	Martiniano et al. 2016	York	2nd–4th century AD*	45,995,965	1.1	Male	R1b1a2a1a2b-S28	H2+195
6DRIF-23	Martiniano et al. 2016	York	2nd–4th century AD*	25,256,982	0.7	Male	R1b1a2a1a-L52	H6a1b2
6DRIF-3	Martiniano et al. 2016	York	2nd–4th century AD*	68,421,310	1.7	Male	R1b1a2a1a1-M405	J1b1a1
M1489	Martiniano et al. 2016	Melton	210 BC–40 AD	21,802,991	0.6	Female	-	U2e1e
NO3423	Martiniano et al. 2016	Norton on Tees	AD 650–910	43,369,123	1.1	Male	I1-S107	H1a
15579A	Schiffels et al. 2016	Linton	360–50 BC	196,286,837	1.4	Female	-	H1e
12880A	Schiffels et al. 2016	Hinxton	160 BC–AD 26	123,262,472	1.3	Male	R1b1a2a1a2c-L21	K1a1b1b
12884A	Schiffels et al. 2016	Hinxton	170 BC–AD 80	1,017,830,874	11.8	Male	R1b1a2a1a2c1-L21	H1ag1
15558A	Schiffels et al. 2016	Oakington	AD 420–570	418,337,060	3.8	Female	-	U5a2a1
15569A	Schiffels et al. 2016	Oakington	AD 385–535	201,232,078	2.7	Female	-	H1g1
15570A	Schiffels et al. 2016	Oakington	AD 395–540	716,598,871	8.2	Female	-	T2a1a
15577A	Schiffels et al. 2016	Oakington	AD 400–545	422,286,156	6.3	Female	-	H1at1
12881A	Schiffels et al. 2016	Hinxton	AD 666–770	264,114,638	4.4	Female	-	H2a2b1
12883A	Schiffels et al. 2016	Hinxton	AD 631–776	294,092,649	3.8	Female	-	K1a4a1a2b
12885A	Schiffels et al. 2016	Hinxton	AD 690–881	72,434,144	0.9	Female	-	H2a2a1

Tab. 1 A summary table of all 19 samples presented in the two studies and reanalysed here. Ages marked with a star (*) are based on historical context (York was founded in AD 71 and the cemetery was used until the 4th century), other ages are calibrated radiocarbon dates.

Tab. 1 Eine Zusammenstellung der 19 Proben, die im Rahmen der beiden genannten Untersuchungen analysiert wurden und hier nochmals untersucht worden sind. Datierungen, die mit einem Stern (*) versehen sind, beruhen auf geschichtlichen Zusammenhängen (York wurde im Jahr 71 n. Chr. gegründet und der Friedhof wurde bis ins 4. Jh. genutzt), bei den übrigen Daten handelt es sich um kalibrierte ^{14}C-Daten.

Genetic Analyses

In the focal study (Schiffels et al. 2016), we sampled teeth from a total of 29 individuals, and extracted DNA in clean room facilities at the Australian Centre for Ancient DNA in Adelaide. The resulting sequencing libraries were then initially sequenced in small amounts, to assess the amount of human DNA. Ten libraries were selected for deeper sequencing based on their preservation quality (i. e. the amount of endogenous human DNA), age, and provenance.

Combining these ten samples with the nine samples from Martiniano et al. (2016), we generated genotype calls for all 19 individuals and projected the genotypes for the ancient samples onto the first two principal components of

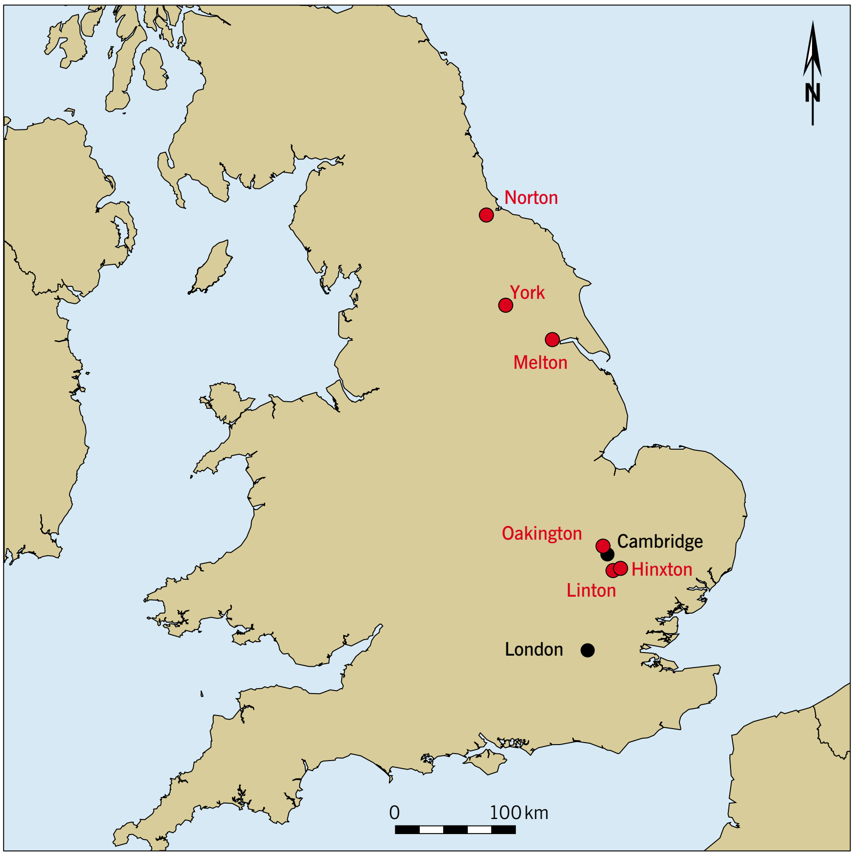

Fig. 4 A map with the archaeological sites of the samples analysed here. Sampling locations are shown in red. The locations of Cambridge and London are shown for orientation.

Abb. 4 *Karte der Fundstellen der besprochenen Proben. Die entsprechenden Fundstellen sind rot markiert. Cambridge und London sind lediglich zur Orientierung angegeben.*

866 modern European individuals, published in I. Lazaridis et al. (2014; Fig. 5).

Figure 5 shows that 18 of 19 ancient samples (black symbols) fall into the cluster of other central and western European individuals, close to modern French and English samples. However, one ancient Roman individual clusters most closely with the modern Palestinian and other Near Eastern populations, suggesting a Near Eastern ancestry of this one Roman soldier from York. This striking finding was reported by Martiniano and co-workers (Martiniano et al. 2016) and provides genetic evidence to support a growing body of isotopic data that points to high levels of individual mobility amongst the soldiery, officers, and administrators of the Roman Empire (Leach et al. 2010; Eckardt et al. 2014). Apart from this outlier, the 18 other samples are genetically close to other European populations, with some subtle differences between the Early and Middle Anglo-Saxon samples (which are closer to modern Scottish and Norwegian samples) and the Iron Age and Roman samples (which are closer to modern French samples).

While Principal Components Analysis reveals differences in ancestry when source populations are sufficiently divergent, as seen in the example of the Near Eastern Roman outlier (see Fig. 5), its resolution is limited when trying to resolve closely related ancestries, as seen in the bulk of our samples. This resolution limit is a problem of the visualisation method, not of the data itself. Because Principal Components Analysis seeks to visualise the major components of genetic variance, it is biased towards segregating high-frequency mutations in the population. These mutations are primarily of very ancient origin and are not specific to any particular subpopulation, but are found nearly everywhere in Europe and the world today.

A simple change of perspective can be achieved by focusing on rare genetic variation, which does not contribute much to the population-level genetic variance, but is very specific to particular subpopulations. Here we consider a panel of 524 modern European individuals for which there is whole genome sequencing data available (The Genome of the Netherlands Consortium 2014; The 1000 Genomes Project Consortium 2015), and focus on mutations that are only seen once in all samples. In a particular ancient sample, we can then search for these rare mutations and count how many of them are shared with each subpopulation in the reference panel (Fig. 6).

We used this method to determine relative allele sharing[2] between all our ancient samples and the modern Dutch population. As shown in Fig. 6b and 7, the ancient samples analysed here are stratified substantially with respect to these relative allele sharing ratios (Fig. 7).

We found that among all the ancient samples analysed, the Iron Age individuals from Linton, Melton, and Hinxton have the lowest numbers of rare Dutch alleles, while two Early and four Middle Anglo-Saxon samples from Oakington, Hinxton, and Norton have the highest numbers. This suggests a marked change in ancestry from the Iron Age

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[2] »Allele sharing« is the amount of similar genotypes between two samples.

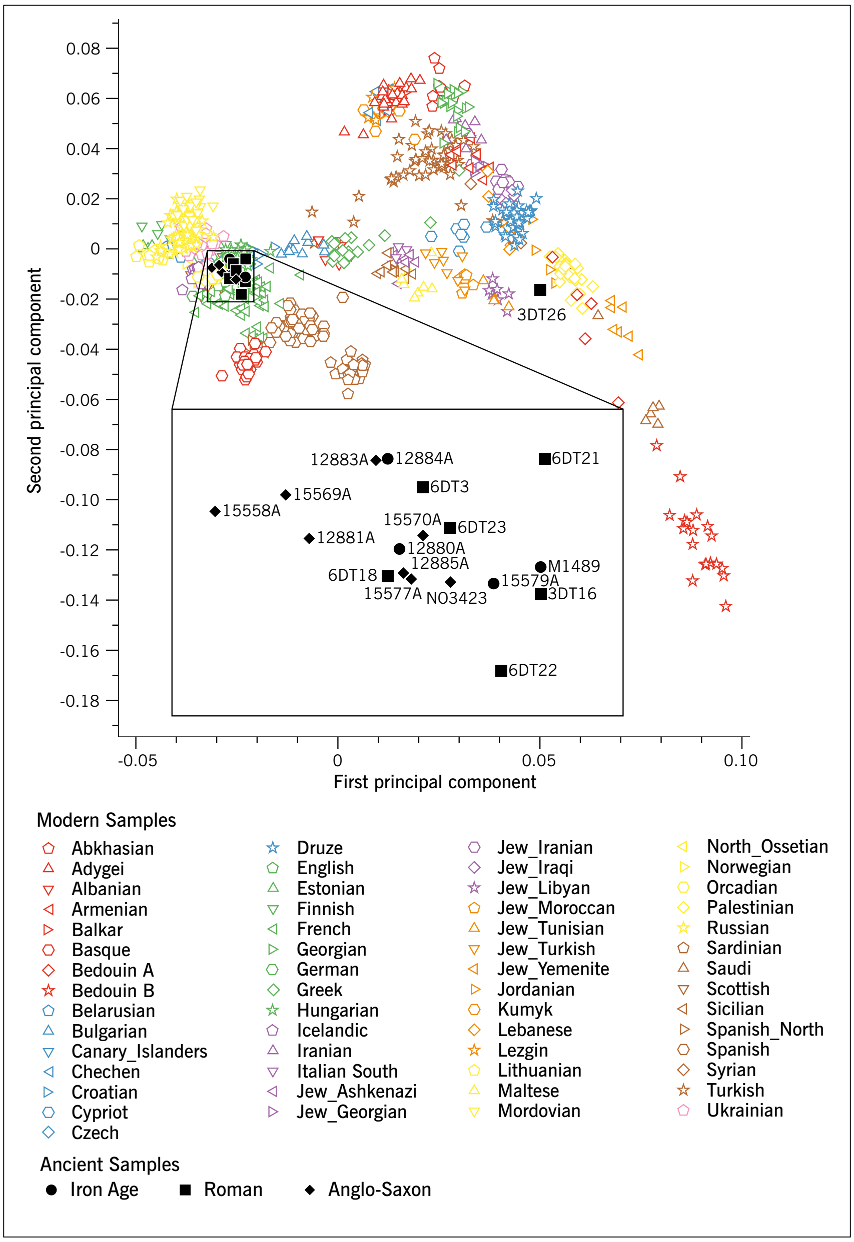

Fig. 5 Principal Components Analysis. All 19 samples analysed here are projected onto the principle components computed from genotype data from 866 modern individuals from 57 European populations. The zoomed area gives the exact sample names of the ancient individuals. One outlier (3DT26) falls into contemporary Near-Eastern populations and is not part of the zoomed area.

Abb. 5 *Hauptkomponentenanalyse. Alle 19 hier untersuchten Proben sind auf die Hauptkomponenten von Genotypdaten von 866 modernen Individuen aus 57 europäischen Bevölkerungsgruppen übertragen. Der vergrößerte Ausschnitt zeigt die genauen Probenbezeichnungen der historischen Individuen. Ein Ausreißer (3DT26) stimmt mit zeitgenössischen Bevölkerungsgruppen aus dem Nahen Osten überein und liegt somit außerhalb des vergrößerten Ausschnitts.*

through the Early and Middle Anglo-Saxon period, with a substantial increase of continental ancestry related to modern Dutch samples. The Roman samples (excluding the outlying Near Eastern individual) broadly resemble the earlier Iron Age samples, with one notable outlier, 6DT3, which apparently shares a similar number of rare alleles with modern Dutch samples as the Anglo-Saxon samples. If we include the Near Eastern outlier described above, we find that two out of the six sampled Roman soldiers from York appear to descend not from the local (Iron Age) population but from sources outside of the British Isles: one from a Near Eastern source related to modern Palestinian samples, and one from a source related to modern Dutch samples.

Two further outliers are seen in the Early Anglo-Saxon samples, 15577A and 15570A, which have substantially lower amounts of Dutch sharing compared to the other six. As reported in Schiffels et al. (2016), these two samples are probably of Iron Age and mixed Iron Age/Anglo-Saxon ancestry, respectively. This surprising finding suggests that, at least in this community, migrants or descendants of migrants lived together with autochthonous people and were also buried side by side. Furthermore, all four Early Anglo-Saxon samples from Oakington have similar archaeological assemblages in their graves, suggesting no social segregation along biological or ethnic origins within this community. They were buried the same way and they wore similar clothes, suggesting an integrated and interbreeding population.

When we compared the estimates of rare allele sharing between our ancient samples and ten modern British samples, obtained from the UK10K project (The UK10K Consortium 2015), we observed that all the modern British samples fell in-between the two extremes seen in Iron Age samples on the one hand, and Middle Anglo-Saxon samples on the other hand. Using a simple linear model for admixture, we used these allele sharing statistics to compute the average proportion of Anglo-Saxon ancestry in the modern British population. For the East of England, we found this average

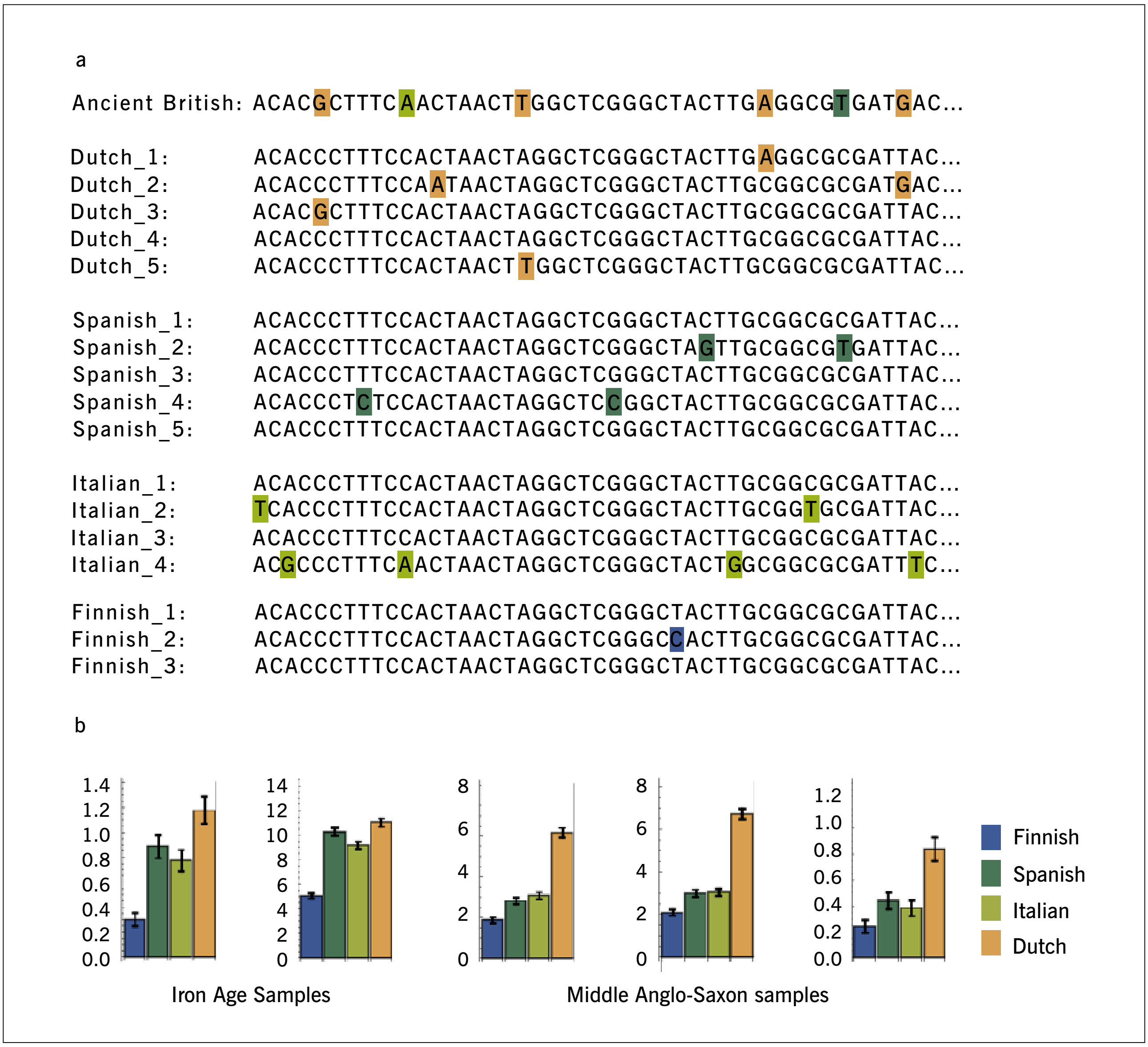

Fig. 6a–b Schematic representation illustrating rare allele sharing. a Schematic illustration of rare allele sharing. An ancient sample is compared to a set of reference genomes for which genome sequencing data is available. Mutations only present once in the reference panel (singletons) may be shared with the ancient sample. The relative counts of ancient singletons shared with different modern subpopulations is informative about the recent ancestry of the ancient sample; b actual counts of singletons shared by selected modern European populations and the five ancient samples from Hinxton, showing clearly elevated Dutch alleles in the Middle Anglo-Saxon individuals.

***Abb. 6a–b** Schematische Aufstellung der gemeinsamen Allele. a Schematische Aufstellung von gemeinsamen seltenen Allelen. Eine historische Probe wird mit einer Reihe von Referenzgenomen verglichen, für die es Genomsequenzdaten gibt. Mutationen, die in der Referenzspalte nur einmal vorkommen (Einzelnachweise) können auch in der historischen Probe vorkommen. Die relative Anzahl gemeinsamer Einzelnachweise in den alten Proben und in verschiedenen modernen Bevölkerungsgruppen gibt Hinweise zur Verwandtschaft der historischen Probe in jüngerer Zeit; b tatsächliche Anzahl gemeinsamer Einzelnachweise in ausgesuchten modernen europäischen Populationen und den fünf historischen Proben aus Hinxton. Es zeigt sich eine deutliche Zunahme holländischer Allelen in den mittelangelsächsischen Individuen.*

proportion to be 38 %, with a large variation among modern samples, ranging from about 25 % to 50 %. We also made the same estimate for modern samples from Wales and Scotland, and found the average proportion to be lower, at 30 %. However, since we have no ancient DNA from Wales and Scotland, our estimate is less robust in these regions. We also caution that this simple linear model of admixture between Iron Age samples and Middle Anglo-Saxon samples assumes that Dutch allele sharing in the modern British population has not altered since the Anglo-Saxon period. This may seem like a bold assumption given the known later influence from Scandinavia and the Normans, but our estimates would only be affected by these later events in so far as they may have altered the Dutch allele sharing (in either direction).

Discussion

The two studies presented and reviewed in this article were the first to generate and analyse whole genomes from ancient British individuals, and represent a valuable new public resource for investigating British history through genetics and changes in ancestry. Furthermore, we have

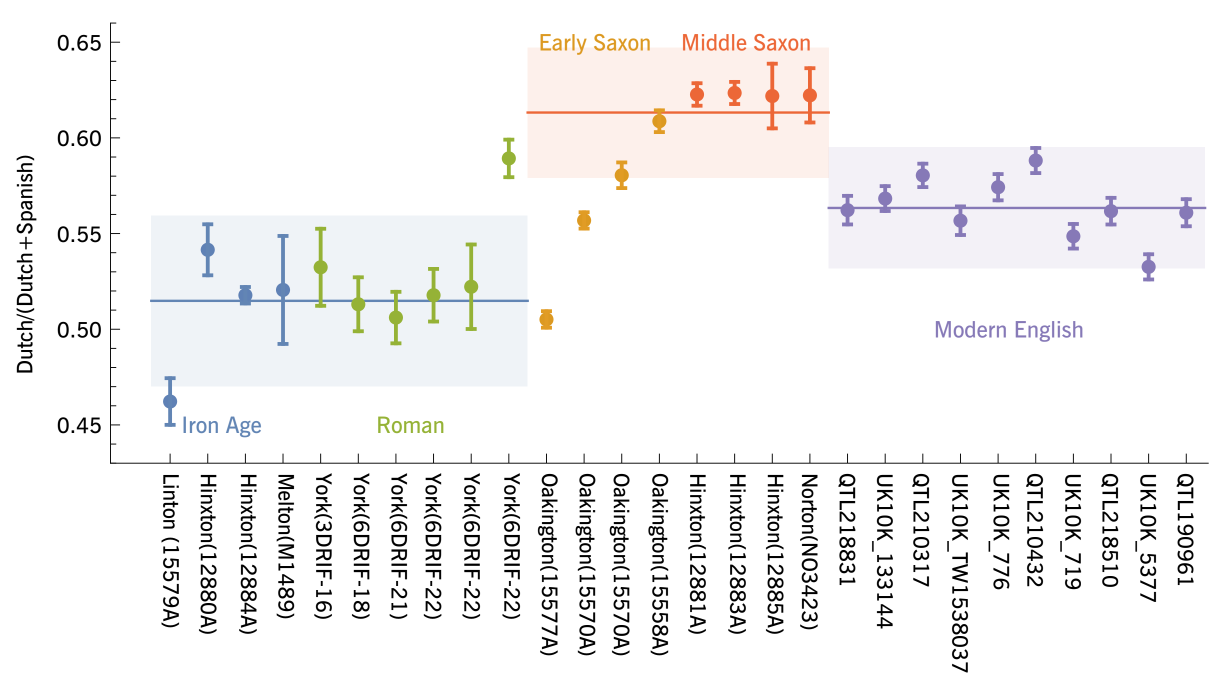

Fig. 7 Relative allele sharing between all ancient samples (except the Near Eastern outlier) and modern Dutch samples, normalised by modern Spanish. Two Early Anglo-Saxon individuals from Oakington (15569A, 15558A), and four Middle Saxons from Hinxton (12881A, 12883A, 12885A) and York (NO3423) have the highest relative sharing with modern Dutch samples. Ten modern British samples fall in-between the earlier Iron Age and the Saxon samples. For the average values, we excluded the Roman soldier 6DT3, as well as the two Early Anglo Saxons, 15570A and 15577A, because they appear to be outlying or mixed, respectively.

***Abb. 7** Gemeinsame Allele in allen historischen Proben (jedoch unter Ausschluss des Ausreißers aus dem Nahen Osten) und modernen holländischen Proben, normalisiert durch gemeinsame Allele mit spanischen Proben. Zwei frühangelsächsische Individuen aus Oakington (15569A, 15558A) und vier Mittelsachsen aus Hinxton (12881A, 12883A, 12885A) und York (NO3423) weisen die zahlreichsten relativen Gemeinsamkeiten mit den modernen holländischen Proben auf. Zehn moderne britische Proben liegen zwischen den früheren eisenzeitlichen und sächsischen Proben. Bei der Berechnung der Durchschnittswerte wurden der römische Soldat 6DT3 sowie zwei Früh-Angelsachsen (15570A und 15577A) entweder als Ausreißer oder als scheinbar vermischt ausgeschlossen.*

shown how large modern genomic data sets can be combined with ancient genomes in a novel way, based on rare allele sharing, providing a means of analysing subtle genetic differences between closely related populations.

The most obvious result from our joint analysis of all 19 samples is the clear evidence for a distinct »Anglo-Saxon« ancestry in most of the samples that were typed archaeologically as Early and Middle Anglo-Saxon (Fig. 7). Given that the archaeological model has moved away from mass migration to more limited elite mobility, this result was not necessarily expected. It is also notable that the samples analysed included many women and were not limited to male warriors or elites. These results confirm that the cultural changes observed on the British Isles after the end of the Roman Empire and throughout the 1st millennium AD were driven by the arrival of new people, rather than by cultural diffusion. Another key result, as partly reported by Martiniano and colleagues (Martiniano et al. 2016), is the fact that the majority of the Roman soldiers from York are genetically similar to the local (Iron Age) population, with only one individual showing evidence of ancestry similar to the Anglo-Saxon samples. Largely, this supports the idea of high levels of continuity from the late Iron Age throughout the Roman period, while at the same time suggesting a continuous flow of migrants even before the end of Roman rule in Britain, albeit at a lower level than what we see after AD 400.

The Roman soldier (6DT3) with a similar genetic ancestry to that of the Anglo-Saxon individuals reminds us of discussions of migration focused on Germanic *Foederati*. This interpretation depends on Gildas' 6th century account *De Excidio et Conquestu Britanniae*, which describes how the British King Vortigern invited some German barbarians, led by Hengest and Horsa, to help him defend against the Picts (lat. *picti*; Roman name for peoples in Scotland) and Scots following Roman withdrawal (Gildas, De Excidio et Conquestu Britanniae; Campbell et al. 1982). Gildas describes how these barbarians then betrayed their hosts and shifted their attention to conquest. Some archaeologists have used these accounts to interpret archaeological finds. For example, quoit or chip-carved belt buckles from sites at Richborough (county Kent), Dorchester-on-Thames (county Oxfordshire), Gloucester (county Gloucestershire), Lankhills (Winchester, county Hampshire) and Mucking (county Essex) have been interpreted as military issue rank insignia for soldiers of Germanic origin in the 4th and 5th centuries (Suzuki 2000) and used to point to: »a pattern of a Romano-Germanic army, of Germanic *laeti* or *foederati* settled behind the frontiers, and their gradual replacement during the 5th century by invading bodies of free Germans.« (Hawkes/Dunning 1961, 40–41)

When found in an Early Anglo-Saxon context, these Romano-British belt buckles are mostly from female graves (Suzuki 2000) and so an exclusively military interpretation is problematic. However, the DNA of this Roman individual (6DT3) does show an important biological connection between the Roman military and Early Anglo-Saxon immigrants, perhaps implying a continuity of connectedness between recruits drawn from the local population and people overseas connected to them by trade or familial ties, providing a mechanism for the migration of individuals and their families well before AD 410.

Our analysis of four Early Anglo-Saxon samples from the cemetery in Oakington adds significantly to our picture of the period. We see evidence of a genetically mixed but culturally Anglo-Saxon community, even in this early period, in contrast to claims for strong segregation between newcomers and the indigenous population (Thomas et al. 2006). The genomes of two sequenced individuals (15558A and 15569A) are consistent with those individuals being of recent immigrant origin, from a source population close to modern Dutch samples; the third sample was genetically similar to native Iron Age samples (15577A); and the fourth was consistent with the individual being of admixed genetic origin (15570A), indicating interbreeding. Despite this, their graves were conspicuously similar, with all four individuals buried in a flexed position, and with similar grave furnishings, indicating that there was no difference in their treatment.

Given this mixing apparent around AD 500, and that the modern population has not more than 40 % Anglo-Saxon ancestry, it is perhaps surprising that the Middle Anglo-Saxon individuals from the more dispersed field cemetery in Hinxton, as well as the Middle Anglo-Saxon sample from Norton (county Durham), look more genetically consistent with unmixed immigrant ancestry. This opens up the exciting possibility that high personal mobility and migration continued for some centuries into the Middle Saxon period (as Bede may have told us in the first quote above). The unmixed Hinxton group, versus the mixing of the Oakington population, shows that early medieval migration took a variety of forms and that these migrants integrated with the incumbent population in different ways. We should not assume that there was only one kind of experience of migration and settlement, and the experiences of the Roman, Early, and Middle Saxon periods were probably quite different. Excitingly, our results extend Anglo-Saxon mobility and immigration earlier into the Roman period, and later into the Middle Saxon period. More ancient genomes from other sites in England from this and later periods will enable us to resolve these questions in more detail.

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Source of figures

1 Data derived from Meaney 1964; Gelling 1978; Gelling 1988
2 Drawn by D. Sayer and adapted from Sayer et al. forthcoming.
3 Drawn by D. Sayer
4 Drawn by D. Sayer and S. Schiffels
5 Drawn by S. Schiffels
6 Drawn by S. Schiffels
7 Drawn by S. Schiffels

Tab. 1 after Schiffels et al. 2016 and Martiniano et al. 2016

Addresses

Dr. Stephan Schiffels
Department for Archaeogenetics
Max Planck Institute for the Science
of Human History
Kahlaische Strasse 10
07745 Jena
Germany
schiffels@shh.mpg.de

Dr. Duncan Sayer
School of Forensic and Applied Sciences
University of Central Lancashire
Preston PR1 2HE
United Kingdom
dsayer@uclan.ac.uk

Bislang erschienene Bände in der Reihe »Tagungsbände des Landesmuseums für Vorgeschichte Halle«

Die Reihe der Tagungsbände des Landesmuseums wurde 2008 ins Leben gerufen. Anlass dazu war die Konferenz »Luthers Lebenswelten«, die im Jahr 2007 in Halle ausgerichtet wurde. Bereits der zweite Tagungsband widmete sich mit dem Thema »Schlachtfeldarchäologie« dem Mitteldeutschen Archäologentag, der seit 2008 jährlich vom Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt veranstaltet und zeitnah publiziert wird. Dem großen Anteil internationaler Autorinnen und Autoren entsprechend, erscheinen viele Beiträge dieser Reihe in englischer Sprache mit deutscher Zusammenfassung.

Mit dem bislang zuletzt erschienenen Tagungsband konnten die Vorträge der Internationalen Tagung »Alchemie und Wissenschaft des 16. Jahrhunderts. Fallstudien aus Wittenberg und vergleichbare Befunde« in zahlreichen Artikeln renommierter Forscher verschiedenster Fachdisziplinen vorgelegt werden.

Lieferbar sind folgende Bände:

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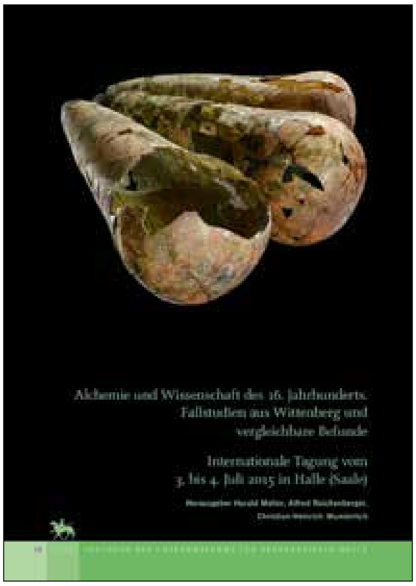

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