Forensic Science International: Reports 8 (2023) 100334

Contents lists available at ScienceDirect

Forensic Science International: Reports

journal homepage: www.sciencedirect.com/journal/forensic-science-international-reports

Forensic genetic population data

English and Irish population comparison using STR markers: Insights into genetic disparities and historical influences

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ARTICLE INFO

Keywords:
Short tandem repeat (STR)
English
Irish
VeriFiler Express PCR Amplification Kit
Population data
Variant allele

ABSTRACT

Short tandem repeat (STR) markers are commonly used in forensic investigations and kinship testing due to their cost-effectiveness and high discriminatory power. In the United Kingdom, STR allele frequency databases are available for different population groups, including the White group, which includes individuals of both English and Irish ethnicity. However, considering differences in historical migrations and influences between England and Ireland, distinct genetic differences might exist between these populations. This study aimed to generate allele frequency data for English and Irish populations using the VeriFiler Express PCR Amplification Kit, which contains loci utilised in national databases. Buccal swabs were collected from 577 English and 500 Irish volunteers with self-proclaimed English and Irish ethnicity respectively. DNA profiling and statistical analyses were performed to assess allele frequencies and forensic parameters, and to perform population comparisons. The results showed minimal genetic differentiation (F_{st} = 0.0013) between the English and Irish populations. Comparison with other European populations revealed close genetic relationships between the English population and Scandinavian countries, while the Irish population displayed closer genetic links to Western European countries. These findings support historical influences such as Viking migrations and highlight the need for further research using additional markers to explore the genetic makeup and history of the English and Irish populations. Although a single allele frequency database may be suitable due to the observed genetic similarity, the establishment of separate databases should be considered to ensure maximum population representation.

1. Introduction

Short tandem repeat (STR) markers are regions of hyper-variable, non-coding DNA widely used in forensic investigation and kinship testing. Compared to other techniques for DNA profiling, they represent a cheap, quick, and simple testing method which can provide a high power of discrimination. An additional advantage of STR typing is the availability of various population data, which aid in the calculation of match probabilities and likelihood ratios. These parameters require the use of the best representative allele frequency database for the population of the individual under evaluation [1].

In the United Kingdom, the Home Office uses separate allele frequency databases for five main population groups. Among these, one is the White group, which includes White British, Irish, and Other White [2]. In order to provide meaningful statistical calculations, it is important to use allele frequency databases representative of the populations in which the STR kits are utilised [3–5]. This is because global databases would lack the necessary individual representation provided by more local databases [6]. However, the British (including English) and Irish populations have nonetheless been combined for the creation of the White allele frequency database despite the differing histories of emigration and immigration of these populations.

One of the first recorded migrations in the history of England and Ireland dates back to A.D. 43, when the Romans invaded and settled in England. Even though they never conquered Ireland, there is evidence of trading between the Romans and the Irish during this time [7,8]. The next recorded mass migration did not take place until A.D. 793, when the Norse Vikings entered England and, in A.D. 795, started raiding Irish monasteries along the coast before moving further inland. In A.D. 849 the Danish Vikings arrived in England and fought the Norse Vikings [9,10]. The final Viking landing took place in 1066 when the Normans, an intermingling population between Norse Viking settlers and indigenous

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https://doi.org/10.1016/j.fsir.2023.100334
Received 23 May 2023; Received in revised form 20 July 2023; Accepted 8 August 2023
Available online 11 August 2023

people [11,12], landed from France, resulting in the Battle of Hastings. Later on, in 1169 the Anglo-Normans invaded Ireland through Wexford, followed shortly thereafter by Henry II's invasion [13,14]. During the 16th and 17th century plantation period, there was a continuous movement of British people to Ireland. Concurrently, Norman and Gaelic lands were being colonised by English and Scottish settlers [13]. Between 1846 and 1851 the Irish Potato Famine killed 1.1–1.5 million Irish from both starvation and famine-related diseases. During this time, 2.1 million Irish emigrated from Ireland to countries all over the world, including North America, Australia, South Africa, and Canada, as well as Britain [15,16]. During the 1920s, Irish migration was predominantly to Britain, while since World War II (WWII) Irish migrants started returning, becoming the main source of immigration into Ireland [17].

Due to the aforementioned shared Viking and Scottish influence and the intermingling of the two populations caused by continuous movements between the two countries, it may be expected that the English and Irish populations would be genetically similar. However, the lack of Roman influence in the Irish genetic pool and the intermixing of Irish DNA with DNA from all over the world resulting from Irish emigration and return post-WWII may have led to distinct differences between the populations.

On this basis, this study was carried out to generate allele frequencies for the English and Irish populations and evaluate if separate databases would be required for these populations. The VeriFiler Express PCR Amplification Kit (Applied Biosystems), one of the most popular STR testing kits available on the market, was selected since it contains, among others, the 'DNA-17' loci utilised in the United Kingdom National DNA Database (NDNAD) [2], the United States Combined DNA Index System (CODIS) markers [18], and the European Standard Set (ESS) loci [19]. This combination of markers makes the kit ideal for the creation of national databases. This kit utilises a 6-dye multiplex technology to amplify 23 autosomal STR loci (D3S1358, vWA, D16S539, CSF1PO, TPOX, D8S1179, D21S11, D18S51, Penta E, D2S441, D19S433, TH01, FGA, D22S1045, D5S818, D13S317, D7S820, D6S1043, D10S1248, D1S1656, D12S391, D2S1338, and Penta D) as well as two sex-determining markers; Y indel and Amelogenin [20]. Data from both populations were also compared with data sets from nearby countries to evaluate genetic differences and gain more insight into genetic distances and closeness between English and Irish populations.

2. Materials and methods

2.1. Population samples

A total of 577 English (341 males and 236 females) and 500 Irish (323 males and 177 females) population samples were collected from unrelated individuals aged 21–60 (mean age 34.2) after obtaining informed consent. All samples were collected from various locations across the United Kingdom from random volunteers with English and Irish self-proclaimed ethnicity for three generations. Efforts were made to ensure a diverse representation of volunteers by including participants with English and Irish ethnic backgrounds from different regions, to obtain a sample pool that reflects the genetic diversity of the broader population in the United Kingdom. Ethical approval was granted by the University of Lincoln (Ethics reference: 2021_6560). The ethical principles outlined in the Helsinki declaration for research involving human subjects were also followed [21].

Prior to sampling, volunteers were requested not to consume any food or drink for 30 min. Buccal swab samples were then collected. The cotton end of the swab was rubbed against the inside of the cheek for 30 s and allowed to air-dry at room temperature for another 30 s. The swab was then placed into a labelled, sealable envelope.

2.2. DNA profiling

DNA was extracted using the Prep-n-Go Buffer (Applied Biosystems) reagent with room temperature protocol, as previously described [22]. DNA quantification was performed on QuantStudio 5 Real-Time PCR System (Applied Biosystems) using Quantifiler HP DNA Quantification Kit (Applied Biosystems) following the manufacturer's recommendations. The DNA samples were then processed employing a reduced volume method for the VeriFiler Express PCR Amplification Kit (Applied Biosystems) [23]. Variant alleles were reprocessed for confirmation.

2.3. Quality control

Developed DNA profiles were checked in Microsoft Excel for any duplicate or closely related profiles using the add-in GenAlEx 6.503 [24]. All population data were then submitted and passed STRidER quality control (STR000410 and STR000411) [25].

2.4. Statistical analysis

Forensic and population genetic parameters, and the principal component analysis (PCA) plot were generated using the online tool STRAF 2.1.51: STR Analysis for Forensics [26]. The English and Irish populations were compared with other European population data (Austria, Belgium, Denmark, France, Germany, Ireland, Norway, Slovenia, Spain, Sweden, and Switzerland) using the phylogenetic tree option available on the STRAF tool, with allele frequencies from the STRidER database.

3. Results and discussion

3.1. Allele frequencies and forensic parameters

Allele frequencies and forensic parameters for both populations are available in Table S1. The alleles with the highest frequency for the English population were allele 8 at locus TPOX (0.5442), allele 16 at locus D22S1045 (0.4090), and allele 11 at locus D5S818 (0.3744). For the Irish population, the highest frequency alleles were allele 8 at locus TPOX (0.5250), allele 12 at locus D5S818 (0.4070), and allele 15 at locus D22S1045 (0.3900). Hence, allele 8 at TPOX was the highest frequency allele in both populations.

For both populations the most discriminatory locus was D1S1656, with PD of 0.9801 and 0.9766 for the English and Irish populations respectively. Evaluation of Hardy-Weinberg equilibrium (HWE) revealed, for each population, one locus below the significant p-value (0.05); locus D5S818 (p-value = 0.0259) in the English population, and locus TPOX (p-value = 0.0453) in the Irish population. These deviations from the HWE could be due to incorrect self-declaration of ethnicity, population size, population substructure, inbreeding, or selection [6,27]. Another common cause of disequilibrium is genotyping error. Primer binding site mutations generating null alleles are frequently encountered during STR typing, potentially leading to rare homozygotes that can generate significant deviations from HWE [28]. Sequence-based STR analysis would reveal more alleles, but the HWE could remain unchanged [29].

3.2. Variant alleles

Variant alleles are alleles not covered by the bin set of a kit [30]. Two variant alleles were detected in the English population; allele 18.1 at locus D1S1656 and allele 29 at locus D12S391. Only one variant allele was detected in the Irish population; allele 14.4 at locus Penta D. Allele 29 at locus D12S391, which was outside the marker range on the VeriFiler Express PCR Amplification Kit, was confirmed by using the SureID 27comp Human DNA Identification Kit (Health Gene Technologies), which also contains locus D12S391, but with different allele sizes and loci order (Fig. 1).

All of these variant alleles have been previously reported in the online database of the National Institute of Standards and Technology

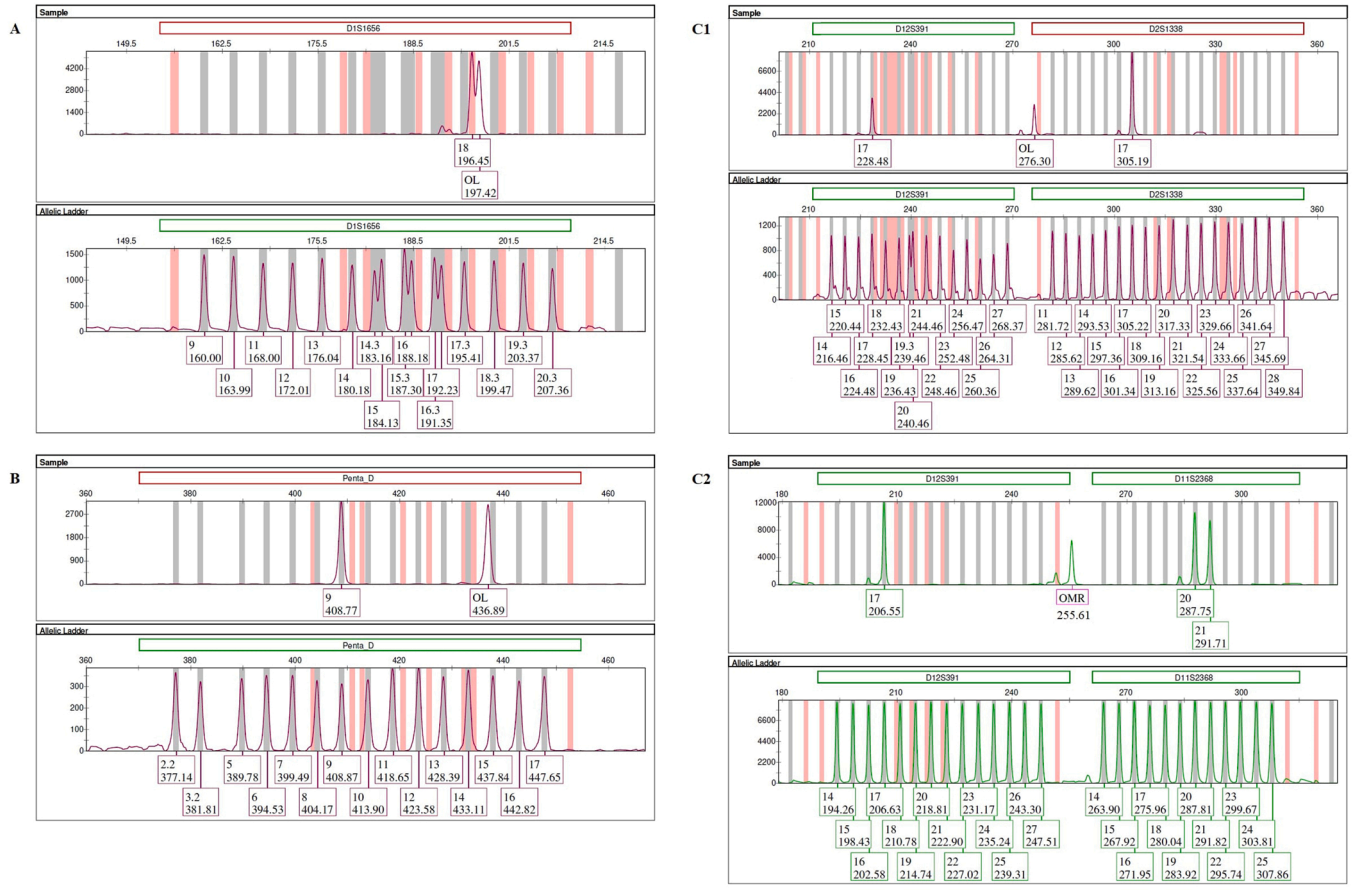

Fig. 1. Electropherograms showing the rare alleles found in the English and Irish population samples: allele 18.1 at locus D1S1656 (A), allele 14.4 at locus Penta D (B), and allele 29 at locus D12S391 (C1), which was confirmed with the SureID 27comp Human DNA Identification Kit (C2). Allelic ladder for the relative markers is also showed. OL = Off Ladder, OMR = Outside Marker Range.

(NIST) Population Dataset (STRBase; https://strbase.nist.gov/) [31]. However, they have not been reported in other databases, such as The European Network of Forensic Science Institutes (ENFSI) DNA working group STR population database (STRidER; https://strider.online/) [25] and ALFRED, the Allele Frequency Database (https://alfred.med.yale.edu/) [32].

3.3. English and Irish populations comparison

The principal component analysis of the English and Irish populations revealed high genetic similarity between them (Fig. 2). In fact, the first two principal components (PC1 and PC2) accounted for only a small percentage of the total variance (0.88% and 0.86% respectively), highlighting nearly equal variances.

In addition, the pairwise F_{st} value calculated between the two populations was 0.0013, confirming the lack of genetic differentiation when employing the STR markers used in this study. Generally, smaller F_{st} values indicate geographical relationships and are observed between populations with shared origins [33]. The size of this F_{st} also resembles the F_{st} estimate obtained between populations of Britain and Irish of Gaelic ancestry in a previous study [34].

3.4. Comparison with other European populations

In the population comparison study carried out on STRAF tool, only 14 loci (D3S1358, D16S539, D8S1179, D21S11, D18S51, D2S441, D19S433, TH01, FGA, D22S1045, D10S1248, D1S1656, D12S391, and D2S1338) shared with other populations from the STRidER database were used to generate the phylogenetic tree shown in Fig. 3.

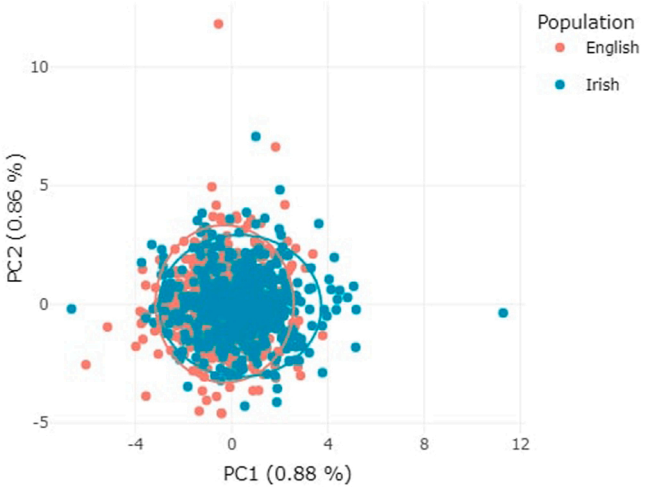

Fig. 2. PCA plot showcasing the genetic relationship between English and Irish populations. PC1 = Principal Component 1, PC2 = Principal Component 2.

This phylogenetic tree indicated a close genetic relationship between the Irish population retrieved on the STRidER database and this study's Irish population. Both these Irish populations clustered in the same group and exhibited close genetic links to Austrian, Belgian, German, and Swiss populations. The English population, on the other hand, appeared more closely related to Danish, Swedish, and Norwegian populations.

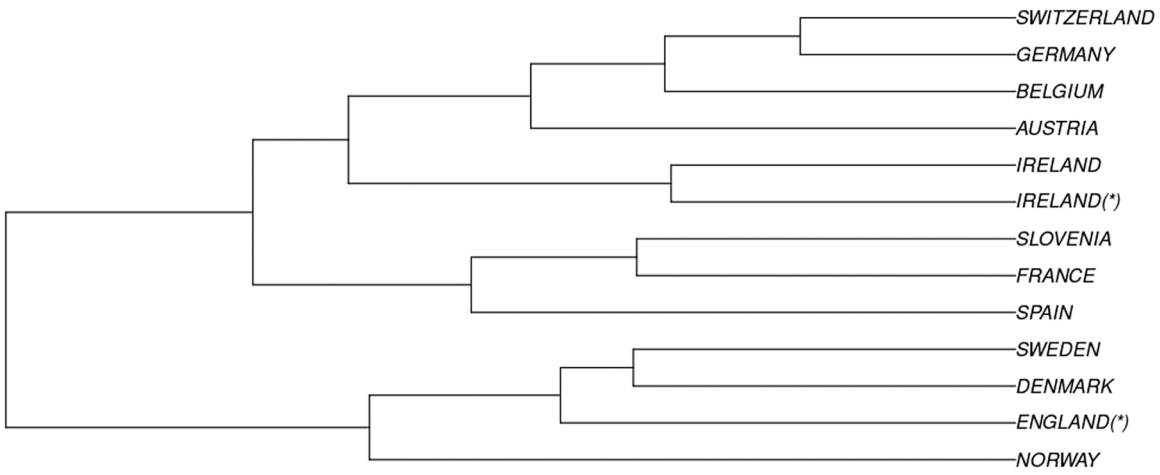

Fig. 3. Phylogenetic tree showing the English and Irish populations from this study, denoted with an asterisk (*), in comparison with 11 European populations from the STRidER database.

The history of England and Ireland suggests that the English and Irish populations experienced strong genetic influence from Scandinavia, along with potential French influence. A genome-wide ancient DNA study by Gretzinger et al. [35] found English DNA, and not Irish, to have experienced significant French influence, while this study revealed a closer genetic relationship between French and Irish rather than French and English populations. Gretzinger et al. also reported close genetic relationships between England, Germany, and Denmark, and while the present study supports the finding of genetic closeness between England and Denmark, it also indicates that Ireland might be more closely linked to the German rather than the English population.

Krzewińska et al. [36] used next-generation sequencing to study mitochondrial DNA polymorphisms and found the Viking-age Norwegian population to be genetically similar to modern Scandinavian, English, and Scottish populations. This substantiates the genetic distance results obtained between England, Norway, Sweden, and Denmark in the present study.

A genome sequencing investigation by Margaryan et al. [37] found Norwegian-like ancestry to be present in Ireland. However, the current study did not identify any close genetic relationships between Ireland and Norway, instead, genetic closeness was observed between England and Norway. Margaryan et al. also reported the presence of Danish-like ancestry in England, but the Viking Age Danish-like ancestry in the British Isles cannot be distinguished from Angles, Saxons, and Jutes, who migrated from present-day northern Germany and Denmark around 1,500 years ago. The Danish influence on English DNA is supported by the genetic closeness observed between England and Denmark in the current study. However, while Ireland and Germany showed genetic closeness, a similar genetic relationship would have been expected between England and Germany, which in this case was not observed.

The Roman invasion could also have influenced the English genetic pool as they settled in England but never invaded Ireland [8,9]. However, historical records report that auxiliary units from the western Roman empire, especially Batavians from Germania Inferior province, Tungrians from Gallia Belgica province, and Gallians from Gallia Lugdunensis province, were recruited by the Romans for this conquest [38]. This would support the findings of Gretzinger et al. [35] and would indicate little influence of Italian DNA in the English genetic pool, but due to the limited number of available populations on the STRidER database, the relationship with the Italian population was not explored in the current investigation.

4. Conclusions

In this study, allele frequencies for the English and Irish populations were generated using the VeriFiler Express PCR Amplification Kit. Forensic parameters, genetic similarities between the two populations, and genetic relationships with other nearby countries were also determined.

The results showed minimal genetic differentiation, and instead, close genetic similarity between the English and Irish populations, which could be due to shared genetic ancestry, historical influences, and geographical proximity. Comparison with other European populations revealed distinct genetic relationships, with the English population appearing more closely linked to Scandinavian countries and the Irish population exhibiting closer genetic links to Western European countries. Interestingly, the genetic links obtained in this study appeared both in accordance and in contrast with previous published data.

The findings suggest that historical migrations and the intermingling of populations between England and Ireland have contributed to their genetic similarities. However, certain factors such as the lack of Roman influence in the Irish genetic pool and the impact of Irish emigration and return post-WWII may have led to distinct differences between the two populations which may not have been captured by the kit used in the current investigation.

While the observed genetic similarity supports the use of a single allele frequency database for both populations, further research using additional genetic markers is warranted to better understand the genetic makeup and history of England and Ireland, as well as their genetic relationship with other nearby countries. Additionally, the study highlights the need to explore the establishment of separate databases to ensure maximum representation for statistical calculations and forensic purposes.

Overall, this research contributes to our knowledge of the genetic relationships between English and Irish populations and provides insights into their shared ancestry and genetic characteristics.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fsir.2023.100334.

References

[1] S. Gittelson, T.R. Moretti, A.J. Onorato, B. Budowle, B.S. Weir, J. Buckleton, The factor of 10 in forensic DNA match probabilities, Forensic Sci. Int. Genet. 28 (2017) 178–187, https://doi.org/10.1016/j.fsigen.2017.02.007.

[2] Home Office, Data to support the implementation of National DNA Database, 2014. ⟨https://www.gov.uk/government/statistics/dna-population-data-to-support-the-implementation-of-national-dna-database-dna-17-profiling⟩ (accessed 23 May 2023).

[3] P.M. Schneider, Scientific standards for studies in forensic genetics, Forensic Sci. Int. 165 (2007) 238–243, https://doi.org/10.1016/j.forsciint.2006.06.067.

[4] P.M. Schneider, Beyond STRs: the role of diallelic markers in forensic genetics, Transfus. Med. Hemotherapy. 39 (2012) 176–180, https://doi.org/10.1159/000339139.

[5] J.M. Butler, The future of forensic DNA analysis, Philos. Trans. R. Soc. B Biol. Sci.. 370 (2015), e20140252, https://doi.org/10.1098/rstb.2014.0252.

[6] S. Iyavoo, O. Afolabi, B. Boggi, A. Bernotaite, T. Haizel, Population genetics data for 22 autosomal STR loci in European, South Asian and African populations using SureID® 23comp Human DNA Identification Kit, Forensic Sci. Int. 30 (2019) 174–181, https://doi.org/10.1016/j.forsciint.2019.05.033.

[7] N. Edwards. The Archaeology of Early Medieval Ireland, first ed., Routledge, London, 1996 https://doi.org/10.4324/9780203433782.

[8] E. Saur, The Roman invasion of Britain (AD 43) in imperial perspective: A response to Frere and Fulford, Oxf. J. Archaeol. 21 (2002) 333–363, https://doi.org/10.1111/1468-0092.00167.

[9] D.Ó. Corráin, The Vikings and Ireland, in: S. Brink, N. Price (Eds.), The Viking World, Routledge, London, 2008, pp. 428–433, https://doi.org/10.4324/9780203412770.

[10] A. Walsh, Scandinavian Relations with Ireland During the Viking Period, Good Press,, 2021.

[11] Britannica, The Editors of Encyclopaedia, "Norman", Encyclopedia Britannica, 2022. https://www.britannica.com/topic/Norman-people (accessed 2 May 2023).

[12] M. Hanson, The Normans, 2022. https://englishhistory.net/middle-ages/the-normans/ (accessed 2 May 2023).

[13] R.P. Byrne, R. Martiniano, L.M. Cassidy, M. Carrigan, G. Hellenthal, O. Hardiman, D.G. Bradley, R.L. McLaughlin, Insular Celtic population structure and genomic footprints of migration, PLoS Genet. 14 (2018), e1007152, https://doi.org/10.1371/journal.pgen.1007152.

[14] A. Hadfield, Briton and Scythian: Tudor Representations of Irish Origins Author, Ir. Hist. Stud. 28 (1993) 390–408, https://doi.org/10.1017/S0021121400011354.

[15] J.H. Relethford, M.H. Crawford, J. Blangero, Genetic Drift and Gene Flow in Post-Famine Ireland, Hum. Biol. 69 (1997) 443–465.

[16] K. Kenny, Diaspora and Comparison: The Global Irish as a Case Study, J. Am. Hist. 90 (2003) 134–162, https://doi.org/10.2307/3659794.

[17] P. Mac Éinrí, A. White, Immigration into the Republic of Ireland: a bibliography of recent research, Ir. Geogr. 41 (2008) 151–179, https://doi.org/10.1080/00750770802076943.

[18] Federal Bureau of Investigation, Combined DNA Index System (CODIS). ⟨https://le.fbi.gov/science-and-lab/biometrics-and-fingerprints/codis⟩, (accessed 23 May 2023).

[19] ENFSI DNA Working Group, DNA Database Management Review and Recommendations, 2019. ⟨https://enfsi.eu/wp-content/uploads/2021/09/ENFSI-DOCUMENT-ON-DNA-DATABASE-MANAGEMENT-2019.pdf⟩ (accessed 23 May 2023).

[20] Applied Biosystems™, VeriFiler™ Express PCR Amplification Kit user guide, 2021. Publication No.: 100043588 ⟨https://assets.thermofisher.com/TFS-Assets/LSG/manuals/100043588_VFE_UG.pdf⟩ (accessed 2 May 2023).

[21] World Medical Association, WMA Declaration of Helsinki – ethical principles for medical research involving human subjects, 2022. ⟨https://www.wma.net/policies-post/wma-declaration-of-helsinki-ethical-principles-for-medical-research-involving-human-subjects/⟩ (accessed 11 July 2023).

[22] S. Iyavoo, S. Knights, M. Mavrommatis, T. Haizel, Implementation of Prep-n-GoTM Buffer for DNA extraction from buccal swabs, Forensic Sci. Int. Genet. Suppl. Ser. 7 (2019) 211–213, https://doi.org/10.1016/j.fsigss.2019.09.081.

[23] J. Perry, T. Munshi, T. Haizel, S. Iyavoo, Validation of reduced volume VeriFilerTM Express PCR Amplification Kit for buccal swab samples extracted using Prep-n-GoTM Buffer, J. Forensic Sci. 67 (2022) 1971–1978, https://doi.org/10.1111/1556-4029.15084.

[24] R. Peakall, P.E. Smouse, GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research - an update, Bioinformatics 28 (2012) 2537–2539, https://doi.org/10.1093/bioinformatics/bts460.

[25] M. Bodner, I. Bastisch, J.M. Butler, R. Fimmers, P. Gill, L. Gusmão, N. Morling, C. Phillips, M. Prinz, P.M. Schneider, W. Parson, Recommendations of the DNA Commission of the International Society for Forensic Genetics (ISFG) on quality control of autosomal Short Tandem Repeat allele frequency databasing (STRidER), Forensic Sci. Int. Genet. 24 (2016) 97–102, https://doi.org/10.1016/j.fsigen.2016.06.008.

[26] A. Gouy, M. Zieger, STRAF – A convenient online tool for STR data evaluation in forensic genetics, Forensic Sci. Int. Genet. 30 (2017) 148–151, https://doi.org/10.1016/j.fsigen.2017.07.007.

[27] S.J. Walsh, C.M. Triggs, J.M. Curran, J.R. Cullen, J.S. Buckleton, Evidence in Support of Self-Declaration as a Sampling Method for the Formation of Sub-Population DNA Databases, J. Forensic Sci. 48 (2003), e2002364, https://doi.org/10.1520/jfs2002364.

[28] J. Graffelman, B.S. Weir, The transitivity of the Hardy-Weinberg law, Forensic Sci. Int. Genet. 58 (2022), 102680, https://doi.org/10.1016/j.fsigen.2022.102680.

[29] K.B. Gettings, L.A. Borsuk, C.R. Steffen, K.M. Kiesler, P.M. Vallone, Sequence-based U.S. population data for 27 autosomal STR loci, Forensic Sci. Int. Genet. 37 (2018) 106–115, https://doi.org/10.1016/j.fsigen.2018.07.013.

[30] K.B. Gettings, R.A. Aponte, P.M. Vallone, J.M. Butler, STR allele sequence variation: Current knowledge and future issues, Forensic Sci. Int. Genet. 18 (2015) 118–130, https://doi.org/10.1016/j.fsigen.2015.06.005.

[31] C.M. Ruitberg, D.J. Reeder, J.M. Butler, STRBase: A short tandem repeat DNA database for the human identity testing community, Nucleic Acids Res. 29 (2001) 320–322, https://doi.org/10.1093/nar/29.1.320.

[32] H. Rajeevan, U. Soundararajan, J.R. Kidd, A.J. Pakstis, K.K. Kidd, ALFRED: an allele frequency resource for research and teaching, Nucleic Acids Res. 40 (Database issue) (2012) D1010–D1015, https://doi.org/10.1093/nar/gkr924.

[33] C. Tian, R. Kosoy, R. Nassir, A. Lee, P. Villoslada, L. Klareskog, L. Hammarström, H. J. Garchon, A.E. Pulver, M. Ransom, P.K. Gregersen, M.F. Seldin, European Population Genetic Substructure: Further Definition of Ancestry Informative Markers for Distinguishing among Diverse European Ethnic Groups, Mol. Med. 15 (2009) 371–383, https://doi.org/10.2119/molmed.2009.00094.

[34] E. Gilbert, S. O'Reilly, M. Merrigan, D. McGettigan, A.M. Molloy, L.C. Brody, W. Bodmer, K. Hutnik, S. Ennis, D.J. Lawson, J.F. Wilson, G.L. Cavalleri, The Irish DNA Atlas: Revealing Fine-Scale Population Structure and History within Ireland, Sci. Rep. 7 (2017), 17199, https://doi.org/10.1038/s41598-017-17124-4.

[35] J. Gretzinger, D. Sayer, P. Justeau, E. Altena, M. Pala, K. Dulias, C.J. Edwards, S. Jodoin, L. Lacher, S. Sabin, A.J. Vågene, W. Haak, S.S. Ebenesersdóttir, K.H. S. Moore, R. Radzeviciute, K. Schmidt, S. Brace, M.A. Bager, N. Patterson, L. Papac, N. Broomandkhoshbacht, K. Callan, E. Harney, L. Iliev, A.M. Lawson, M. Michel, K. Stewardson, F. Zalzala, N. Rohland, S. Kappelhoff-Beckmann, F. Both, D. Winger, D. Neumann, L. Saalow, S. Krabath, S. Beckett, M.V. Twest, N. Faulkner, C. Read, T. Barton, J. Caruth, J. Hines, B. Krause-Kyora, U. Warnke, V. J. Schuenemann, I. Barnes, H. Dahlström, J.J. Clausen, A. Richardson, E. Popescu, N. Dodwell, S. Ladd, T. Phillips, R. Mortimer, F. Sayer, D. Swales, A. Stewart, D. Powlesland, R. Kenyon, L. Ladle, C. Peek, S. Grefen-Peters, P. Ponce, R. Daniels, C. Spall, J. Woolcock, A.M. Jones, A.V. Roberts, R. Symmons, A.C. Rawden, A. Cooper, K.I. Bos, T. Booth, H. Schroeder, M.G. Thomas, A. Helgason, M. B. Richards, D. Reich, J. Krause, S. Schiffels, The Anglo-Saxon migration and the formation of the early English gene pool, Nature 610 (2022) 112–119, https://doi.org/10.1038/s41586-022-05247-2.

[36] M. Krzewińska, G. Bjørnstad, P. Skoglund, P.I. Olason, J. Bill, A. Götherström, E. Hagelberg, Mitochondrial DNA variation in the Viking age population of Norway, Philos. Trans. R. Soc. B Biol. Sci. 370 (2015), e20130384, https://doi.org/10.1098/rstb.2013.0384.

[37] A. Margaryan, D.J. Lawson, M. Sikora, F. Racimo, S. Rasmussen, I. Moltke, L. M. Cassidy, E. Jørsboe, A. Ingason, M.W. Pedersen, T. Korneliussen, H. Wilhelmson, M.M. Buś, P.B. Damgaard, R. Mariniano, G. Renaud, C. Bhérer, J. V. Moreno-Mayar, A.K. Fotakis, M. Allen, R. Allmäe, M. Molak, E. Cappellini, G. Scorrano, H. McColl, A. Buzhilova, A. Fox, A. Albrechtsen, B. Schütz, B. Skar, C. Arcini, C. Falys, C.H. Jonson, D. Błaszczyk, D. Pezhemsky, G. Turner-Walker, H. Gestsdóttir, I. Lundstrøm, I. Gustin, I. Mainland, I. Potekhina, I.M. Muntoni, J. Cheng, J. Stenderup, J. Ma, J. Gibson, J. Peets, J. Gustafsson, K.H. Iversen, L. Simpson, L. Strand, L. Loe, M. Sikora, M. Florek, M. Vretemark, M. Redknap, M. Bajka, T. Pushkina, M. Søvsø, N. Grigoreva, T. Chrisensen, O. Kastholm, O. Uldum, P. Favia, P. Holck, S. Sten, S.V. Arge, S. Ellingvåg, V. Moiseyev, W. Bogdanowicz, Y. Magnusson, L. Orlando, P. Pentz, M.D. Jessen, A. Pedersen, M. Collard, D.G. Bradley, M.L. Jørkov, J. Arneborg, S.M. Sindbæk, L. Hedeager, K. Kristiansen, R. Nielsen, T. Werge, E. Willerslev, Population genomics of the Viking world, Nature 585 (2020) 390–396, https://doi.org/10.1038/s41586-020-2688-8.

[38] D.B. Cuff, 2010, The *auxilia* in Roman Britain and the Two Germanies from Augustus to Caracalla: Family, Religion and 'Romanization' (Doctoral thesis, Department of Classics, University of Toronto). ⟨https://tspace.library.utoronto.ca/bitstream/1807/24732/1/Cuff_David_B_201006_PhD_thesis.pdf⟩.