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SUPPLEMENTARY INFORMATION

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Ancient genomes indicate population replacement in Early Neolithic Britain

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Ancient Genomes Indicate Population Replacement in Early Neolithic Britain SUPPLEMENTARY MATERIAL

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Section 1: Archaeological information

Tom Booth, Ian Barnes & Rick Schulting

This includes archaeological information for all newly-reported samples. Archaeological information for previously-published samples can be found in Olalde et al., 2018[1]. All quoted radiocarbon dates have been calibrated using the IntCal13 curve in OxCal 4.3[2] apart from Ogof-yr-Ychen_1 (UBA-32282) and CnocCoig_1 (SUERC-69249) which were calibrated using a mixed IntCal13/Marine13 curve[2-3]. Proportions of marine/terrestrial contribution were calculated in each case from carbon stable isotope results assuming observed marine and terrestrial endpoints of -12.0‰ and -21.0‰ respectively[4]. The estimated % contribution of marine C to collagen for Cnoc Coig and Ogof-yr-Ychen were on average 90±10% and 63±10% and marine offsets calculated using ΔR values of -68±90 and -33±93 respectively[5-8]. Contextual dates listed here (denoted by 'BCE' rather than 'cal. BCE') and in Supplementary Table S1 are used for samples that have not been dated directly but where absolute dates on associated material or typological associations infer a particular date range.

Aveline's Hole, Somerset, England, UK

Contacts: Linda Wilson and Graham Mullan

Aveline's Hole is a cave located near the village of Burrington in the Mendip Hills of northern Somerset. The cave was first discovered in 1797 AD by two young men chasing a rabbit[9]. The presence of a large assemblage of human remains was noted from the time of its discovery and it is clear that this deposit was disturbed and diminished until it was excavated by the University of Bristol Spelaeological Society (UBSS) in 1912-1914. As well as human bones, the deposit included stone tools and faunal remains, some of which showed signs of butchery. Perforated periwinkle shells were found scattered through the deposits and may have been grave goods. Post-excavation assessments of the human remains suggested that there were around 50 individuals represented. Unfortunately, the UBSS collections were damaged by an air-raid on Bristol in 1940, destroying a large proportion of the Aveline's Hole assemblage. The extant human assemblage represents the remains of at least 21 individuals. Early accounts may be of questionable reliability, but suggest that at least some skeletons were in correct anatomical articulation, suggesting that fleshed bodies had been placed in the cave soon after death. There was also some suggestion from early accounts of the discovery of the cave that a large stone slab had sealed the entrance.

Prior to this study, 23 radiocarbon dates were available on human remains from Aveline's Hole. These dates were consistent with one continuous phase of Early Mesolithic burial activity from 840-8290 cal. BCE to 8260-8140 cal. BCE (95% probability), lasting only 70-180 years (68% probability). The number of bodies that were deposited in Aveline's Hole over this relatively short period of time suggested that the site was a place where disparate groups met to inter their dead. However, further radiocarbon dating for this paper suggests that Aveline's Hole was later reused for the deposition of human remains, possibly limited to crania, in the Early Neolithic. The Aveline's Hole human remains assemblage is curated at the UBSS in Bristol. Palaeogenetic data from three samples of petrous portions of temporal bones and one

sample of a left tibia (Aveline_9) have been included here, two dating to the Early Mesolithic and two to the Early Neolithic:

Aveline_3/SB343C/I6745/M1.15(3): 8750-8459 cal. BCE (9340±50 BP, OxA-34338)

Aveline_9/SB337B/I6744/M1.14(55): 8596-8302 cal. BCE (9230±50 BP, OxA-34339)

Aveline_1/SB350C/I6746/M1.11(326): 3695-3384 cal. BCE (4809±45 BP, UBA-30800)

Aveline_13/SB338B/I3005/M1.11(325): 3780-3650 cal. BCE (4934±35 BP, OxA-34336)

Burn Ground, Gloucestershire, England, UK

Contact: David Rice

Burn Ground is a megalithic tomb covered by an earthen long barrow and belongs to the Cotswold-Severn group of Neolithic tombs[10-11]. The architecture of the tomb is an unusual hybrid, including both a transverse and a transepted lateral passageway. It is located near the village of Hampnett, outside Cheltenham in Gloucestershire and was excavated in 1940-1 by Professor W.F. Grimes. Human remains representing a minimum of ten adults and three subadults were recovered from the transverse passageway and the transepts. The bones from the transverse passageway accounted for six adults and three subadults, but were incomplete, highly disarticulated and commingled, and no specific individuals could be identified. In contrast, the human bones from the transepts mostly comprised the disarticulated remains of single individuals, suggesting two discrete depositional traditions. No cut marks or modifications indicative of excarnation were found on any of the bones, and the most likely scenario was that bodies were deposited fleshed before the bones were manipulated and disturbed after bodies had decomposed.

Nine radiocarbon dates have been obtained from the Neolithic Burn Ground human remains; 8 on individuals deposited in the transepts and one on a disarticulated bone from the transverse passageway[11]. All of the radiocarbon dates place the death of individuals in the British Early Neolithic and many of the dates are amongst the oldest obtained for British human remains from Neolithic tombs, with some placed in the centuries before 3800 BCE and one potentially pre-dating 4000 BCE. This early date may be attributable to the deposition of human remains that had been curated for an extended period of time. There were no differences in dates of human remains from the different passageways, suggesting that the assemblage may represent contemporaneous discrete depositional practices. The human remains are currently curated by Bournemouth University of behalf of Gloucester City Museum. Palaeogenetic data from a sample of a petrous portion of a temporal bone originating from a disarticulated assemblage of remains of a single individual from one of the transepts (Deposit 5) that had produced a particularly early radiocarbon date was included in this study:

BurnGround/SB488B/I6760/Deposit 5(A2615): 3943-3711 cal. BCE (5023±34 BP, OxA-17173)

Bryn yr hen Bobl, Anglesey, Wales, UK

Contact: Elizabeth Walker

Bryn yr hen Bobl ('hill of the old people') is a chambered cairn monument located near Plas Newydd on the island of Anglesey in North Wales[12]. It is composed of a 'kidney-shaped' cairn with an extended terrace continuing some six metres to the south. The entrance to the cairn leads into a single chamber. The entrance is flanked by two protruding 'horns', creating a forecourt. The cairn chamber was originally opened by workmen in 1754, and after this point there were several more visits by individuals who noted the presence of a large assemblage of human bones in the chamber. The cairn was on the estate of the Marquess of Anglesey and was excavated by W.J. Hemp in 1929 on behalf of the Marquess.

The chamber contained a mixed deposit of human and animal bone, as well as pottery sherds, stone tools, axes and arrowheads dating typologically to the Neolithic. The human bone assemblage comprised disarticulated, commingled and incomplete skeletons representing the remains of around 20 individuals of variable age and sex. One of the crania had been trephinated. The finds are currently curated at the National Museum of Wales in Cardiff. Palaeogenetic data from a petrous portion of a temporal bone was included in this study. The cranium had been radiocarbon dated to the Late Neolithic.

Bryn_Yr_Hen_Bobl_1/SB568A/I5357/39.578/23: 2911-2698 cal. BCE (4233±32 BP, OxA-12741)

Carsington Pasture Cave, Brassington, Derbyshire, England, UK

Contact: Andrew Chamberlain

Carsington Pasture Cave is located in the southern Peak District, around one kilometre east of Brassington village, Derbyshire[13-14]. The cave was originally explored and excavated in 1998 by members of the Pegasus Caving Cub and archaeologists from the University of Sheffield, revealing three successive chambers joined by near-vertical passages. New explorations have periodically produced more finds from the cave, which are held in the collections of Andrew Chamberlain at the University of Manchester.

Large quantities of disarticulated human and faunal bone were recovered all chambers and adjoining passages. The human bone was mostly concentrated in the second chamber and represented the remains of at least 20 individuals, mostly mature adults and neonatal infants. The neonatal infant remains were mostly complete, in partial articulation and concentrated in the centre of the second chamber, suggesting that this area was reserved for primary deposition of young infants. The adult bones were dispersed through the three chambers although skeletal part representation suggested that whole bodies were originally interred, with sediment and carnivore action (as indicated by tell-tale gnaw marks on a small proportion of bone surfaces) distributing the remains through the chambers over time. Very few dateable finds were recovered from the cave, but a bone pin and a worked antler fragment dating typologically to the Bronze Age and Neolithic respectively were found in the second chamber. Roman pottery and coins found in passages leading off from the entrance chamber and evidence for post-medieval mining suggested that the cave was continuously accessible.

Radiocarbon dating of human remains from the cave have produced Early Neolithic, Early Bronze Age and Iron Age dates.

Palaeogenetic data for this project were obtained from the petrous portion of the temporal bone of a mostly-complete, partially articulated adult male skeleton known as 'Sven'. This individual had been radiocarbon dated to the Early Neolithic:

Carsington_Pasture_1/SB381/I6747/'Sven': 3656-3521 cal. BCE (4808±35 BP, UB-29004)

Cave Ha 3, Giggleswick Scar, Yorkshire Dales, England, UK

Contact: Tom Lord

The Cave Ha Complex refers to a group of four rock shelters on the Giggleswick Scar limestone located near the town of Settle in the North Yorkshire Dales[15]. Ancient human and faunal remains were recovered from these rockshelters during excavations in the 1870s and the 1940s-50s. However, human remains were only recovered from Cave Ha 3 and 4. Archives of the excavation reports are currently held at Craven Museum in Skipton.

Cave Ha 3 consists of a medium-sized rock shelter with two natural recesses located on the back wall, adjacent to a large hearth. The faunal assemblage included domesticated cattle bones that showed evidence of having been highly processed. A charcoal sample recovered during the excavations which produced the cattle bone gave a date in the early Beaker period. Finds recovered from Cave Ha 3 included 2 Neolithic flint scrapers and a limestone pestle. The flints were located close to the human remains from the cave and may have been grave goods.

The human bones recovered from Cave Ha 3 represented incomplete, disarticulated and commingled remains remains of at least four individuals: a mature adult male (Individual 1), a neonate (Individual 2), a 9 to 12-month-old infant (Individual 3) and a two-year-old child (Individual 4). The two natural recesses seem to have formed the focal point for the deposition of these remains. The bones had been deposited directly onto tufa, with many of the bones having been encased in this material. A lack of cortical weathering and correct anatomical articulation of some skeletal elements suggested that these individuals had been deposited in the cave fairly soon after death. The incompleteness of the skeletons therefore suggests that the bodies had been revisited and manipulated at a later stage. Direct evidence for manipulation was found in the left tibia of the adult male, which had been split longitudinally whilst fresh. Individual 1 and Individual 4 were both radiocarbon dated to the Early Neolithic. The human remains from Cave Ha 3 are currently held in Tom Lord's private collections at Lower Winskill Farm. Palaoegenetic data generated from a sample of temporal bone from Individual 2 were included in this study. As this individual was a child, sex could not be estimated osteologically; however, the genetic data indicated that they were male.

CaveHa3_1/SB467A/I3059/Individual 4: 3654-3523 cal. BCE (4595±40 BP, OxA-14226).

Cnoc Coig, Oronsay, Inner Hebrides of Scotland, UK

Contact: Alison Sheridan

Cnoc Coig is one of a series of five monumental Mesolithic shell midden sites located on the small island of Oronsay, in the Inner Hebrides of Scotland[16-19]. These middens are complex monuments and include evidence for different types of activity, including hearths and structures[16]. The site was originally excavated in 1911 and 1912, before being excavated more extensively in 1973-79 by Paul Mellars. These shell middens are the only Mesolithic sites from Britain which included human remains dating to the 5th Millennium BCE[17]. This is testament to the paucity of British Late Mesolithic human remains, presumably because their predominant mortuary rite was one that left no archaeological trace. Oronsay would have been too small in of itself to sustain a large population of people and it is likely that Mesolithic hunter-gatherers visited the island seasonally to fish and hunt marine mammals, as well as disposing of human remains. Carbon and nitrogen stable isotope analysis of several human remains from these middens has suggested that they obtained the majority and perhaps all of their dietary protein from marine resources, indicating that their a subsistence strategies were highly dependent on coastal environments[7, 18].

Human remains recovered from all of these Mesolithic shell middens comprise collections of disarticulated isolated skeletal elements, usually from several individuals[18]. At Cnoc Coig, the small bones of the hands and feet were represented most often. The tendency for these kinds of bones to disarticulate from the body first during decomposition has led to suggestions that Mesolithic communities were excarnating bodies on shell middens for a short while before moving the bulk of the remains to another location[19]. At least six individuals were represented by the remains recovered from Cnoc Coig.

When calibrated for the marine reservoir effect, radiocarbon dates of human remains from Cnoc Coig date from 4370-3800 BCE, overlapping with the earliest Neolithic radiocarbon dates from Britain and western Scotland specifically, suggesting that Mesolithic hunter-fisher-gatherers and Britain's earliest farmers may have lived side-by-side for a century or more[7, 17]. The human remains from Cnoc Coig are currently curated by National Museums Scotland. Palaeogenetic data from a disarticulated petrous portion of a temporal bone were included in this study. The bone has been radiocarbon dated recently as part of a separate study[8]:

Cnog_Coig_1/SB514B/I3065/CC 18143: 4256-3803 cal. BCE (5492±36 BP, SUERC-69249)

Coldrum, Trottiscliffe, Kent, England, UK

Contact: Heather Bonney

Coldrum is a megalithic chambered tomb belonging to the Medway group of monuments, which is made up of nine structures grouped around the River Medway in Kent[20-21]. It is composed of a rectilinear tomb covered by an earthen long barrow defined by a series of sarsen megaliths. The architecture of the tomb has often been used to suggest that it is amongst the earliest British Neolithic tombs typologically and bears some resemblance to Middle Neolithic monuments from adjacent areas of Continental Europe, particularly France

(Pas-de-Calais) and Belgium. The western part of the chamber was excavated by F.J. Bennett in 1910 and the rest was excavated by E.W. Filkins in the 1920s[20].

The excavations of the chamber revealed two superimposed platforms that were thought to represent different phases of activity. Human remains representing at least 17 individuals, five adult males, four adult females, two older subadults four older children and two younger children were recovered from the main chamber. Deposits on both terraces comprised commingled disarticulated and incomplete remains of several individuals. Cut marks identified on certain bones suggested that some of the bodies had been ritually defleshed. The lack of cortical modifications associated with exposure suggested that whole bodies had originally been interred soon after death, with skeletons being disturbed and manipulated after bodies had decomposed. Carbon and nitrogen stable isotope analysis suggested that individuals deposited at Coldrum derived most of their protein from terrestrial sources and there was no evidence for the consumption of marine protein[20].

Radiocarbon dating of 22 bones from the Coldrum assemblage confirmed that the two platforms represented different phases of deposition. Chronological modelling of the radiocarbon dates using Bayesian inference suggested that the individuals represented by the lower terrace died during the earliest part of the British Neolithic from 3980-3800 to 3930-3750 cal. BCE, and the individuals represented in the upper terrace all died from 3730-3540 to 3310-2980 cal. BCE, in the British Early-Middle Neolithic[21]. However, evidence for manipulation of remains may mean that some of the individuals represented had been long dead and their bones curated before they were deposited at Coldrum.

The archive of the site is divided between the Cambridge University Duckworth Laboratory, the Natural History Museum, London and Maidstone Museum and Art Gallery. It was thought that the cranial remains mostly went to the Duckworth Laboratory, whilst the post-crania were deposited in the Maidstone Museum and the Natural History Museum[21]. However, research for this project identified cranial remains originating from Coldrum in the collections at the Natural History Museum. It is unclear which platform and therefore which phase these cranial remains belong to. Palaeogenetic data from a petrous portion of a temporal bone are included in this study:

Coldrum_1/SB451B/I6753/ 5901 NN1: 3980-3800 to 3930-3750 BCE or 3730-3540 to 3310-3980 BCE.

Embo, Sutherland, Scotland, UK

Contact: Alison Sheridan

Embo is an Orkney-Cromarty-type double-chambered round cairn located in the village of Embo, near the town of Dornoch, in Sutherland, the Highlands of Scotland[22]. The cairn was originally excavated in 1956[23] but these works were mainly concentrated on intrusive Bronze Age cists and cremations. The cairn chambers were excavated in 1960 as part of a rescue excavation in advance of the construction of a new car park. The two chambers of the cairn were accessible by separate short passageways, one to the north and one to the south. The southern entrance led to the main chamber which contained a collection of disarticulated,

commingled and incomplete skeletons representing the remains of at least six adults and nine children. The human remains in this chamber had been deposited in two layers separated by soil infilling. The first deposit consisted of the remains of at least three adults, a child and an infant. The second included bones from at least three adults one adolescent, four children and two infants. A series of stone slabs had been used to seal the chamber after these remains had been deposited.

The second chamber had been severely disturbed and mostly included faunal remains, although some disarticulated human bones representing at least one individual were also present. The presence of small bones of the hands and feet suggested that whole bodies had originally been interred in the chambers soon after death and that there was subsequent manipulation, disturbance and retrieval of skeletal elements after bodies had decomposed. Several human bones from the chambers and the intrusive cairns have been radiocarbon dated, producing dates that correspond to Middle-Late Neolithic and Beaker periods. The human remains are currently curated at National Museums Scotland. Palaeogenetic data from two petrous portions of temporal bones recovered from the primary chamber were included in this study.

Embo_1/SB519A2/I16766/Chamber I Ch II: 3500-2700 BCE

Embo_3/SB515A/I6764/Chamber ia Ch IV: 3500-2700 BCE

Gop Cave, Flintshire, Wales, UK

Contact: Elizabeth Walker

Gop Cave is a located on Gop Hill, close to the large prehistoric round cairn known as The Gop, which is situated on the hill's summit. Gop Hill forms part of the eastern boundary of the Vale of Clwyd in Flintshire, Wales. Gop Cave and The Gop were excavated by Boyd Dawkins in 1886 and 1887 at the behest of Mr Pochin of Bodnant Hall[24]. Gop Cave consists of a wide rockshelter that contracts into a narrow passageway. The cave was filled almost to the ceiling with debris when it was discovered and contained two main sedimentary layers which, based on the finds and the faunal assemblage broadly dated to the Pleistocene and Holocene.

The Holocene deposits, referred to as 'The Prehistoric Accumulations' by Boyd-Dawkins included quantities of charcoal, a possible hearth, disarticulated bones of domesticated animals and a series of limestone slabs. Many of the human remains were found beneath these slabs. A limestone chamber had been constructed against the back wall of the cave and was found to contain human bones representing the remains of at least 14 individuals. Gop Cave is one of several examples from Britain of caves that have been modified with internal structures to resemble a Neolithic tomb. The bodies had been compacted into the chamber, which was only four feet six inches by five feet by four feet. The skeletons were mostly complete and in various states of articulation in crouched postures, suggesting that each had been interred soon after death, with decomposition of preceding bodies making room for successive interments. This pattern of deposition suggested to Boyd Dawkins that the chamber represented a familial tomb. Finds included two jet belt sliders and sherds of Middle Neolithic Peterborough ware pottery. Three human bones from the Gop Cave chamber have

been radiocarbon dated, with two producing dates in the Early Neolithic and one in the Late Neolithic[25]. Palaeogenetic data generated from a sample of an undated temporal bone from Gop Cave was included in this study. This bone is assumed to be Neolithic based on the association with the other radiocarbon dated human remains from the chamber. The human remains from Gop Cave are currently curated at the National Museum of Wales.

Gop_Cave_2/SB577A/I6770/47.97/97: 4000-2500 BCE.

Gough's Cave, Cheddar Gorge, Somerset, England

Contact: Heather Bonney

Gough's Cave is located near the village of Cheddar in the Mendip Hills in northern Somerset, England, UK. In 1903, workmen digging a new drainage ditch for a new show cave (Gough's New Cave) uncovered the almost-complete skeleton of an adult male that probably died in his early twenties who came to be known as Cheddar Man (GC1)[26-27]. Reliable precise details of the position of the skeleton when it was uncovered are elusive; however, most accounts suggest that it was articulated and in a flexed posture and had been deposited in the cave soon after death. A large cavity on the frontal bone had been taken to indicate that Cheddar Man had met a violent death as a result of blunt force trauma, but more recently this lesion could be an infectious abscess or the result of post-mortem taphonomic damage. No artefacts can reliably be confirmed to have accompanied the skeleton as grave goods, although it is possible that the excavators missed artefacts, as well as the remains of any additional individuals. The skeleton was mostly covered by stalagmite rather than sediment. The stalagmite was in contact with certain bones indicating that Cheddar Man had been subject to a shallow burial in the cave sediment, if he had been buried in sediment at all.

The Cheddar Man skeleton has been radiocarbon dated twice. Both attempts produced calibrated dates in the late 9th millennium BCE, which corresponds with the Early Mesolithic in Britain. Most British Early Mesolithic remains have been recovered from caves, suggesting that Cheddar Man had probably been deposited in the cave as a form of funerary treatment. In particular the remains of several individuals who were more-or-less contemporary with Cheddar Man were recovered from Aveline's Hole, another cave in the Mendip Hills. However, the possibility that Cheddar Man happened to die in Gough's Cave, rather than being buried there, cannot be ruled out. The skeleton is currently owned by the Longleat Estate but is on loan to the Natural History Museum, London. Palaeogenetic data from the petrous portion of the temporal bone of Cheddar Man were included in this study:

Cheddar_man/SB524A/SB424B/I6767/GC1: 8607-7982 cal. BCE (9100±100 BP, OxA-814)

Jubilee Cave

Contact: Tom Lord

Jubilee Cave (also known as Tratman's Cave) is located at the north end of Kingscar, part of Attermire Scar, near the village of Langcliffe in the North Yorkshire Dales[15]. It consists of a triple entrance leading into several chambers and narrow fissures. The cave has been subject to several excavations. Recorded excavations took place in 1871 and through the early 1930s. Finds recovered during these excavations included Mesolithic microliths, Middle Neolithic Peterborough Ware pottery and Romano-British artefacts. The faunal osteological assemblage mostly comprised bones of domesticated species.

The human bone assemblage from Jubilee Cave represents at least five individuals. However, the majority of this assemblage comes from the mostly-complete skeleton of a single adult male (Individual 1). Individual 1 was recovered from a side fissure beneath a rock shelf. The completeness of the skeleton and position of the bones suggested that it represented a primary deposit that had been disturbed post-skeletonisation. Osteological analysis indicated that this individual was around 40 when they died and had suffered from severe osteoarthritis. The rest of the assemblage comprised the disarticulated and fragmented bones from an additional adult male (Individual 2), two adult females (Individual 3 and 4) and a 9 to 11-year-old child (Individual 5). These skeletal elements were disarticulated, commingled and scattered along the corridor of the fissure. Individual 2 was only represented by two cranial fragments. Individual 3 comprised fifteen bones including fragments from the skull and long bones of the right side of the body. It was possible that this deposit represented the remains of more than one individual. The biased representation of bones from one side suggested that this may represent a primary burial that had been disturbed or partially cleared. Individual 4 was represented only by a fragment of right femur and Individual 5 consisted of two fragments from a mandible and pelvis (Leach 2015).

Taphonomic analysis of the bones revealed that while Individual 1 showed no weathering, consistent with the body having been deposited in the cave soon after death, the bones of the other four individuals showed more extensive modifications, some of which were indicative of trampling. This suggested that the individuals represented by these bones may have been exposed or buried elsewhere before being redeposited in Jubilee Cave. The bones alternatively may have originally been deposited in a different part of the cave where they were subject to more extensive weathering, before being redeposited in the fissure corridor.

A radiocarbon date from the tibia of Individual 1 produced a date in the Early Neolithic. The temporal bone of Individual 3 was radiocarbon dated as part of this project, producing an Early Neolithic date consistent with the one obtained from Individual 1. Individual 1 and 3 represent a single phase of Early Neolithic depositional activity in the site, consistent with results from other caves in the Craven area of the North Yorkshire Dales. Palaeogenetic data generated from a sample of the temporal bone of Individual 3 were included in this study. The results suggested that this individual was male, contrary to the osteological assessment. However, it is possible that Individual 3 actually represented the remains of at least two individuals.
Jubilee_cave/SB470A/I6757/Individual 3: 3648-3377 cal. BCE (4766±48 BP, UBA-32285)

Kent's Cavern, Torquay, Devon, England

Contact: Barry Chandler

Kent's Cavern is a limestone cave located in the boundaries of the City of Torquay, Devon, England, UK[27-28]. It has two entrances to the north and south that which would have provided

access to the cave throughout the Holocene. The cave is composed of three connected chambers; the Vestibule, the Sloping Chamber and the Great Chamber. The Sloping Chamber is connected to the Vestibule through the Passage of Urns. The cave has been excavated numerous times since 1824 and is most famous for its extensive Pleistocene faunal remains, as well as a maxilla that is the oldest anatomically modern human bone from Britain.

The excavations most relevant to the bones discussed here were those undertaken by William Pengelly between 1864 and 1879. The Pengelly excavations were concentrated on the uppermost 'black mould' layer of sediment in the cave, which was found to contain a range of organic materials and artefacts dating from the Mesolithic to Medieval periods. This layer was almost entirely removed from the Great Chamber, and large sections were also removed from the Sloping Chamber and Vestibule. The excavations in the Sloping Chamber yielded, amongst other things, several hundred pieces of disarticulated human bone. This assemblage which included an ulna which has been radiocarbon dated to the late 8th millennium BCE, falling just after the Late Mesolithic transition as defined by the shift to narrow blade microliths[27]. A maxilla including four teeth was recovered from the Vestibule and produced a radiocarbon date that is statistically consistent with the one obtained from the ulna[27]. It is possible that both elements belong to the same individual. Cut marks and breakage pattern identified on the ulna suggest that the individual had been defleshed and possibly cannibalised[28]. Stable isotope analysis of carbon and nitrogen from the ulna suggest that they obtained most of their dietary protein from terrestrial sources. The human remains are currently curated by Torquay Museum. Palaeogenetic data from a tooth in the Mesolithic human maxilla were included in this study.

KentCavern_1/SB428B/I3025/A2540: 7478-7146 cal. BCE (8270±45 BP, OxA-23812)

Little Lodge, Powys, Wales, UK

Contact: Heather Bonney

Little Lodge is a megalithic chambered tomb covered by a long barrow located near the village of Three Cocks in Powys, Wales and is named after the nearby Little Lodge Farm[29]. The tomb was excavated in 1928-9 by Vuliamy (Vuliamy 1929). A main complex of stone chambers was discovered near the centre of the mound, with two smaller chambers on the south side. Human bones representing the remains of at least six adults: five adult males, one adult female, and 2-3 children were recovered from the main chamber. The bones were generally disarticulated and commingled, although the bones of an adult male were slightly separate from the rest and the child bones seemed to have been placed at its feet. Some of the human bones had been deposited in gaps between stone slabs. The description of the skeletons suggested that complete bodies were successively interred in the Little Lodge tomb with some disturbance, manipulation and removal of skeletal elements. Bones of red deer, cattle, sheep and goat were also recovered from main chamber, as well as some charcoal. No bones from Little Lodge have been radiocarbon dated, however the typology of the monument would suggest that they are likely to date to the Early Neolithic. The human remains from Little Lodge are currently curated at the Natural History Museum.. Palaeogenetic data from a sample of a temporal bone were included in this study.

Little_Lodge/SB415A/I3023/PASK1643: 4000-3500 BCE

Ogof Yr Ychen, Caldey Island, Pembrokeshire, Wales

Contact: Elizabeth Walker

Caldey Island is located just off the southeast coast of the Pembrokeshire peninsula in Wales, UK. Ogof yr ychen ('Ox cave') is one of a series of caves on Caldey that has yielded fragmentary and disarticulated human remains[4, 27, 30]. Radiocarbon dating of human remains from these caves have produced Mesolithic, Neolithic and later dates; this and the presence of artefacts dating to later periods suggests that these caves were visited at various times through history and prehistory[29]. Carbon and nitrogen stable isotope analysis of the Mesolithic human remains from these caves suggests that their diet included a variable but substantial contribution (35-70%) from marine protein, indicating some dependence on coastal resources, whereas the Neolithic and later human remains exhibit isotopic values consistent with predominantly terrestrial diets.

Ogof yr ychen was discovered by van Nedervelde and Davies in 1970 and excavated from 1970-74 and 1984 following quarrying near the site[4]. This cave has yielded bones and artefacts dating from the Middle Pleistocene to the Romano-British period. The human bone assemblage is composed of fragmentary disarticulated bones representing at least six individuals. These human bones have produced radiocarbon dates ranging from the 8th to the 6th millennium BCE, suggesting that there were several phases of Late Mesolithic funerary activity at Ogof yr Ychen[27]. Radiocarbon dating of previously undated material for this project identified one petrous portion of the temporal bone as belonging to the Early Neolithic. Artefacts recovered from Ogof yr Ychen had already suggested that the site was visited during the Neolithic, however this date is the first evidence for Neolithic funerary treatment, some 2000 years after the latest Mesolithic mortuary deposit. The Ogof yr Ychen assemblage is owned by the Cistercian Monks of Caldey Island and Tenby Museum, but is currently curated by the National Museum of Wales. Palaeogenetic data from two petrous portions of temporal ones, one dating to the Late Mesolithic and another to the Early Neolithic, were included in this study.

Ogof_Yr_Ychen_1/SB460A/I6754/98.2H/55: 7593-7204 cal. BCE (8597±54 BP, UBA-32282)

Ogof_Yr_Ychen_3/SB462A/I3033/98.2H/276: 3695-3520 cal. BCE (4819±42 BP, UBA-32284)

West Kennet, Wiltshire, England

Contact: Marta Lahr

The West Kennet long barrow is situated in the Upper Kennet Valley near the village of Avebury, Wiltshire. It consists of a megalithic chambered tomb composed of five chambers defined by sarsen orthostats; an end (West) chamber and two pairs of opposed (South West,

North West and South East, North East) chambers, covered by an earthen long barrow which is flanked by ditches on either side[31-32]. The entrance has a slight concave shape, producing a small forecourt. The forecourt was sealed off by a series of sarsen megaliths. West Kennet was originally partially excavated by John Thurnam in the 19th Century before being more extensively excavated by Stuart Piggott and Richard Atkinson in the 1950s[31].

Disarticulated, commingled human remains representing at least 36 individuals were recovered from all of the chambers[31]. The representation of skeletal elements and variable articulation and completeness of remains suggested that fleshed bodies had been interred successively, with bones being disturbed, manipulated and selectively removed after bodies had decomposed. There was a clear primary deposit of human remains that was covered by a secondary deposit of material, which included some disarticulated human remains, but also flecks of charcoal, animal bones and pottery sherds.

The human remains from West Kennet have been radiocarbon dated extensively as part of a dating programme designed to produce a robust chronological model of the site[31]. Modelling of 31 radiocarbon dates on bone representing 25 human individuals and an articulated goat skeleton suggests that the tomb was constructed 3670-3635 cal. BCE (81% probability) and that the primary mortuary activity lasted only 1-55 years (94% probability) before the chambers were sealed. The chambers were sealed and there was a hiatus of more than a century before they began to be infilled by the secondary deposits. This infilling continued for around a thousand years before the monument was sealed. The secondary deposit in the South East chamber included a collection of mostly-complete infant skeletons that produced Middle-Late Neolithic radiocarbon dates. Palaeogenetic data from a petrous portion of a temporal bone retrieved from the secondary deposit in the South East chamber was included in this study. The human remains from West Kennet are currently curated by the Duckworth Laboratory at Cambridge University.

WestKennet_1/SB543A/I5387/SE Chamber 305 (immature cranium): 3300-2500 BCE.

Whitehawk, Brighton, Sussex, England

Contact: Andy Maxted

The Whitehawk causewayed enclosure is a scheduled ancient monument located near Brighton racecourse in the east of the town of Brighton, Sussex, UK[33-34]. It was first recognised as a significant monument in 1821 by the Reverend J. Skinner and has been subject to several excavations in the early and late 20th Century. The main excavation activity was undertaken in 1929 and 1932-3 by E. C. Curwen in advance of road construction. The monument occupies six hectares and consists of four concentric ditches, with some evidence for associated banks, divided by causeways. Where they survived, excavations of the banks revealed evidence of a timber post palisade. The enclosure is situated between two low hilltops overlooking the coastal plains to the south. As with most Neolithic causewayed enclosures, the Whitehawk camp is thought to have been occupied periodically for meetings, feasts and ritual ceremonies.

The inner and second ditches contained the greatest number of finds including broken Neolithic Bowl pottery, bones and domestic refuse whilst the fourth ditch was archaeologically

sterile. The third ditch included the complete articulated skeletons of at least four individuals: two young adult females (Skeleton I/128 and II/129), one (I/129) accompanied by an articulated infant around 39 weeks old (Skeleton IIa/129a) and a 6-8-year-old child (Skeleton IV/140). Skeleton II showed evidence for carnivore gnawing on their left rib, suggesting that the body had been exposed for a short while. This skeleton also showed possible perimortem trauma on their right parietal. A fifth articulated skeleton (Skeleton III/139a) representing of a young adult male was recovered from the inner ditch. Disarticulated human remains representing at least six individuals were scattered throughout the first three enclosure ditches: three young adults and one adult of indeterminable sex, one 7-8-year-old child and one juvenile. The individuals represented by the disarticulated material had been defleshed before selected disarticulated remains were interred in the enclosure ditches. A small number of disarticulated fragments showed signs of low-temperature burning. Only one cut mark was identified on an isolated humerus and possibly one on an infant mandible and there were no cortical bone modifications observed indicative of sub-aerial exposure. Therefore it was most likely that these individuals had been buried or deposited in a protected/sheltered environment before certain bones were retrieved for redeposition. The archive of the site (including the human remains) is curated by Brighton Museum and Art Gallery.

Skeleton I and Skeleton II have both been radiocarbon dated to the British Early Neolithic[34]. None of the other human remains have been radiocarbon dated but an extensive programme of radiocarbon dating and modelling has been performed on the Whitehawk deposits as part of the Gathering Time project[35]. The best model of the radiocarbon dates suggest that the Whitehawk monument was used for 75-260 years (95% confidence) from the middle of the 37th century BCE, which gives a latest possible date of death for the disarticulated remains. Ancient DNA data from two disarticulated petrous portions of temporal bones recovered from the enclosure ditches are newly reported in this study.

Whitehawk_1/SB493A/I3039/Skull 7 R3688/133: 3650-3500 BCE

Whitehawk_2/SB495A/I3040/R3688/133b: 3650-3500 BCE

Section 2: Y-chromosome lineage determination

Rui Martiniano

We used Yleaf[36] to determine Y-chromosome lineage labels in Mesolithic and Neolithic samples, requiring at least 1 read overlapping informative alleles and a concordance rate of 0.50. Haplogroup determination results are shown in Supplementary Table S1 and SNPs with derived alleles on Supplementary Table S5.

We found that the vast majority of Mesolithic and Neolithic individuals analysed belonged to haplogroup I, and more specifically to I2a2. This suggests that I2a2 Y-chromosome lineages were already present in Early Mesolithic Britain, and were either absorbed by incoming Neolithic populations or alternatively, these were assimilated in continental Europe and not in Britain, which could fit the small amount of British Mesolithic specific ancestry observed in agriculturalist groups from the region. We identify a single occurrence of haplogroup I2a1b in a sample from Kelco Cave, a lineage also identified in two Late Neolithic/Chalcolithic West Iberians[37].

The presence of I2a lineages in the British Neolithic mirrors previous findings obtained in a larger sample of British prehistoric human remains[1], where almost all Neolithic samples were determined to belong to this haplogroup and were later replaced by R1b-derived Copper/Late Bronze Age individuals with high levels of steppe-related ancestry.

Our results suggest that despite the discontinuity observed between British Mesolithic and Neolithic samples at the autosomal and mitochondrial level, Y-chromosome lineage composition remained stable at the time of the appearance of agriculture in the region, with no evidence supporting the appearance of G2a-derived lineages characteristic of the Anatolian Neolithic[38-39].

Notes regarding lineage determination:

Aveline_9, which dates to the Early Mesolithic, was determined to belong to the IJK clade, although it presented 3 ancestral alleles at SNPs defining haplogroup I and 7 ancestral alleles at J SNPs. We note that this sample also presents a derived allele at R-F356 and R1-CTS2565, but it carries ancestral alleles at SNPs R-F765 and R-CTS8311, we cannot therefore decisively include this sample in the R lineage. Given the low coverage obtained for this sample, we therefore tentatively assign it to IJK. Sample TottyPot_1 was assigned to haplogroup I. This sample also presents a derived allele at I1-Z2842, but this is a C->T mutation and it carries 2 ancestral alleles at other I1 defining SNPs.

Section 3: Pigmentation

Susan Walsh & Manfred Kayser

See Supplementary Table S2 for sequencing data and allelic states that entered the analyses below. Predictions are based on methods and tools published in Walsh *et al.*, 2013[40], Walsh *et al.*, 2017[41] and Chaitanya *et al*., 2018[42].

The probability profiles over the discretized pigmentation categories in this section are interpreted in two ways. In the strict sense, they are only an intermediate result that serves as input for the discriminant function which produces the final classification result by choosing the most likely category. This is the inference that has been validated in Walsh *et al*., 2017[41], and found to produce highly accurate results especially for the darker pigmentation categories.

In an attempt to augment the discrete category system towards a more continuous prediction and exploit the information that may be contained in the probability profile beyond the most likely category, it has recently been proposed that the second most likely category can be seen as modulating the pigmentation level in some cases[42]. Table 2 in Chaitanya *et al*., 2018[42], summarise the preliminary recommendations on how to interpret the probability profiles.

La Braña (Spain, Mesolithic)

Eye colour —All loci are present and have good coverage.

Blue eye	0.459
Int. eye	0.155
Brown eye	0.387

Final prediction: Intermediate (hazel/green) eye colour

Explanation: All probabilities are less than 0.5 so it is a combination of all categories, as brown is relatively high, it is more than likely a light hazel eye colour individual, but perceived green (blue/yellow) cannot be ruled out.

Hair colour—There is 1 locus (*TYRP1* rs683) with low coverage (1x), hence a heterozygote is possible. Prediction is a range that includes what the 1x coverage found (derived G allele) and the possibility of an A ancestral allele being present.

	TYRP1 rs683 (homozygote GG)	*TYRP1* rs683 (heterozygote GA)
Blond	0.018	0.014

Brown	0.612	0.595
Red	0	0
Black	0.37	0.391
Light	0.033	0.025
Dark	0.967	0.975

Prediction range:

Brown	0.612 – 0.595
Black	0.37 – 0.391

Final Prediction: Black/Dark Brown hair colour

Explanation: The probability value of black is >0.25 so it has a significant impact on prediction, and will darken the high brown probability. This individual would be perceived to have black hair. However, Dark Brown cannot be ruled out.

Skin pigmentation—Only 1 locus (*BNC2* rs10756819) is missing; however, the profile contains 3 loci with low coverage (n=1x), hence a heterozygote is possible. When factoring in possible genotype combinations, a prediction range has been generated. The range consists of assuming the 3 loci with low coverage are correct as homozygous for their sequenced allele (*ASIP* rs1667394 A allele (derived), *OCA2* rs1545397 A allele (ancestral), *TYRP1* rs683 A allele (ancestral)) and omitting *BNC* rs10756819 in the prediction model as it has no coverage, to including this SNP with a homozygote ancestral G allele and also derived A allele. The following range for skin pigmentation prediction is possible for this individual with these parameters:

	Omitting rs10756819	G ancestral allele	A derived allele
Very Pale	0	0	0
Pale	0	0	0
Intermediate	0.174	0.042	0.205
Dark	0.463	0.209	0.435
Dark-Black	0.363	0.749	0.360

Prediction range:

Very Pale	0
Pale	0
Intermediate	0.042 - 0.205
Dark	0.209 - 0.435
Dark-Black	0.749 - 0.36

Final prediction: Dark/Dark-to-Black skin

Explanation: The combined effect of probabilities in the dark and dark-to-black colour categories provide an indication that the individual has darkly pigmented skin, it is unlikely that this individual has the darkest possible skin pigmentation, but it cannot be ruled out as the missing SNP does influence that detail, but certainly skin pigmentation is dark in complexion.

Cheddar Man (UK, Mesolithic)

Eye colour —There is 1 locus (*LOC105374875* (formally known as *SLC24A4*) rs12896399) with low coverage (1x) hence a heterozygote is possible. Prediction includes a range that includes what the 1x coverage found (ancestral G allele) and the possibility of an A derived allele being present.

	LOC105374875 rs12896399 (homozygote GG)	*LOC105374875* rs12896399 (heterozygote GA)
Blue eye	0.564	0.711
Int. eye	0.189	0.143
Brown eye	0.247	0.145

Prediction range:

Blue eye	0.564 - 0.711
Int. eye	0.189 - 0.143
Brown eye	0.247 - 0.145

Final prediction: Intermediate (blue/green) eye colour

Explanation: This individual has light or blue/green eye colour, it is not light blue, there are elements of brown/yellow in the eye to give a proposed perceived green colour. Better coverage at the low sequenced SNP would clarify this but blue/hazel cannot be ruled out. It is certainly not a brown eyed or clear blue-eyed individual.

Hair colour—There is 1 locus *PIGU* rs2378249 with low coverage (1x) hence a heterozygote is possible. Prediction is a range that includes what the 1x coverage found, ancestral A allele, but also includes the possibility of a heterozygote being present.

	PIGU rs2378249 (homozygote AA)	*PIGU* rs2378249 (heterozygote CA)
Blond	0.009	0.009
Brown	0.692	0.741
Red	0.006	0.012
Black	0.292	0.237
Light	0.999	0.999
Dark	0.001	0.001

Prediction range:

Brown	0.692 – 0.741
Black	0.292 – 0.237

Final Prediction: Dark Brown/Black hair colour

Explanation: The probability value of black is >0.2 so it has an impact on prediction, and will darken the high brown probability. However, there are light pigment alleles indicating a lighter shade phenotype. Better coverage at the low sequenced SNP would help clarify this. This individual would be perceived as having dark brown hair. However, black cannot be ruled out.

Skin pigmentation—There are 3 loci (*BNC2* rs10756819, *TYR* rs1126809, *MC1R* rs3212355) missing, and the profile does contain 2 loci (*LOC105374875* rs12896399 and *PIGU* rs2378249) with low coverage (n=1x) hence a heterozygote is possible at those sites. When factoring in possible genotype combinations, a prediction range may be generated. The range consists of assuming the two loci with low coverage are correct as homozygote for their sequenced allele (*LOC105374875* rs12896399 G allele and *PIGU* rs2378249 A allele) and omitting the 3 missing loci from the prediction model as they have no coverage, to including these SNPs with their ancestral (*BNC2* rs10756819-GG, *TYR* rs1126809-GG, *MC1R* rs3212355-CC) and also their derived allele counterparts. The following range for skin pigmentation prediction is possible for this individual with these parameters:

	ancestral alleles used	derived alleles used
Very Pale	0	0
Pale	0	0
Intermediate	0.152	0.038
Dark	0	0
Dark-Black	0.848	0.962

Prediction range:

Very Pale	0	
Pale	0	
Intermediate	0.152	- 0.038
Dark	0	- 0
Dark-Black	0.848	- 0.962

If we omit the three missing alleles, our tool produces 0.752 and 0.248 probabilities for the intermediate and dark-black category respectively, changing the prediction ranges to 0.752-0.038 and 0.248-0.962. However, note that this completely removes the locus from the prediction model; hence the prediction will not perform optimally (how the prediction model was made). It is therefore best to have some allele present to infer the most probable range for Cheddar Man and we derive the ranges above from the extreme allele constellations only.

Final prediction: Dark/Dark-to-black skin

Explanation: The missing loci certainly impact on this prediction; however, utilizing the input of all ancestral alleles is the preferred option over the use of the derived alleles at these loci – hence 0.152 for intermediate and 0.848 for Dark-to-Black would be the most probable profile. That being said a broad range is present in both the intermediate and dark-black categories due to the missing loci. Also, this effect of skipping a skin pigmentation prediction category with regards probability values, tends to be observed more often in admixed individuals. What is important to note is the input of the dark-black prediction is significant on the intermediate category and therefore it is acceptable to propose a dark complexion individual over an intermediate/light prediction even though the intermediate range is present. It is unlikely that this individual has the darkest possible pigmentation, but it cannot be ruled out. Better sequencing coverage would clarify to what degree this individual has a dark complexion.

Carsington Pasture 1 (UK, Neolithic)

Eye colour —All loci are present and have good coverage. Artefact bases are proposed for locus *SLC45A2* rs16891982 (T allele).

Blue eye	0.022
Int. eye	0.090
Brown eye	0.887

Final prediction: Brown eye colour

Explanation: The highest probability is well above the threshold 0.7p for brown, so a strong brown prediction is proposed.

Hair colour—All loci are present and most have good coverage. An artefact base is proposed for locus *SLC45A2* rs16891982 (T allele). For loci *SLC45A2* rs28777, *OCA2* rs12441727, *OCA2* rs1470608, they are assumed to be heterozygotes, although coverage is low (1x) for one of the alleles. Artefact bases are proposed for locus *MC1R* rs1110400 (A allele) and *MC1R* rs885479 (A allele) as there is >40x coverage for the more represented allele, therefore it is assumed that it is not a heterozygote at these loci. There is 1 locus (*TYRP1* rs683) with low coverage (1x) hence a heterozygote is possible. Prediction is given as a range that includes what the 1x coverage found (ancestral A allele), and the possibility of a G derived allele being present as a heterozygote at this locus for hair colour prediction.

	TYRP1 rs683 (homozygote AA)	*TYRP1* rs683 (heterozygote GA)
Blond	0.028	0.023
Brown	0.646	0.631
Red	0.001	0
Black	0.325	0.345
Light	0.031	0.024
Dark	0.969	0.976

Prediction range:

Brown	0.646 – 0.631
Black	0.325 – 0.345

Final Prediction: Black/Dark Brown hair colour

Explanation: The probability value of black is >0.25 so it has a significant impact on prediction, and will darken the high brown probability. This individual would be perceived to have black hair. However, Dark Brown cannot be ruled out.

Skin pigmentation—All loci are present and most have good coverage. An artefact base is proposed for locus *SLC45A2* rs16891982 (T allele). For loci *SLC45A2* rs28777, *OCA2* rs12441727, *OCA2* rs1470608, they are assumed to be heterozygotes although coverage is low (1x) for one of the alleles. Additional sequencing of this SNP would clarify this. Artefact bases are proposed for locus *MC1R* rs1110400 (A allele) and *MC1R* rs885479 (A allele) as there is >40x coverage for the more represented allele, therefore it is assumed that it is not a

heterozygote at these loci. There is 1 locus (*TYRP1* rs683) with low coverage (1x) hence a heterozygote is possible. Prediction is given as a range that includes what the 1x coverage found (ancestral A allele), and the possibility of a G derived allele being present as a heterozygote at this locus for skin pigmentation prediction.

	TYRP1 rs683 (homozygote AA)	*TYRP1* rs683 (heterozygote GA)
Very Pale	0.007	0.005
Pale	0.066	0.042
Intermediate	0.462	0.299
Dark	0.213	0.344
Dark-Black	0.252	0.311

Prediction range:

Very Pale	0.007 – 0.005
Pale	0.066 – 0.042
Intermediate	0.462 – 0.299
Dark	0.213 – 0.344
Dark-Black	0.252 – 0.311

Final prediction: Dark/Intermediate skin

Explanation: The effect of probability in the dark-to-black colour category has an impact on the intermediate prediction. However, it is highly unlikely this individual has the darkest possible skin pigmentation as it is >0.25 probability in the Dark-Black category, taken collectively, these probabilities indicate that the individual would fall more into a dark skin pigmentation category. However, intermediate cannot be definitively ruled out.

Loschbour (Luxembourg, Mesolithic)

Eye colour —All loci are present and have good coverage.

Blue eye	0.564
Int. eye	0.189
Brown eye	0.247

Final prediction: Intermediate (blue/green) eye colour

Explanation: This individual has light or blue/green eye colour, it is not light blue, there are elements of brown/yellow in the eye to give a proposed perceived green colour, but blue/hazel cannot be ruled out. It is certainly not a brown eyed or clear blue-eyed individual.

Hair colour—All loci are present and have good coverage. Artefact bases are proposed for locus *TYR* rs1126809 (A allele) and *HERC2* rs1667394 (G allele) as there is >20x coverage for the more represented allele, therefore it is assumed that it is not a heterozygote at these loci.

Blond	0.005
Brown	0.532
Red	0
Black	0.463
Light	0.022
Dark	0.978

Final Prediction: Black/Dark Brown hair colour

Explanation: The probability value of black is >0.25 so it has a significant impact on prediction, and will darken the high brown probability. This individual would be perceived to have black hair. However, Dark Brown cannot be ruled out.

Skin pigmentation—All loci are present and have good coverage.
There is a similar artefact assessment as above for rs1126809 and rs1667394.

Very Pale	0
Pale	0
Intermediate	0.893
Dark	0.069
Dark-Black	0.038

Final prediction: Intermediate skin

Explanation: The highest probability of approximately 0.9 for intermediate indicates a light skinned (white) individual. He would not have the darkest possible skin pigmentation but does have tanning ability, so could be perceived as darker than white (pale) in the summer months.

Summary

Two WHGs (Cheddar Man and La Braña[43] from northern Spain) are predicted to have had dark or dark-to-black skin, whereas one (Loschbour[44] from Luxembourg) is predicted to have had intermediate skin suggesting but we find potential temporal and/or geographical variation in pigmentation characteristics, suggesting that diverse skin pigmentation levels coexisted in WHGs by at least ca.8 kBP. Sven was predicted to have had dark to intermediate to dark skin in line with the current hypothesis that alleles commonly associated with lighter skin in Europeans were introduced to north-western Europe by ANFs[39].

Section 4: Heterozygosity and Lactase Persistence

Yoan Diekmann & Mark G Thomas

The Mesolithic Cheddar Man and the Neolithic sample from Carsington Pasture Cave, Derbyshire ('Sven') had sufficient coverage to estimate heterozygosity. Consistent with recent ancestry from larger or more admixed populations, Sven showed slightly higher levels of heterozygosity than Cheddar Man (Supplementary Figure S10). None of the Mesolithic and

Neolithic British individuals analysed here had a derived lactase persistence allele (see Supplementary Table S2).

Section 5: Stable Isotope Analysis

Sophy Charlton & Rick Schulting

Stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ was undertaken on two individuals from Carsington Pasture Cave, five individuals from Aveline's Hole, two individuals from Ogof-yr-Ychen, and one individual from Jubilee Cave, from which genome-wide information had already been obtained. Isotopic analysis was undertaken in an attempt to determine the subsistence pathways of the individuals (i.e. hunter-gatherer-fisher vs. farming), particularly given their Early Neolithic date, and the Late Mesolithic date of one of the Ogof-yr-Ychen samples (Supplementary Table S6). This was particularly pertinent given the genetic differences exhibited by the Carsington Pasture, Jubilee Cave and three of the Aveline's Hole Early Mesolithic individuals when compared to the Late Mesolithic individuals from Cnoc Coig and Ogof-yr-Ychen, which have previously been shown to have a diet dominated by marine protein[4, 7, 17, 27]. Isotopic analysis therefore aimed to explore whether genetic change could be seen to coincide with dietary change. The data from these samples also contribute to the existing isotopic dataset for the British Mesolithic and Neolithic.

Analysis followed a modified Longin collagen extraction protocol using ultrafiltration (30kDa MWCO)[7, 48-49]. For the Carsington Pasture Cave individuals, c.500mg of bone per sample was initially cleaned manually using a scalpel, and then demineralised in 0.6M aq. HCl solution at 4°C, and the resulting insoluble fraction gelatinised in pH3 HCl for 48h at 80°C. The supernatant solution was then ultrafiltered (30kDa MWCO, Amicon) to isolate the high molecular weight fraction, which was then lyophilised. Purified collagen samples (1mg) were analysed in duplicate by Elemental Analysis Isotope Ratio Mass Spectrometry (EA-IRMS) on a Sercon GSL analyser coupled to a Sercon 20-22 Mass Spectrometer at the University of York. The analytical error, calculated from repeated measurements of each sample, a bovine control, and international standards, was <0.2‰ (1σ) for both $\delta^{13}C$ and $\delta^{15}N$.

For the Aveline's Hole, Ogof-yr-Ychen, and Jubilee Cave individuals, c.0.5-1g of bone sample was ground using a percussion mortar and demineralised in 2% HCl, followed by treatment with 0.1M sodium hydroxide and additional 2% HCl. The resulting insoluble fraction was gelatinised in pH2-3 HCl for 15h at 70°C, and this gelatin solution was filtered using pre-baked 7 micron and 12 micron glass fibre filters. The filtrate was then ultrafiltered (15-30kDa MWCO, Vivaspin Turbo) to isolate the high molecular weight fraction, which was then lyophilised. Purified collagen samples were analysed in duplicate by Elemental Analysis Isotope Ratio Mass Spectrometry (EA-IRMS) on a Thermo Delta V EA-IRMS at the ^{14}Chrono Centre for Climate, the Environment and Chronology, Queen's University Belfast[50].

All individuals yielded sufficient amounts of collagen of suitable quality for $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis. Collagen quality fell within prescribed quality ranges[51-52]. Collagen yields were calculated from retentate samples only, following ultrafiltration. All samples also exhibited

acceptable atomic C:N ratios, of c.3.2 (Supplementary Table S6). Stable isotope values are presented here relative to the internationally defined standards of VPDB for $\delta^{13}C$ and AIR for $\delta^{15}N$.

The $\delta^{13}C$ and $\delta^{15}N$ values obtained from Carsington Pasture Cave, Aveline's Hole, Jubilee Cave and one individual from Ogof-yr-Ychen are all indicative of a diet based upon terrestrial protein and C3 plants, and show good concordance between sites (Supplementary Table S6). In particular, the Carsington Pasture Cave samples show remarkable similarity between the two individuals, perhaps indicating an isotopically homogeneous population, as has been seen at other British Neolithic sites[53-54]. However, it must be noted that little faunal isotope data is available from these sites, and therefore without these faunal baselines a more detailed interpretation of the $\delta^{13}C$ and $\delta^{15}N$ data is not possible at present.

The $\delta^{13}C$ and $\delta^{15}N$ values obtained from the Neolithic individuals (as defined both through AMS dating (Supplementary Table S6) and genetically) are directly comparable to isotopic data from other British Neolithic sites. Typically, Neolithic individuals show $\delta^{13}C$ values c.-21‰ ±1‰ and $\delta^{15}N$ values c.10‰ ±1-2‰. The individuals analysed here can be seen to fall within this broad dietary trend, and show isotopic affinity to individuals from sites such as Hambledon Hill and Quanterness (Supplementary Figure S17).

The $\delta^{13}C$ and $\delta^{15}N$ isotopic values obtained from the Early Neolithic individuals also indicate no significant marine protein contribution within their diets, in contrast to the Late Mesolithic individual analysed here from Ogof-yr-Ychen (sample 98.2H/55, Supplementary Table 7), and previously published individuals both from Cnoc Coig and Ogof-yr-Ychen, which can be seen to have a diet dominated by marine protein[4, 7, 17, 27] (Supplementary Figure S18). The $\delta^{13}C$ and $\delta^{15}N$ values of the Mesolithic Ogof-yr-Ychen individual (sample 98.2H/55) fall completely in line with previous isotopic values obtained from Mesolithic individuals from the site[4], indicating a subsistence strategy highly dependant on marine foods year-round. These Late Mesolithic individuals, now known to cluster genetically with WHGs, therefore exhibit a very different diet to the Early Neolithic individuals from Carsington Pasture Cave, Aveline's Hole, Jubilee Cave and other sites now known to show ANF ancestry (Supplementary Figure S18). Interpretation of this is not straightforward, however, since the comparison is between coastal Late Mesolithic and mainly inland Neolithic sites. The results from the inland Early Mesolithic site of Aveline's Hole also shows no significant contribution of marine protein. Nevertheless, the new Neolithic results reported here are entirely consistent with the pattern of an overwhelmingly terrestrial diet previously noted for the British Neolithic, regardless of coastal or inland location.

Section 6: Newly-Reported Radiocarbon Dates and Chronological Modelling

Tom Booth

Several radiocarbon dates are presented here for the first time. Details of the newly-reported dates, including associated stable isotope analyses are listed in Supplementary Table S6. All

quoted radiocarbon dates have been calibrated using the IntCal13 curve in OxCal 4.3 apart from Ogof-yr-Ychen_1 (UBA-32282) and CnocCoig_1 (SUERC-69249) which were calibrated using a mixed IntCal13/Marine13 curve[2-3].
Proportions of marine/terrestrial contribution were calculated in each case from carbon stable isotope results assuming observed marine and terrestrial endpoints of -12.0‰ and -21.0‰ respectively[4]. The estimated % contribution of marine C to collagen for marine component of Cnoc Coig and Ogof-yr-Ychen were on average estimated as 90±10% and 63±10% and marine offsets calculated using ΔR values of -68±90 and -33±93 respectively[2-7] . Other recent radiocarbon dates performed on samples included here have been reported previously in Olalde et al[1].

In order to estimate the date by which continental Neolithic farmers arrived in Britain and the speed with which they moved into different regions of Britain, we modelled direct radiocarbon dates from ancient individuals with ANF ancestry dating to the Early Neolithic (4000-3500 BCE) from five broad regions (Western Britain, Central England, Eastern England, Western Scotland and the Orkney Isles) using Bayesian methods implemented in OxCal 4.3 (Supplementary Figure S19)[2-3]. Details of all the dates used in the model can be found in Supplementary Table S1.

The Agreement indices and further outputs of the model can be found in Supplementary Table S7. The Agreement indices are acceptable under the standard that they may be problematic if they drop below 60 (Amodel = 69.2, Aoverall = 67.0)[2]. The Agreement is affected by an early date for a human bone from McArthur Cave, western Scotland which shows poor individual agreement (A=26.1). We only used samples that had been directly dated in our model, meaning that many individuals with ANF ancestry were excluded. This includes undated individuals from sites that have otherwise been intensively dated and subject to chronological modelling using similar methods to those used here, as without direct dating of samples it was impossible to know exactly where they fitted in the chronology of each site.

Our model suggests that ANF ancestry first arrives in Britain by 3975-3722 cal. BCE (95% confidence) or 3856-3736 cal. BCE (68% confidence). This is 27 years before to 481 years after (95% confidence) or 375-119 years after (68% confidence) the death of our latest Mesolithic individual from Cnoc Coig who is also the latest to show no ANF component. The model suggests that the earliest appearance of ANF ancestry is in western Scotland at 3872-3707 cal. BCE (95% confidence) or 3811-3713 cal. BCE (68% confidence), followed by western Britain at 3865-3677 cal. BCE (95% confidence) or 3789-3715 cal. BCE (68% confidence), eastern England at 3789-3517 cal. BCE (95% confidence) or 3680-3561 cal. BCE (68% confidence), the Orkney Isles at 3747-3537 cal. BCE (95% confidence) or 3691-3566 cal. BCE (68% confidence) and central England at 3705-3542 cal. BCE (95% confidence) or 3656-3553 cal. BCE (68% confidence). The estimated time between the arrival of ANF ancestry in Britain and its latest regional arrival (in central England) is 59-386 years (95% confidence) or 120-275 years (68% confidence).

The results of our model suggest that continental farmers move through Britain rapidly after they first arrive sometime between the 40th and 38th century BCE, which is broadly consistent with chronological modelling of radiocarbon dates associated with the arrival and spread of Neolithic cultural practices[55-56]. Our results are seemingly at odds with previous chronological models suggesting that the earliest appearance of Neolithic cultural traits is in the South East

of England slightly before 4000 BCE[55]. However, while our study includes a sample from the earliest dated Neolithic tomb from South East England (Coldrum) we could not include the associated dates in our chronological model, as the particular individual we sampled has not been dated directly. The resolution of our model is much coarser than chronological models related to the spread of Neolithic cultural traits, and there is not much difference in our model between the earliest appearance of ANF ancestry in different regions of Britain. Given these factors, our results cannot be said to deviate significantly from previous chronological analyses of Neolithic radiocarbon dates[55-56].

The CQL Code for the model is as follows:

```
Plot()
{
 Sequence("British Neolithic Ancestry")
 {
  Boundary("Britain Neolithic Ancestry start");
  Phase("Neolithic Britain")
  {
   Sequence("Orkney Sequence")
   {
    Boundary("Orkney Start");
    Phase("Neolithic Orkney")
    {
     R_Date("SUERC-68641", 4697, 33);
     R_Date("SUERC-68642", 4754, 36);
     R_Date("SUERC-68638", 4851, 34);
     R_Date("SUERC-68639", 4796, 37);
    };
    Boundary("Orkney End");
   };
   Sequence("Western Scotland Sequence")
   {
    Boundary("Western Scotland start");
    Phase("Neolithic Western Scotland")
    {
     R_Date("SUERC-68701", 5052, 30);
     R_Date("SUERC-68702", 4914, 27);
     R_Date("SUERC-69074", 4856, 33);
     R_Date("SUERC-68704", 4881, 25);
     R_Date("PSUAMS-2154", 4725, 20);
     R_Date("PSUAMS-2155", 4730, 25);
     R_Date("PSUAMS-2068", 4770, 30);
    };
    Boundary("Western Scotland end");
   };
   Sequence("Britain West")
   {
    Boundary("Britain West start");
```

```
   Phase("West")
   {
    R_Date("OxA-17173", 5023, 34);
    R_Date("PSUAMS-2513", 4715, 20);
    R_Date("UBA-30800", 4809, 45);
    R_Date("OxA-34336", 4934, 35);
   };
   Boundary("Britain West end");
  };
  Sequence("England Central")
  {
   Boundary("England Central start");
   Phase("Central")
   {
    R_Date("OxA-13539", 4808, 32);
    R_Date("UBA-32285", 4766, 48);
    R_Date("OxA-13538", 4801, 31);
    R_Date("UB-29004", 4808, 35);
    R_Date("UBA-29003", 4820, 34);
    R_Date("OxA-14226", 4595, 40);
   };
   Boundary("England Central end");
  };
  Sequence("England East")
  {
   Boundary("England East start");
   Phase("East")
   {
    R_Date("OxA-34470", 4775, 34);
    R_Date("Poz-83483", 4710, 35);
   };
   Boundary("England East end");
  };
 };
 Boundary("Britain Neolithic Ancestry End");
};
Plot("Cnoc_Coig_plot")
{
 Curve("IntCal13","IntCal13.14c");
 Curve("Marine13","Marine13.14c");
 Delta_R("LocalMarine",-68,90);
 Mix_Curve("Mixed","IntCal13","LocalMarine",90,10);
 R_Date("SUERC-69249", 5492, 36);
};
Difference("CC W Scotland diff", "SUERC-69249", "Western Scotland start");
Difference("CC Britain diff", "SUERC-69249", "Britain Neolithic Ancestry start");
Difference("Britain Orkney diff", "Britain Neolithic Ancestry start", "Orkney Start");
```

Difference("Britain England Central diff", "Britain Neolithic Ancestry start", "England Central start");
Difference("Britain England East diff", "Britain Neolithic Ancestry start", "England East start");
};

Section 7: Haplotype-based Analyses

Lucy van Dorp

In this section we describe work that explores patterns of allele and haplotype sharing amongst our high coverage novel ancient genomes relative to other publicly available high coverage ancient samples and to a large modern reference panel. We additionally use statistical models to represent both modern populations and ancient individuals as mixtures of other sampled groups or individuals. This approach can consider the relative ancestry contributions of all groups at the same time, whilst also making use of the rich information gained by using haplotype-based approaches when analysing high coverage ancient genomes.

Methods

Description of dataset analysed

We merged our new British Mesolithic genome (Cheddar 2X coverage) and British Neolithic genome (Carsington_Pasture_1 10X coverage) with other relevant high coverage ancient genomes (>7X) published in the literature. This included the German WHG "Loschbour"[44], the Caucasus hunter-gatherer (CHG) "KK1"[57], the early Iranian farmer "WC1" [58], the Anatolian early farmer (ANF) "Bar8"[38], the German Neolithic farmer "LBK"[59], the Hungarian farmer "NE1"[59], an early-Neolithic Iberian farmer "I0412"[60], a mid-Neolithic Iberian farmer "I0408"[60], an Irish Neolithic farmer "Ballynahatty"[61], an Early Bronze Age Yamnaya genome from Karagash "Yamnaya_Karagash"[62], a Bronze Age Hungarian genome "BR2"[59], a Bronze Age Irish Genome "Rathlin1"[61], and a 4,500 year old Ethiopian farmer "Mota"[63].

Diploid genotype calls were generated for these ancient genomes using ATLAS[64] and sites were selected with a minimum read depth of at least 2 and a minimum quality score of at least 20. Resulting calls were merged with a modern reference panel comprising data from Hellenthal *et al*. 2014[65], Busby et al 2015[66], and Leslie et al 2015[67]. This comprised 47 North-West European populations (including 35 groups from within the UK), 10 populations from East Europe, nine populations from South Europe and 30 populations from the Middle East, as well as other global populations from East Asia, the Americas, and Africa. After quality filtering for low genotyping call rates (<95%), excluding duplicate or related individuals (based on a PLINK[68] inferred PI_HAT >0.2), and selecting positions for a perfect SNP overlap in our included high coverage ancient samples, this resulted in a dataset merge of 159,287 total SNPs across 4,944 individuals, including 16 ancient genomes. The dataset was jointly phased using SHAPEITv2[69] with build 37 genetic maps.

Inferring Allele and Haplotype Sharing Profiles

We followed the approach described in Lawson et al 2012[70] to compare a "recipient" chromosome to that of a set of "donors". This method, implemented in CHROMOPAINTER[70], calculates the genome-wide amount of DNA (in cM) for which a "recipient" chromosome is most closely related to a particular "donor" individual, given their joint genotype data across all SNPs, thus explicitly modelling linkage disequilibrium information to inform inference.

We used an approach where modern individuals were used as donors, to form both modern and ancient individuals as recipients, excluding a modern individual as a donor when analysing that modern individual as a recipient. We first estimated the CHROMOPAINTER switch rate (N, "-n switch") and mis-copying parameter (M, "-M switch") on every 10th individual across chromosomes 1, 4, 15 and 22 using expectation-maximisation (E-M) over 10 iterations (i.e. "-I 10 -in -iM"). We averaged the inferred values of each parameter across chromosomes, weighting the average by the number of SNPs. We then took the average across individuals. This resulted in mean estimates of N=155.13 and M=6.5x10^{-4} respectively. These values were fixed in the final analysis using the CHROMOPAINTER -n and -M flags. The resulting output provides, for every recipient, the total proportion of genome-wide DNA for which each recipient is inferred to be most closely related to a donor chromosome. This can be defined as f_d^r, where for each recipient,r, we provide the total amount of genome-wide DNA for which this individual is inferred to be most closely related to a donor chromosome from group d. We refer to this as a haplotype sharing profile.

We additionally repeated our painting process using the same panel of donors and recipients using the CHROMOPAINTER unlinked model, -u switch[70]. As before, we use modern individuals as donors and modern and ancient individuals as recipients. However here, instead of considering the correlations between neighbouring SNPs, SNPS are matched between recipient and donors independently. The resulting output thus provides the genome-wide allele matching of any recipient individual (or group) to every donor. We thus refer to this as an allele sharing profile. By generating allele sharing profiles in tandem to haplotype sharing profiles we evaluate the robustness of both our genotype calls and phasing protocol to our inferred demographic patterns.

Evaluating differences in inferred allele sharing and haplotype sharing profiles

In order to quantify the differences in the inferred allele sharing or haplotype sharing profiles, we apply the distance metric total-variation-distance (TVD), as originally applied in Leslie *et al*.[66]. We first normalise f_d^r so that it now defines the genome-wide proportion of DNA that a recipient individual (or group) r copies from each of donor individuals or groups $d \in [1, \ldots, D]$. Then, to compare the haplotype (or allele) sharing profiles of any two recipient individuals $X$and Y we calculated TVD_{XY} as $TVD_{XY} = \frac{1}{2}\sum_{d=1}^{D} \quad |f_d^X - f_d^Y|$.

Inferring "proportions of ancestry" using mixture modelling

A priori a donor group with a disproportionately large number of sampled individuals may have a relatively higher amount of matching to recipient groups, potentially leading to a biased interpretation of results. To account for this we implemented additional Bayesian mixture

modelling implemented in SOURCEFIND[71], which constructs the haplotype sharing profile of an individual of interest (we term the target) as a mixture of the haplotype sharing profiles of a defined set of other groups (we term the surrogates). These mixture proportions can be used to identify which sampled groups are most closely related to each other genetically, reflecting shared common ancestry relative to other groups due to admixture or other historical processes such as shared drift.

In all cases we ran SOURCEFIND with 200,000 MCMC iterations, sampling every 1,000 steps. Additionally, for each target we perform estimation 50 times, weight-averaging these estimates by the posterior probability to obtain one posterior value per target for every surrogate included in the mixture. We express the uncertainty around our inference as the standard error.

We performed several SOURCEFIND mixture modelling analyses which differ in the specification of targets and surrogates. In particular, we considered the inferred proportions when i) forming ancient targets as a mixture of modern populations as surrogates and ii) forming modern target groups as a mixture of ancient individuals. In cases where individuals or groups are specified as both a target and a surrogate, we exclude the possibility of being formed as a mixture of that surrogate in particular, as this would lead to the haplotype (or allele) sharing profiles matching exactly. Additionally, when forming modern target groups from ancient individual surrogates, we also include the modern-day Yoruba and Han groups, since our included ancient samples contain no good proxies for sub-Saharan African and East Asian ancestry.

Results

Across the haplotype sharing profiles of our ancient recipient individuals we inferred a mean of 20 SNPs per chunk (11-28 95% CI), suggesting despite the relatively low SNP count of our final dataset merge, there are still sufficient sites included for haplotype-based techniques to be useful. Further, the pairwise differences, measured by TVD, between each of our ancient samples under the unlinked “allele-sharing” approach and linked “haplotype-sharing” approach, are broadly consistent, Supplementary Figure S20. In both instances, the TVD metric tends to score a greater similarity between the allele/haplotype sharing profiles of ancient individuals from the same time period and/or culture. For example, our British Mesolithic individual (Cheddar), has the lowest TVD with the other WHG in our dataset, Loschbour. Our British Neolithic sample (Carsington_Pasture_1, here labelled Car_P1), has the lowest TVD with the Irish Neolithic individual (Ballynahatty), followed by the two Neolithic individuals sampled from Iberia (I0408 and I0412). Hierarchical clustering based on the TVD distance matrix of our Neolithic genomes (see main text Figure 5), clusters the British Neolithic individual with Irish and Iberian Neolithic samples. Neolithic individuals from Germany and Hungary form a separate clade, with the North-Western Anatolia Neolithic individual from Barcin (Bar8) forming an out-group, main text Figure 5.

We evaluated the relative matching to donor populations of our ancient recipient individuals based on the inferred allele-sharing and haplotype-sharing profiles. When comparing our British Mesolithic WHG to the Loschbour WHG we notice a greater affinity of populations within the British Isles to Loschbour over the local British Mesolithic individual, Supplementary Figure S21. One interpretation is that the introgressing WHG component in British today is better represented by a Central European hunter-gatherer than the resident WHG. However,

alternative explanations are that the Loschbour genome is more genetically diverse than Cheddar, of higher coverage, and is more recent in time, all of which could result in it acting as a better representative.

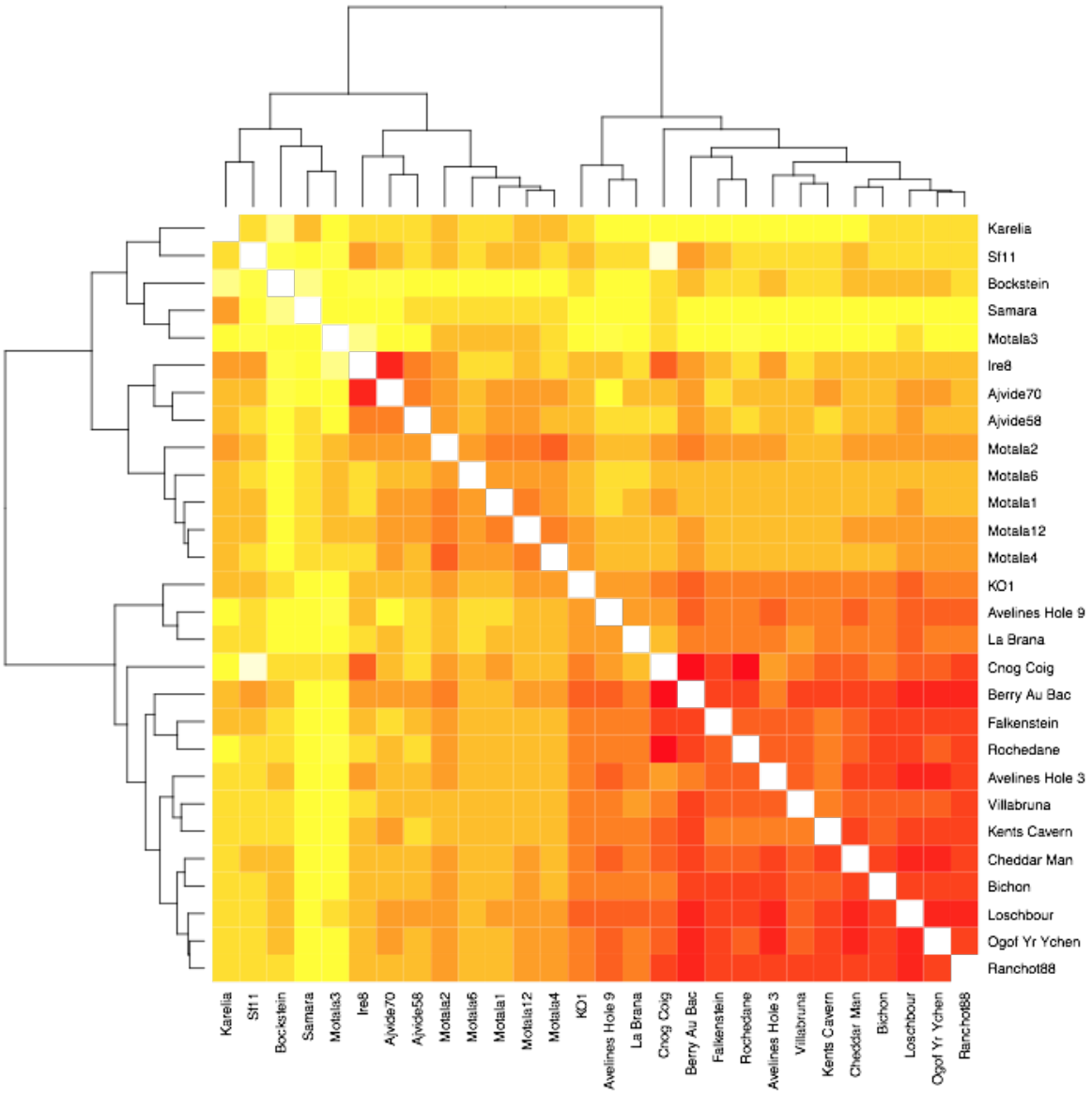
Relative to WHG, all of our Neolithic samples tend to match more haplotypes to modern populations from Southern Europe and the Middle East compared to North-West European populations. When comparing our Central European-like Neolithic samples (NE1, LBK) to our Iberian-like Neolithic individuals from Iberia, Ireland and Britain (I0408, I0412, Ballynahatty, Carsington_Pasture_1), we observe more haplotypes shared with modern populations from Spain, Basque, Sardinia and France in the latter, Supplementary Figure S22. Consistent with their lower TVD, Supplementary Figure A, when compared to the Hungarian Neolithic genome (NE1), the Iberian, Irish and British Neolithic genomes have very similar patterns of haplotype matching to modern populations ($r^2 > 0.9$; Supplementary Figure S22).

To explicitly model proportions of ancestry in modern and ancient genomes, we apply a Bayesian mixture modelling approach[71] to construct target sharing profiles as multiple different specifications of surrogate individuals/populations. Forming our high coverage genomes as a mixture of all others, excluding the more recent Bronze Age samples (Yamnaya_Karagash, BR2, and Rathlin1), demonstrates a high affinity of Cheddar and Loschbour to each other (Cheddar to Loschbour: 0.78 [0.11 SE]; Loschbour to Cheddar: 0.85 [0.11]), Supplementary Table S8, Figure 5b main text. The British Neolithic sample was inferred to share highest proportions of the ancestry mixture with Iberian Neolithic samples (total 0.34 [0.21 SE]), and the Irish Neolithic genome (0.2567 [0.123 SE]). All Iberian, Irish and British Neolithic samples showing high matching to each other compared to the proportions inferred in Central European Neolithic individuals, such as LBK (German) and NE1 (Hungary).

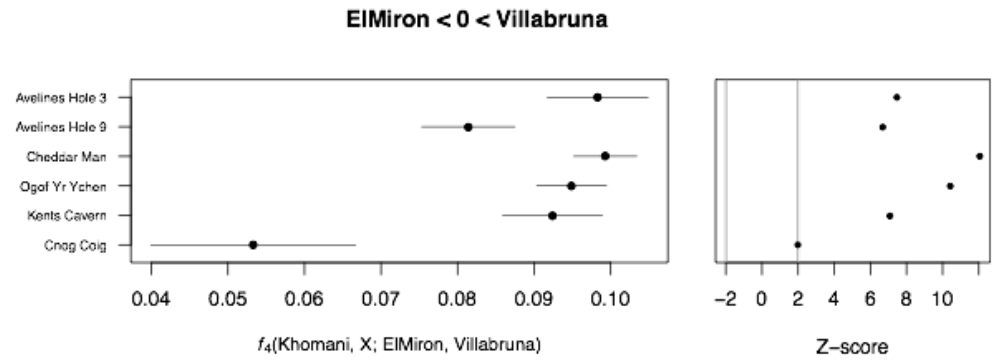
When modelling both the allele sharing and haplotype sharing profiles of each ancient Neolithic genome as mixtures of modern-day surrogates we identify a large French and Spanish affinity in the Early Iberian (Spanish:0.52 [0.14 SE]; Sardinia:0.12 [0.02 SE]), Middle Iberian (Spanish:0.56 [0.15 SE]; Sardinia:0.1 [0.02 SE]), British (French:0.9193 [0.26 SE]) and Irish (French:0.83 [0.37 SE]) Neolithic samples, Supplementary Table S11. This is markedly different to the proportions observed in the Anatolian (West Sicilian:0.70 [0.32 SE]; South Italian: 0.10 [0.22 SE]), German (Tuscan:0.23 [0.16 SE]; North Italian:0.20 [0.26 SE]; West Sicilian:0.11 [0.18 SE]), and Hungarian (North Italian:0.58 [0.34 SE]; French:0.15 [0.23 SE]) Neolithic genomes which match more strongly to Southern Europe (main text Figure 5c, Supplementary Table S9).

This suggests that British Neolithic groups primarily descend from Iberian-Neolithic related populations with a possible route of entry to Britain across the Channel via Northern and/or Southern France (see main text Discussion).

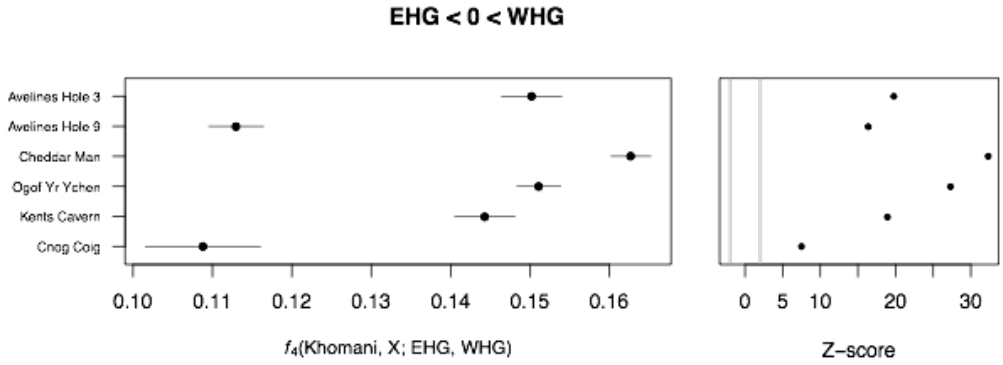
Supplementary Figures



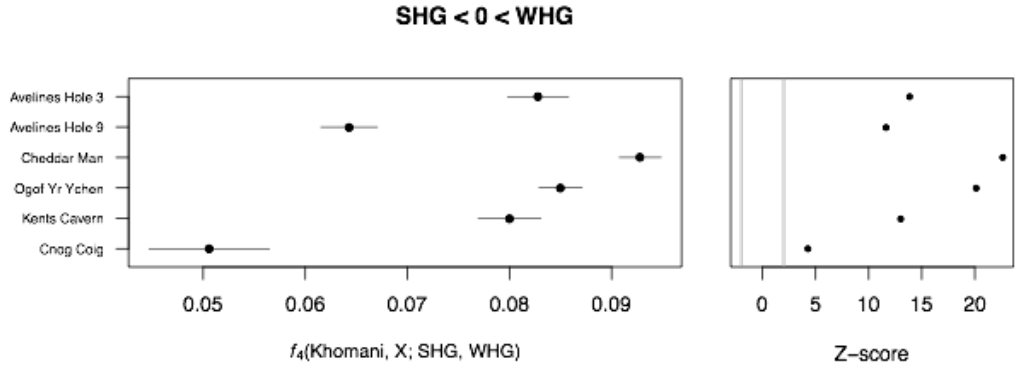
Supplementary Figure S1: *Heatmap of Mesolithic individuals.* Heatmap of pairwise outgroup f_3 statistics between Mesolithic individuals presented here and a set of ancient Eurasians from different hunter-gatherer groups such as Western-, Eastern- and Scandinavian hunter-gatherers (see Supplementary Table S1 for references).



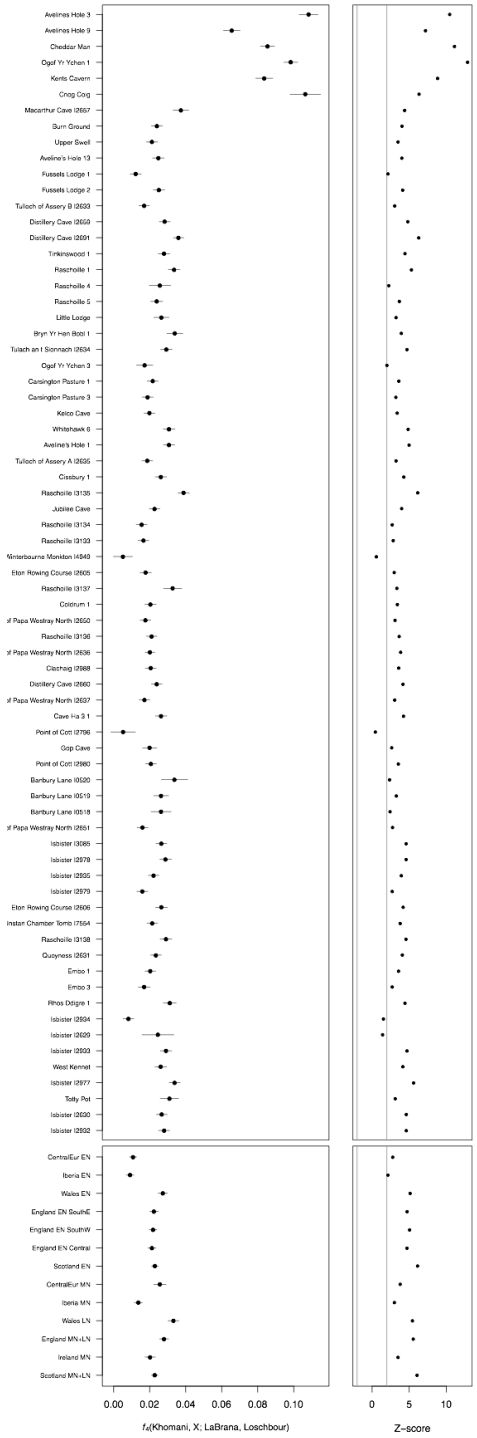
Supplementary Figure S2: *f_4 statistics between hunter-gatherer groups.* We compare the affinities of the Mesolithic individuals presented here to El Mirón and Villabruna.



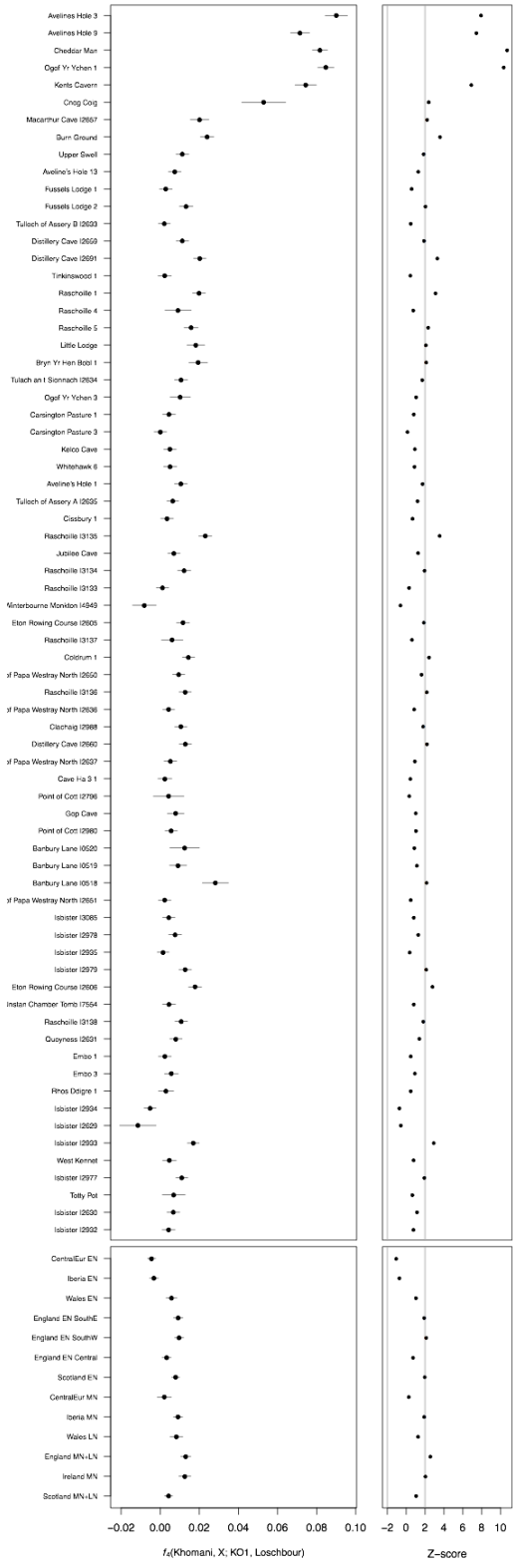
Supplementary Figure S3: *f_4 statistics between hunter-gatherer groups.* We compare the affinities of the Mesolithic individuals presented here to Eastern- (EHG) and Western hunter-gatherers (WHG). See Supplementary Table S1 for the information which individuals were grouped to form EHG and WHG.



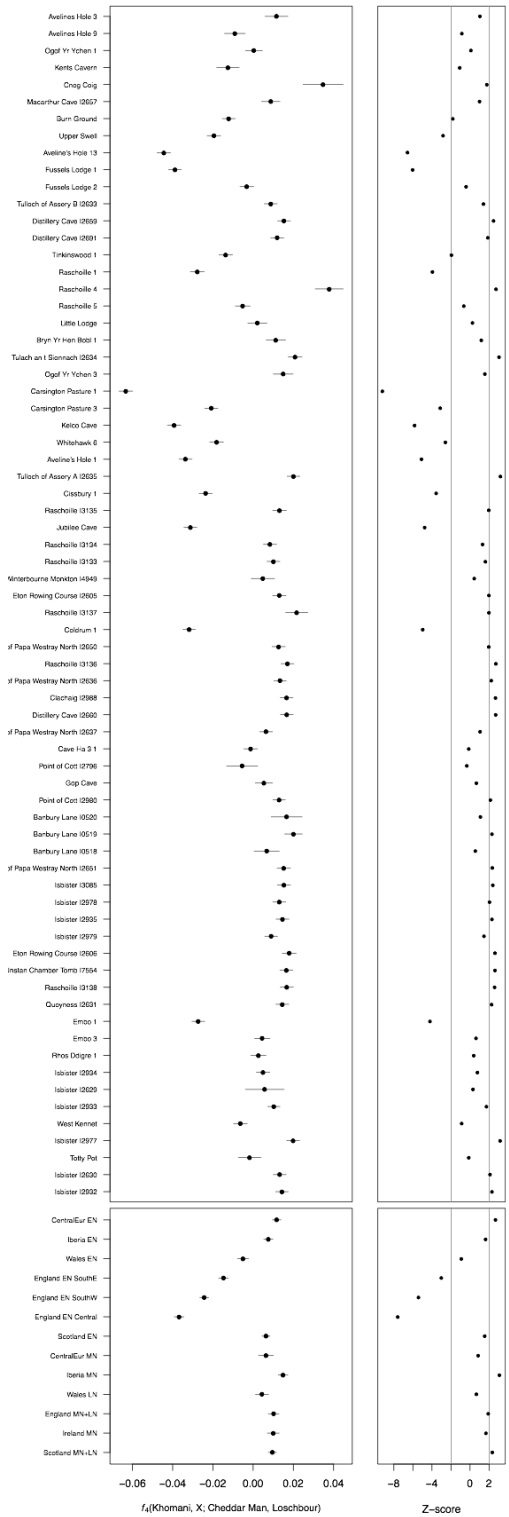
Supplementary Figure S4: *f_4 statistics between hunter-gatherer groups.* We compare the affinities of the Mesolithic individuals presented here to Scandinavian- (SHG) and Western hunter-gatherers (WHG). See Supplementary Table S1 for the information which individuals were grouped to form SHG and WHG.



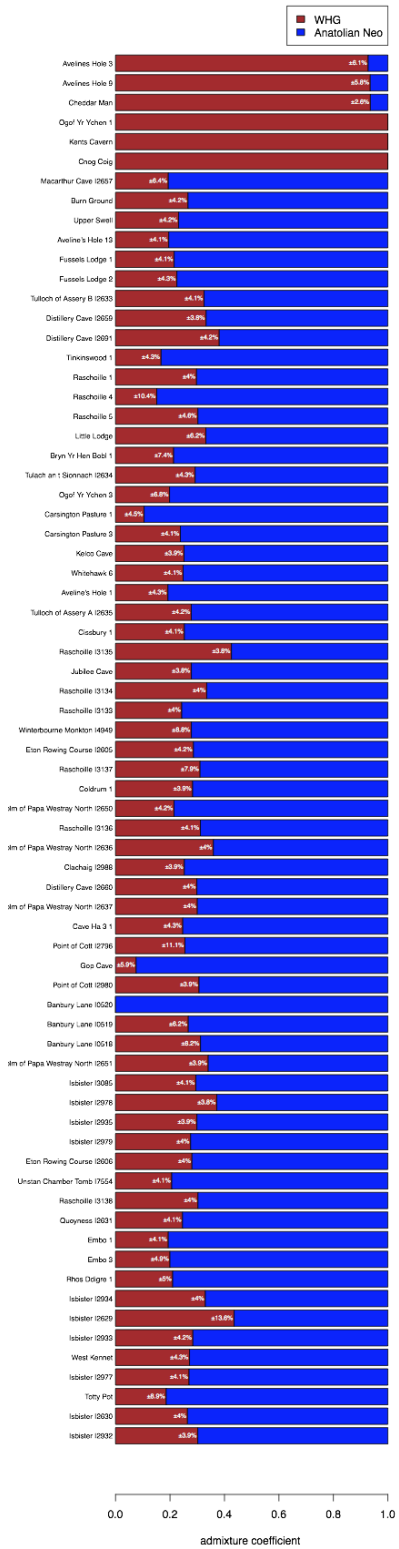
Supplementary Figure S5: *f_4 statistics between different WHG individuals.* The upper panel compares affinities of each ancient British individual analysed here to the Mesolithic individuals La Braña and Loschbour. The lower panel repeats the analysis grouping individuals temporally and where possible geographically, see Supplementary Table S1 for the information which individuals were grouped.



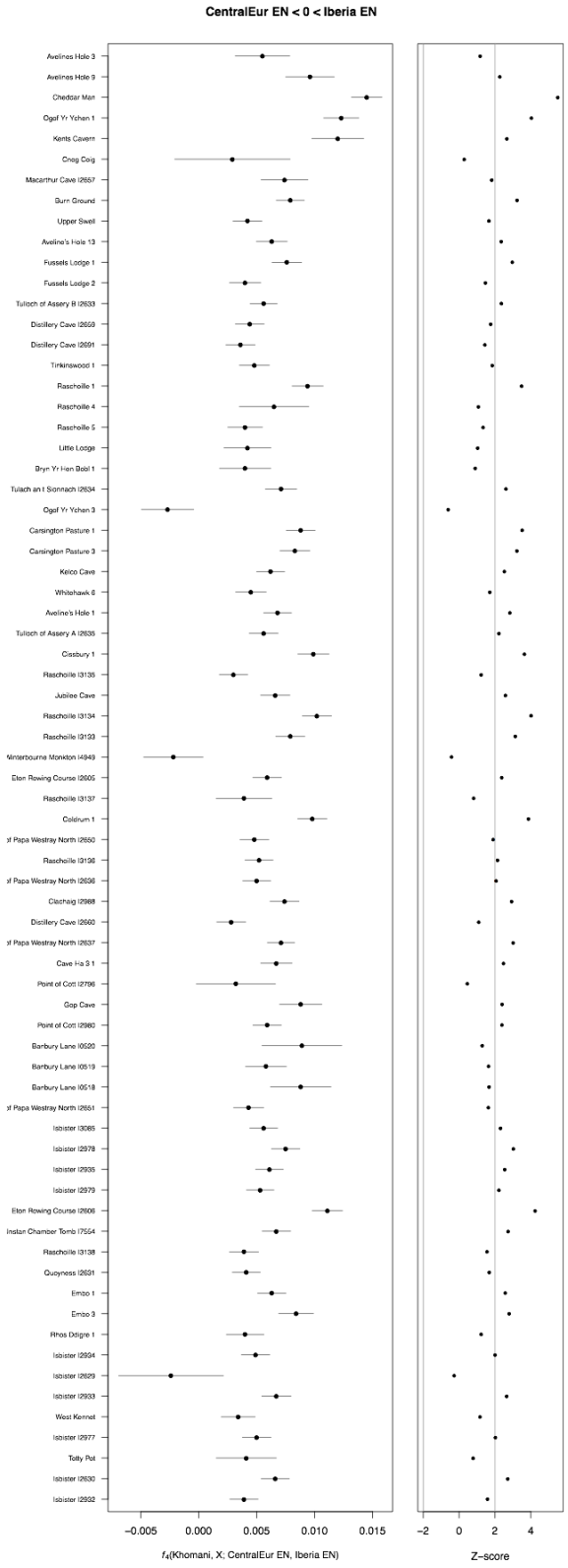
Supplementary Figure S6: *f_4 statistics between different WHG individuals.* The upper panel compares affinities of each ancient British individual analysed here to the Mesolithic individuals KO1 and Loschbour. The lower panel repeats the analysis grouping individuals temporally and where possible geographically, see Supplementary Table S1 for the information which individuals were grouped.



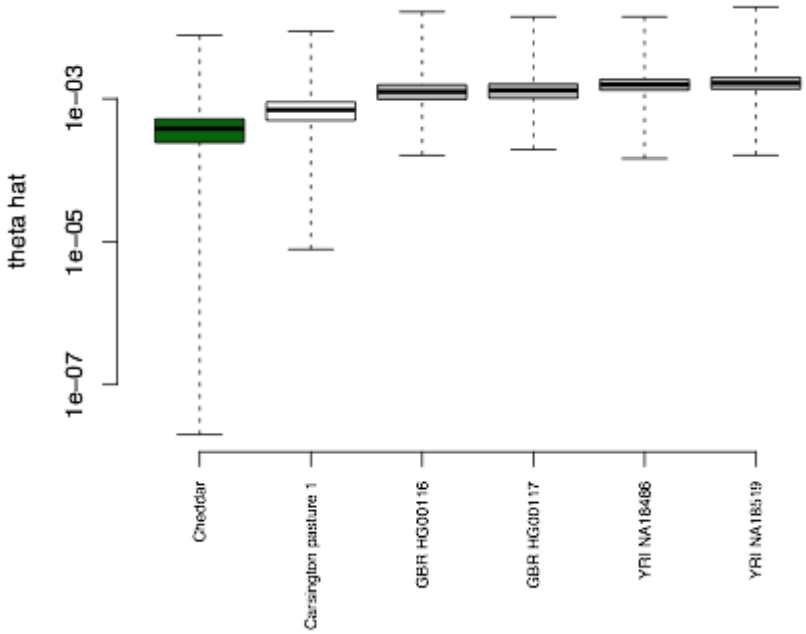
Supplementary Figure S7: *f_4 statistics between different WHG individuals.* The upper panel compares affinities of each ancient British individual analysed here to the Mesolithic British Cheddar Man, whose genome is presented here, and Loschbour. The lower panel repeats the analysis grouping individuals temporally and where possible geographically, see Supplementary Table S1 for the information which individuals were grouped.



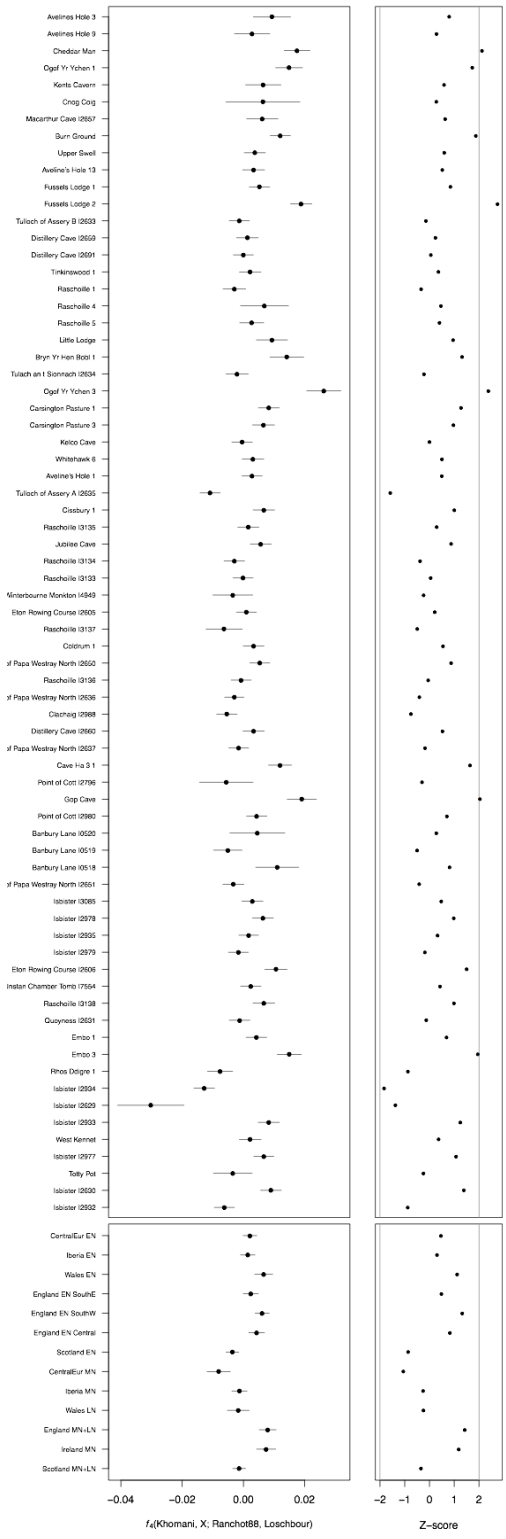
Supplementary Figure S8: *Individual f_4 admixture proportions*. We estimate the WHG and Anatolian farmer ancestry proportions for each ancient British individual analysed here.



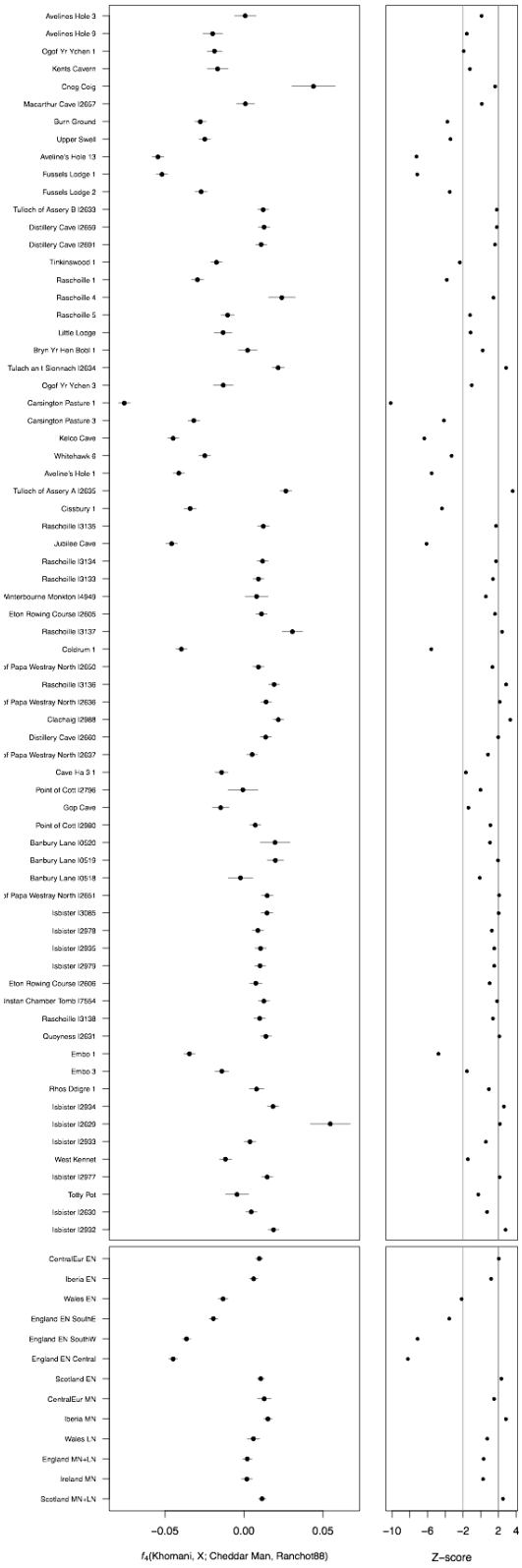
Supplementary Figure S9: *f_4 statistics between different Central European and Iberian Early Neolithic.* We compare the affinities of all individuals presented here to Central European (CentralEur EN) and Iberian Early Neolithic (Iberia EN) populations. See Supplementary Table S1 for the information which individuals were grouped to form the CentralEur EN and Iberia EN).



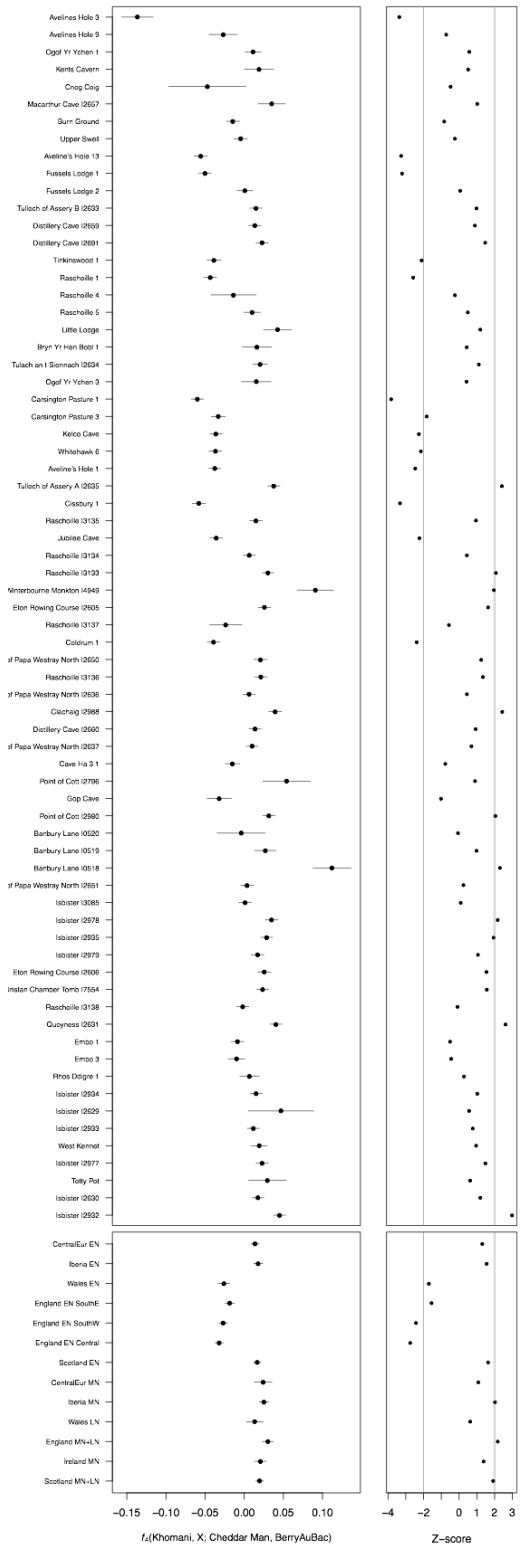
Supplementary Figure S10: *Heterozygosity estimates for ancient and modern British individuals*. We compare heterozygosity estimates between British Mesolithic Cheddar Man, British Neolithic Carsington Pasture 1 ('Sven'), and two modern British and two modern Yoruba individuals from the 1000 genome project[38].



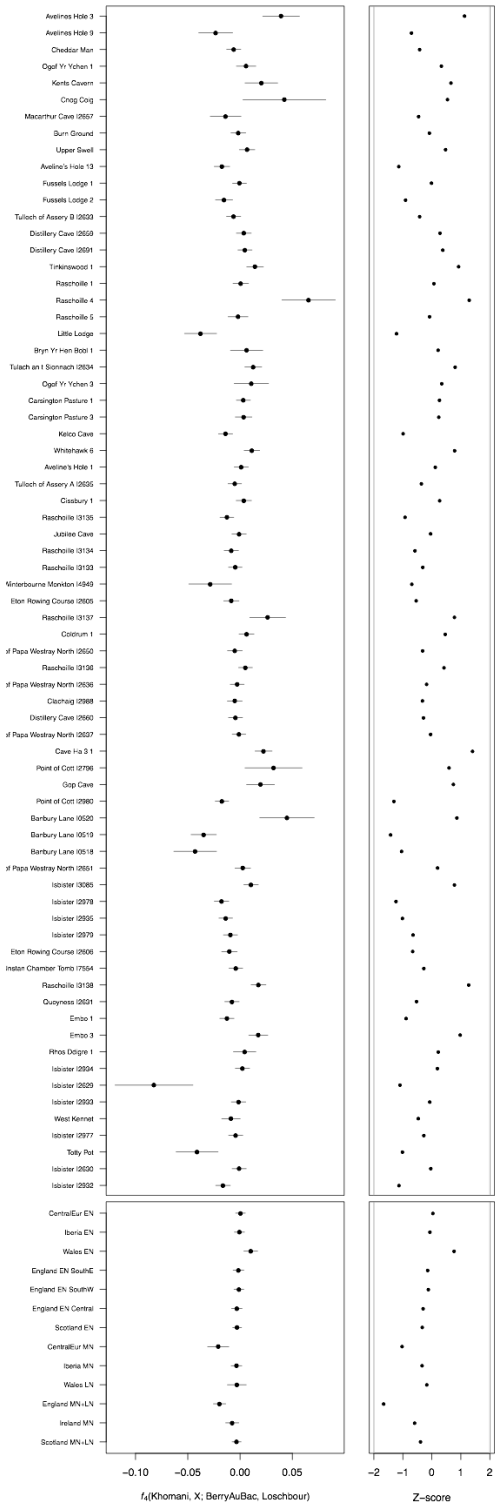
Supplementary Figure S11: *f_4 statistics between different WHG individuals.* The upper panel compares affinities of each ancient British individual analysed here to the Mesolithic individuals Ranchot88, and Loschbour. The lower panel repeats the analysis grouping individuals temporally and where possible geographically, see Supplementary Table S1 for the information which individuals were grouped.



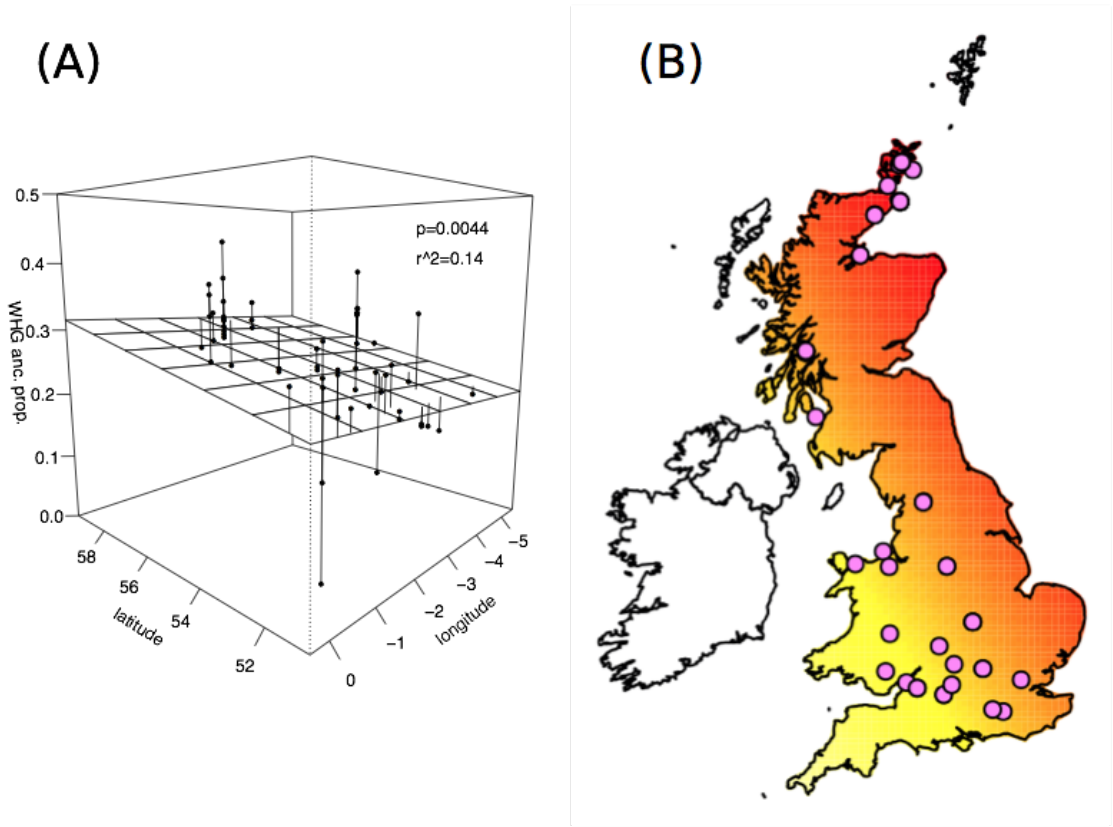
Supplementary Figure S12: *f_4 statistics between different WHG individuals.* The upper panel compares affinities of each ancient British individual analysed here to the Mesolithic British Cheddar Man, whose genome is presented here, and Ranchot88. The lower panel repeats the analysis grouping individuals temporally and where possible geographically, see Supplementary Table S1 for the information which individuals were grouped.



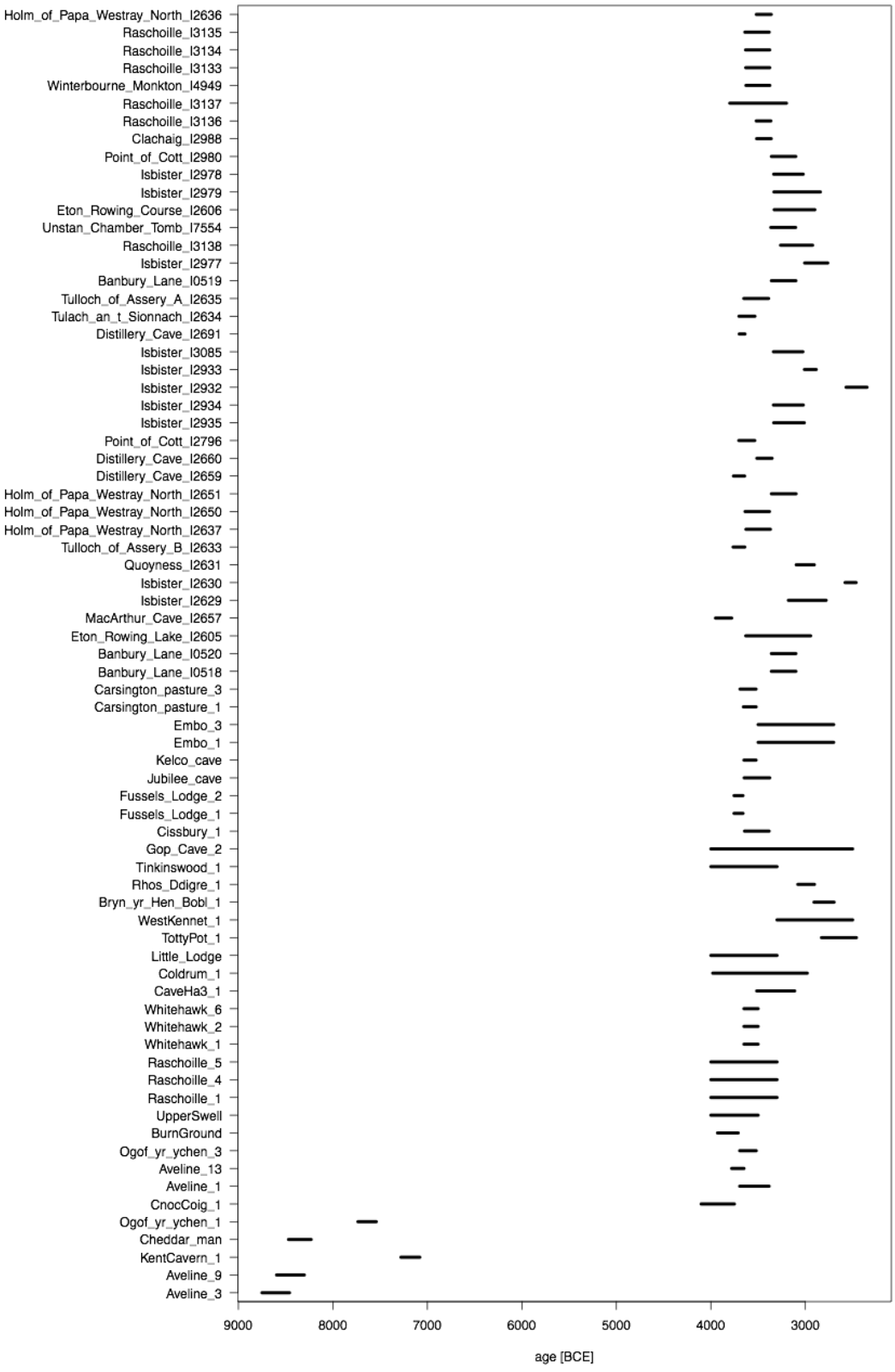
Supplementary Figure S13: *f_4 statistics between different WHG individuals.* The upper panel compares affinities of each ancient British individual analysed here to the Mesolithic British Cheddar Man, whose genome is presented here, and Berry au Bac. The lower panel repeats the analysis grouping individuals temporally and where possible geographically, see Supplementary Table S1 for the information which individuals were grouped.



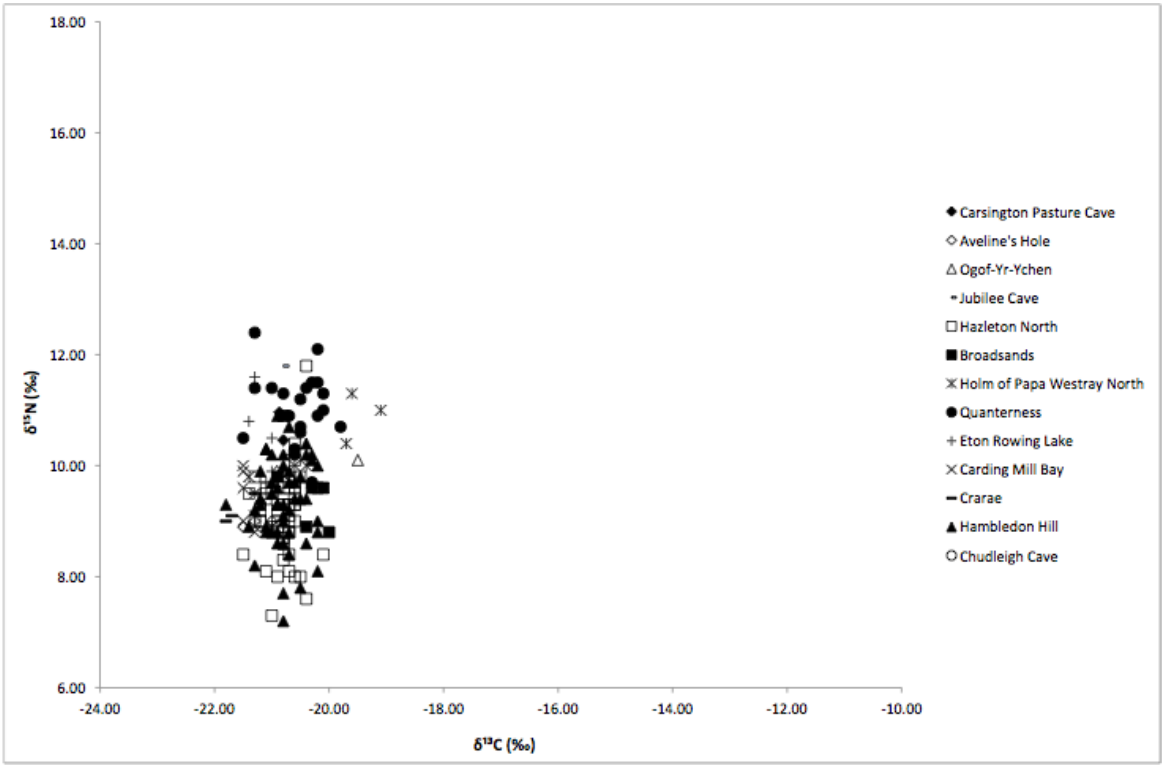
Supplementary Figure S14: *f_4 statistics between different WHG individuals.* The upper panel compares affinities of each ancient British individual analysed here to the Mesolithic individuals Berry au Bac, and Loschbour. The lower panel repeats the analysis grouping individuals temporally and where possible geographically, see Supplementary Table S1 for the information which individuals were grouped.



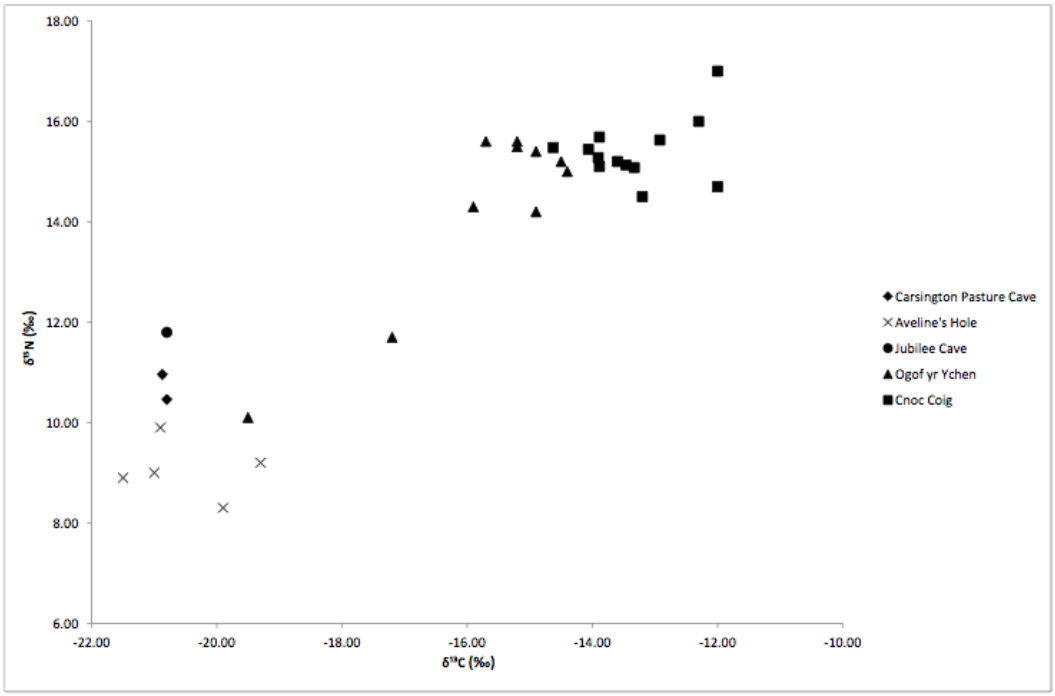
Supplementary Figure S15: *WHG f_4 admixture proportions regressed over latitude and longitude.* Panel A shows individual WHG f_4 admixture proportions represented in Supplementary Figure S8 regressed over latitude and longitude as listed in in Supplementary Table S1, excluding individuals with recent introgression events (Distillery_Cave_I2659, Raschoille_I3135, Raschoille_I3134, Raschoille_1; see Supplementary Table 3) and those with no statistical support for a WHG ancestry component (Banbury_Lane_I0520; see Supplementary Figure S8). Panel B shows a projection of the regression plane onto the contour map of the British Isles. The linear regression is generated using R's 'lm' function, and plotted with the R 'rworldmap' package.



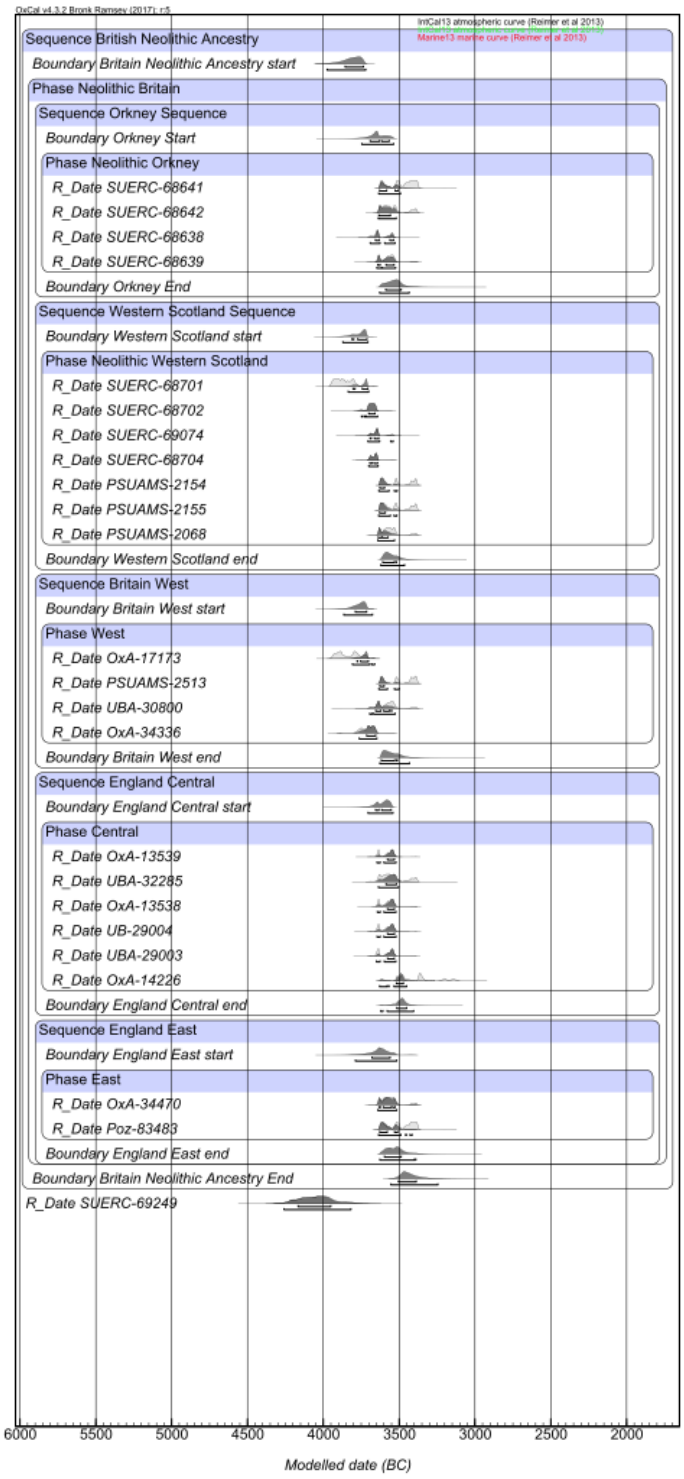
Supplementary Figure S16: *Dates for all ancient samples with new sequencing data presented here.* Graphical representation of ^{14}C dates when available, otherwise contextual dates, for each sample with newly presented data. See Supplementary Table S1 for the numerical values.



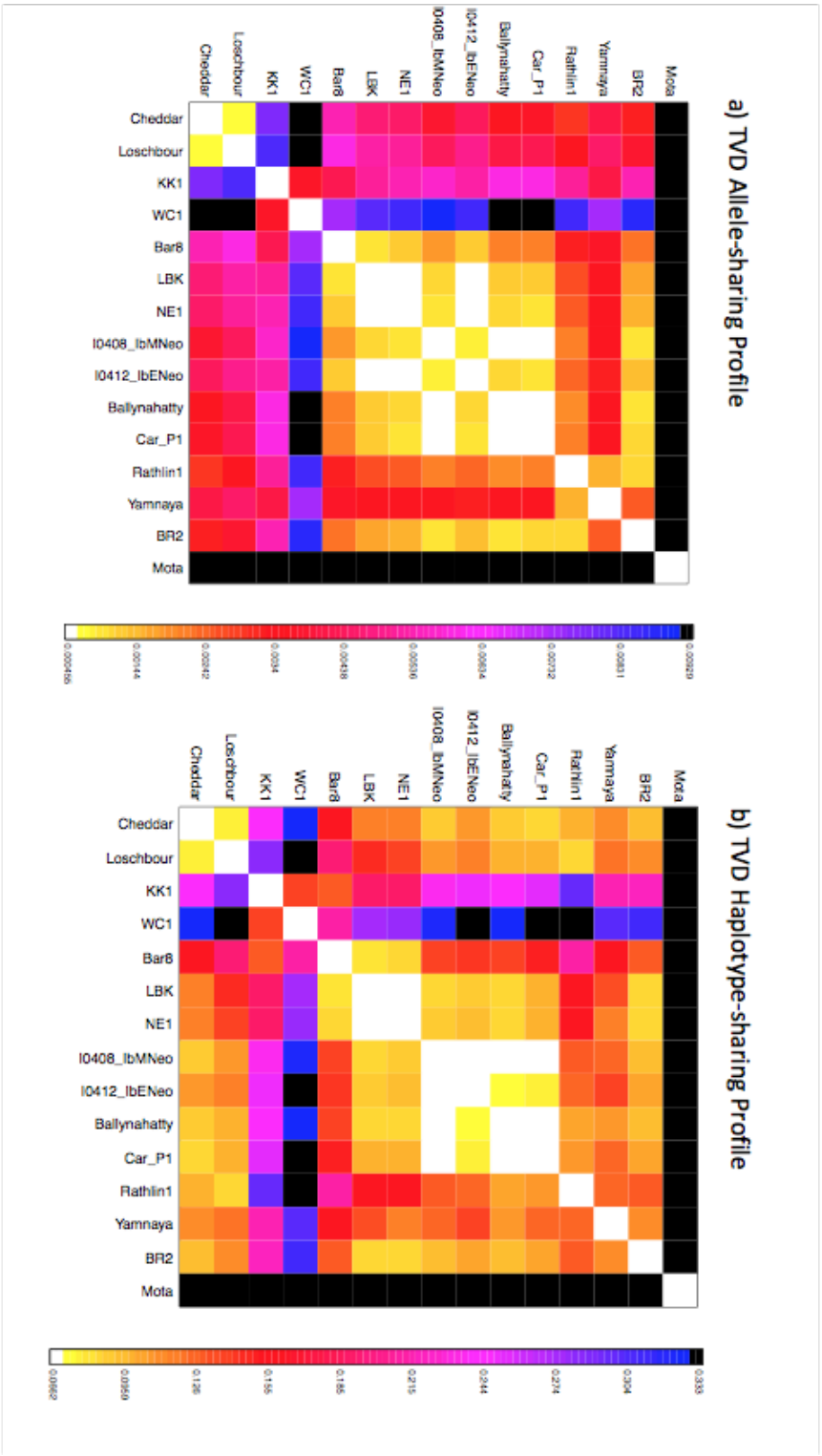
Supplementary Figure S17: Plot of $\delta^{13}C$ and $\delta^{15}N$ values for human remains from Carsington Pasture Cave, Aveline's Hole, Ogof yr Ychen, Jubilee Cave, Hazleton North, Broadsands, Holm of Papa Westray North, Quanterness, Eton Rowing Lake, Carding Mill Bay, Crarae, Hambledon Hill, and Chudleigh Cave[4, 53-54, 72-74].



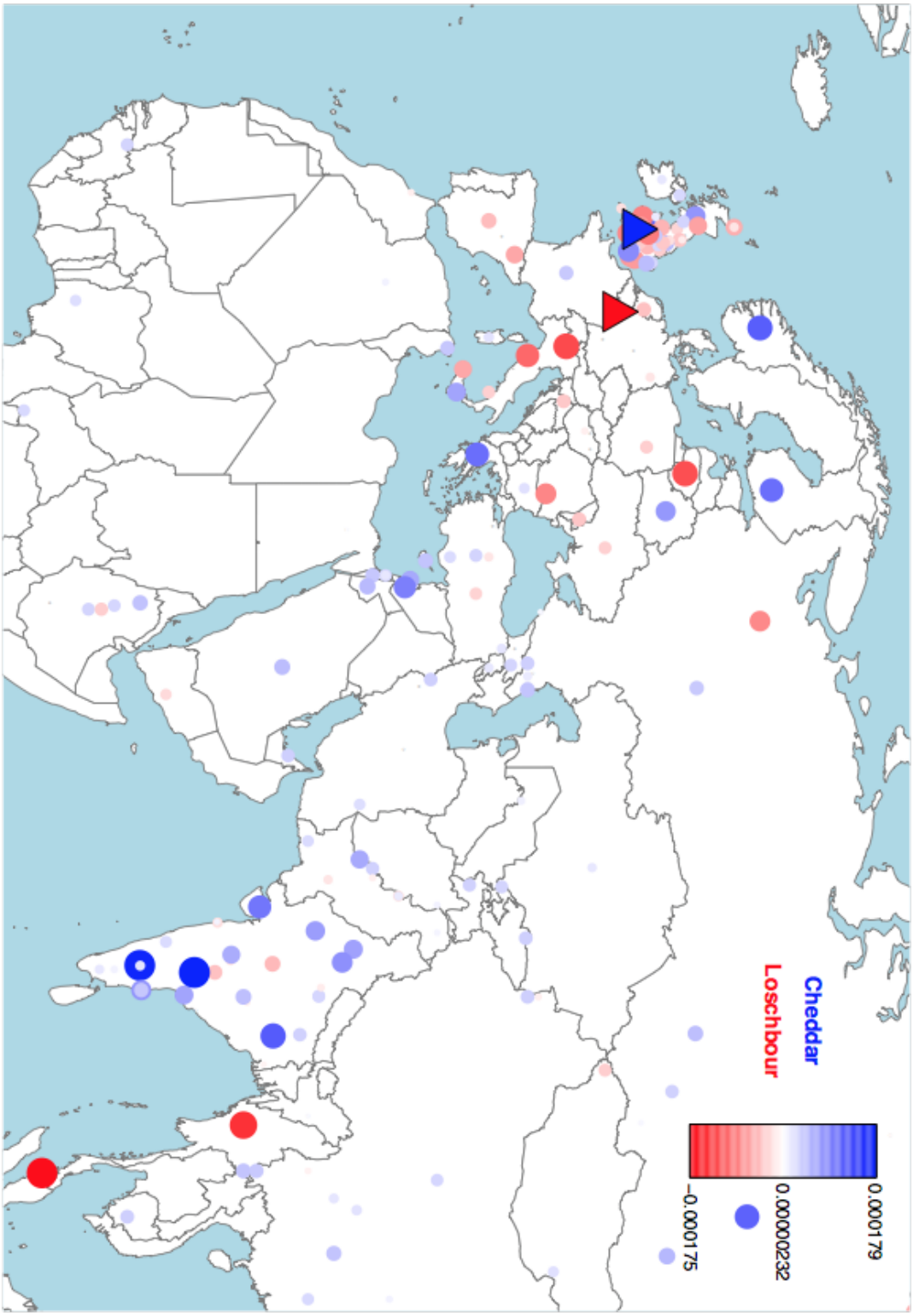
Supplementary Figure S18: Plot of $\delta^{13}C$ and $\delta^{15}N$ values for human remains from Carsington Pasture Cave, Aveline's Hole, Jubilee Cave, Cnoc Coig and Ogof yr Ychen[4, 7,17, 27].



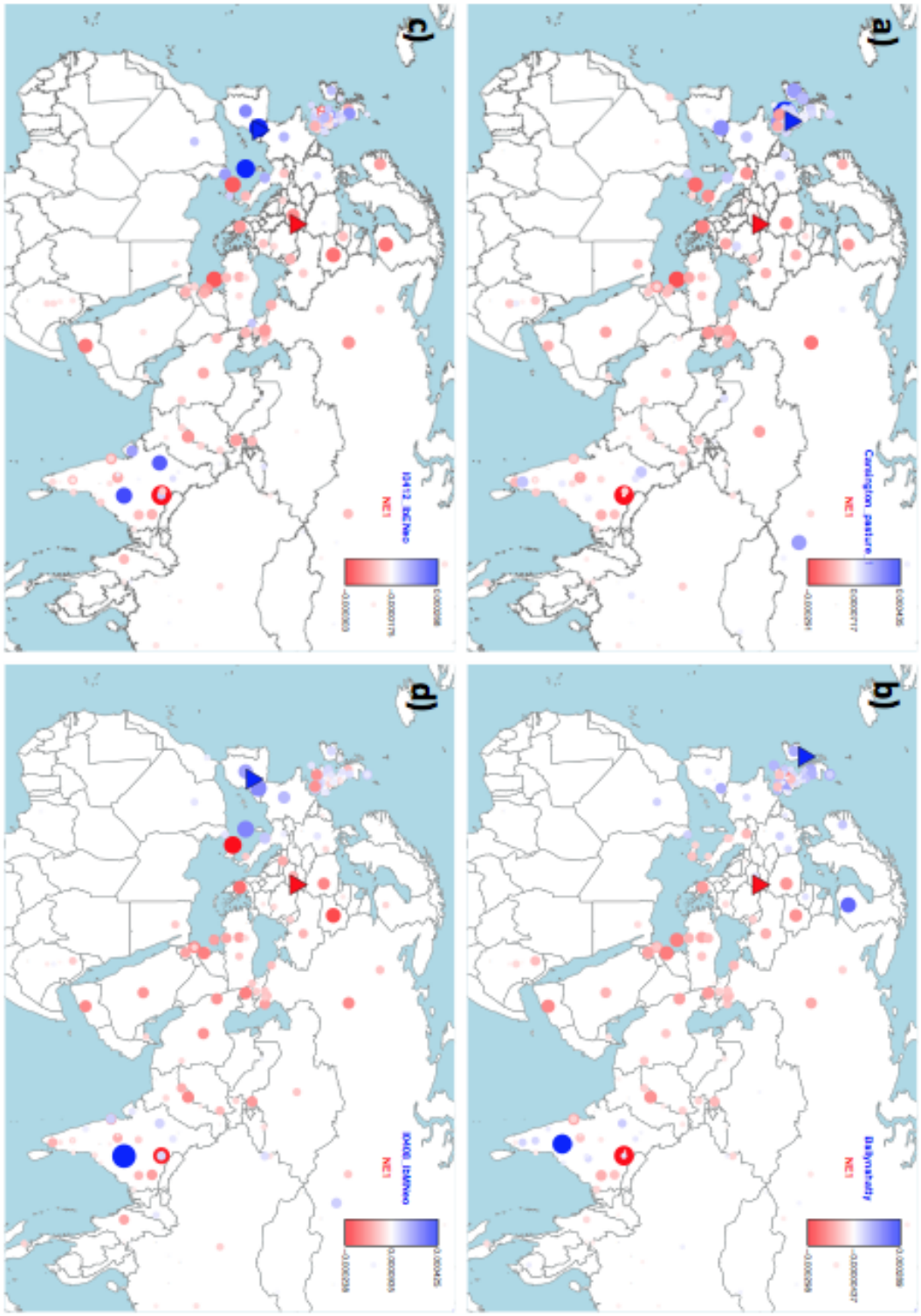
Supplementary Figure S19: Model used in OxCal 4.3[2] and IntCal/Marine13[3] to produce chronologies for the arrival and spread of ANF ancestry around Britain.



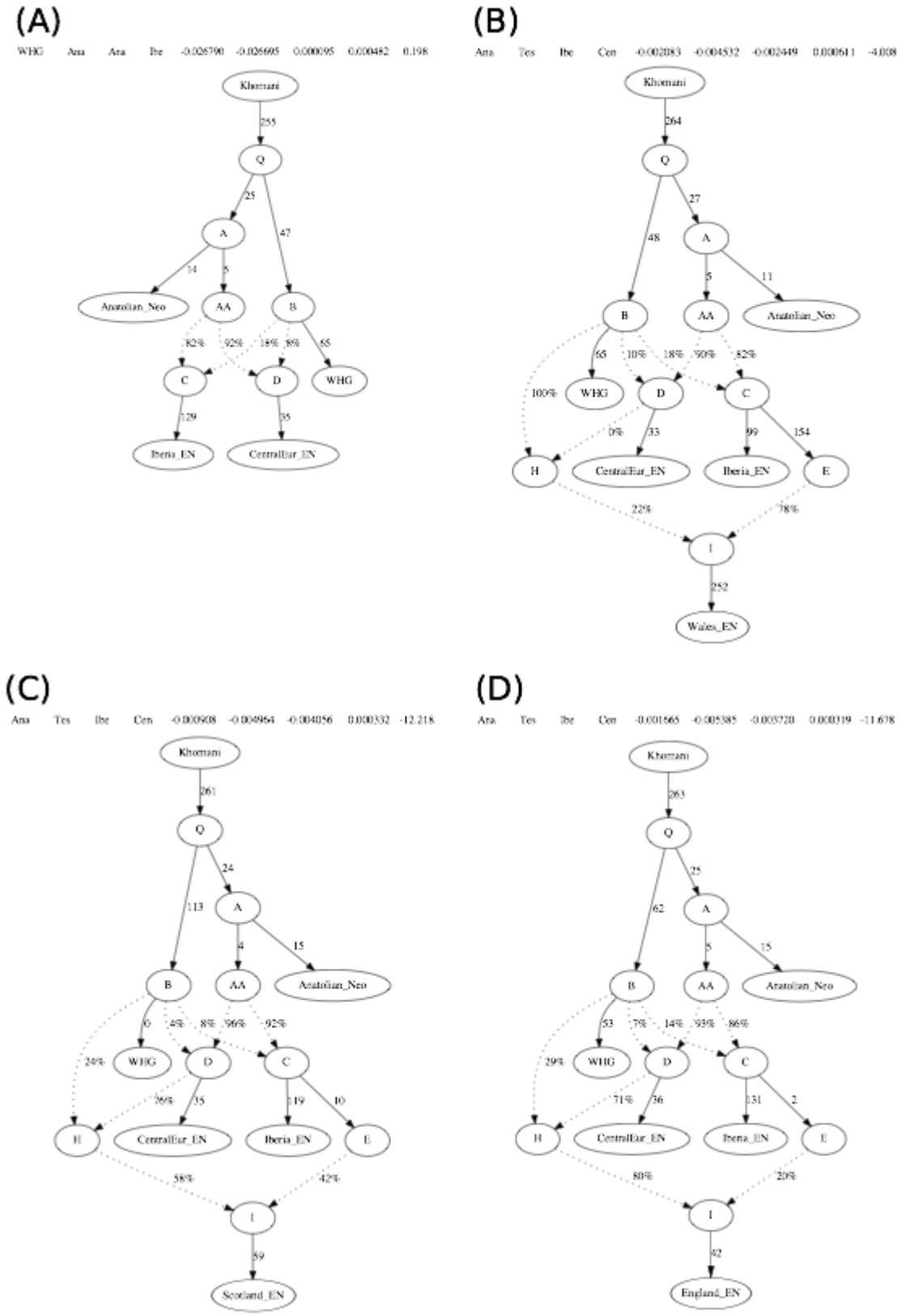
Supplementary Figure S20: a) Pairwise total-variation-distance (TVD) heatmap between high coverage ancient genomes based on the allele sharing profiles inferred under an unlinked chromosome painting approach. b) Pairwise total-variation-distance (TVD) heatmap between high coverage ancient genomes based on the haplotype sharing profiles inferred under a linked chromosome painting approach.



Supplementary Figure S21: Modern groups with an increasingly higher (respectively lower) inferred proportion of haplotype sharing with the British Mesolithic individual (Cheddar, blue triangle) compared to the German Mesolithic genome (Loschbour, red triangle). An increasingly stronger blue colour (respectively red colour) provides a greater affinity of Cheddar (respectively Loschbour) to these populations. Circle sizes provides the relative absolute proportion of this difference.



Supplementary Figure S22: Modern groups with an increasingly higher (respectively lower) inferred proportion of haplotype sharing with the tested Neolithic individual (blue triangle) compared to the Hungarian Neolithic genome (NE1, red triangle). Circle sizes provides the relative absolute proportion of this difference. Results are provided for comparisons of the a) British Neolithic "Carsington_Pasture_1", b) Irish Neolithic "Ballynahatty", c) Early Iberian Neolithic "I0412" and d) Middle Iberian Neolithic "I0408".



Supplementary Figure S23: *Population models fitted with qpGraph*. Panel (A) shows the base model without test population, panel (B), (C), and (D) expand the base model so that the test population is modelled as a mixture of Iberian_EN, and CentralEur_EN with the possibility of additional WHG ancestry. See Supplementary Table S11 for table of outliers.

Supplementary Table legends

Supplementary Table S1: *Summary of sequencing data per individual with relevant Metadata.* We list all individuals analysed as part of this paper, as well as which individuals constitute the groups of individuals like WHG, SHG etc. used throughout the paper. Number of reads are before removing duplicates and MAPQ filtering. Coverage is computed as the number of bases divided by the total number of nuclear positions in the reference genome without counting positions that belong to intervals of five or more consecutive N's. Read depth refers to the average number of times a set of positions is covered given a position is covered at least once. Duplicates are marked with Picard tools and counted with Samtools[38].
Abbreviations: nuclear (NUC), Mitochondrial (MT), number of (nb.)

Supplementary Table S2: *Functional variation.* List of SNPs and alleles found in the individuals newly sequenced here based on which phenotypic characteristics have been predicted.

Supplementary Table S3: *Admixture dates.* Dating of admixture events generated with ALDER[39] for pairs or groups of individuals listed on the bottom of the table.

Supplementary Table S4: *Pairwise comparison of WHG admixture proportions.* We analytically compute the probability that a WHG admixture proportion is greater than another by comparing the Normal distributions generated by *qpAdm* via $P(X > Y) = \frac{1}{2} erfc\left(\frac{\mu_y - \mu_x}{\sqrt{2(\sigma_x^2 + \sigma_y^2)}}\right)$, where erfc is the complementary error function .

Supplementary Table S5: *Y-chromosomal lineages.* Results of Yleaf[27] for the 19 ancient British male Mesolithic and Neolithic individuals, including positions with derived alleles.

Supplementary Table S6: *New radiocarbon dates and stable isotopes.* Newly-reported results of radiocarbon dating and stable isotope analyses on a selection of the individuals included in this study. The radiocarbon date and stable isotopes data for the Cnoc Coig sample were generated as part of a separate PhD study[7].

Supplementary Table S7: *Chronological model outputs*. Output of our chronological model of direct radiocarbon dates on British human remains showing ANF ancestry generated in OxCal[2] using IntCal13 and Marine13[3] curves.

Supplementary Table S8: *SOURCEFIND inferred proportions of ancient ancestry.* SOURCEFIND inferred proportions of ancestry and standard errors for all pre-Bronze age ancient individuals included in our analysis using pre-Bronze Age high coverage ancient genomes as surrogates, see Supplementary Materials Section 7.

Supplementary Table S9: *SOURCEFIND inferred proportions of modern ancestry.* SOURCEFIND inferred proportions of ancestry and standard errors for all pre-Bronze age ancient individuals included in our analysis using modern genomes as surrogates, see Supplementary Materials Section 7. Modern groups are labelled as in the original publications with data from Hellenthal et al. 2014[64] and Busby et al. 2015[65] prefixed "HellBus:" and data from Leslie et al. 2015[66] prefixed "POBI".

Supplementary Table S10: *qpGraph outliers.* Outliers of the f_4 statistics underlying the *qpGraph* models presented in Supplementary Figure S23.

References

[1]Olalde I, Brace S, Allentoft ME, et al. The Beaker phenomenon and the genomic transformation of northwest Europe. *Nature*, **555**, 190-196 (2018).

[2]Bronk Ramsey, C. Bayesian analysis of radiocarbon dates. *Radiocarbon*, **51**, 337-360 (2009).

[3]Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M. and Grootes, P.M. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*, **55**, 1869-1887 (2013).

[4]Schulting, R.J. and Richards, M.P. Finding the coastal Mesolithic in southwest Britain: AMS dates and stable isotope results on human remains from Caldey Island, South Wales. *Antiquity,* **76**, 1011-1025 (2002).

[5]Russell, N. Cook, G.T. Ascough, P.L and Scott, E.M. A period of calm in Scottish seas: a comprehensive study of ΔR values for the northern British Isles coast and the consequent implications for archaeology and oceanography. *Quat Geochronol* **30**, 34-41 (2015).

[6]Cook, G.T. Ascough, P.L. Bonsall, C. Hamilton, W.D. Russell, N. Sayle, K.L. Scott, E.M. and Bownes, J.M. Best practice methodology for 14C calibration of marine and mixed terrestrial/marine samples. *Quat Geochronol* **27**, 164-171 (2015).

[7]Charlton, S., Alexander, M., Collins, M., Milner, N., Mellars, P., O'Connell, T.C., Stevens, R.E. & Craig, O.E. Finding Britain's last hunter-gatherers: A new biomolecular approach to 'unidentifiable' bone fragments utilising bone collagen. *J Archaeol Sci,* **73**, 55-61 (2016).

[8]Bownes, J. Reassessing the Scottish Mesolithic-Neolithic transition: questions of diet and chronology. *PhD Thesis, University of Glasgow* (2018).

[9]Schulting, R.J. Pursuing a rabbit in Burrington Combe': New research on the Early Mesolithic burial cave of Aveline's Hole. *Proceedings of the University of Bristol Spelaeological Society*, **23**(3), 171-265 (2005)

[10]Grimes, W.F. Excavations on Defence Sites, 1939-1945. HM Stationary Office, London (1960).

[11]Smith, M. & Brickley, M. The Date and Sequence of use of Neolithic Funerary Monuments: New AMS Dating Evidence from the Cotswold-Severn Region. *Ox J Archaeol,* **25,** 335–355 (2006).

[12]Hemp, W.J. IX. The chambered cairn known as Bryn yr Hen Bobl near Plas Newydd, Anglesey. *Archaeologia* **85**, 253-292 (1936).

[13]Chamberlain, A.T. Carsington Pasture Cave, Brassington, Derbyshire: a prehistoric burial site. *Capra* **1** (1999).

[14]Chamberlain, A.T. Radiocarbon Dates from Carsington Pasture Cave, Brassington, Derbyshire. *Capra* **3** (2001).

[15]Leach, S. *Going Underground: an anthropological and taphonomic study of human skeletal remains from caves and rock shelters in Yorkshire*. Yorkshire Archaeological Society, Leeds (2015).

[16]Mellars, P. *Excavation and economic analysis of Mesolithic shell middens on the island of Oronsay (Inner Hebrides)*. Duckworth, London (1978).

[17]Richards, M.P. & Mellars, P.A. Stable isotopes and the seasonality of the Oronsay middens. *Antiquity* **72**, 178-184 (1998).

[18]Richards, M.P. & Sheridan, J.A. New AMS dates on human bone from Mesolithic Oronsay. *Antiquity* **74**, 313-315 (2000).

[19]Meiklejohn, C., Merrett, D.C., Nolan, R.W., Richards, M.P. & Mellars, P.A. 2005. Spatial relationships, dating and taphonomy of the human bone from the Mesolithic site of Cnoc Coig, Oronsay, Argyll, Scotland. *Proc Prehist Soc* **71**, 85-105 (2005).

[20]Ashbee, P. Coldrum revisited and reviewed. *Archaeologia Cantiana* **118**, 1-43 (1998).

[21]Wysocki, M., Griffiths, S., Hedges, R., Bayliss, A., Higham, T., Fernandez-Jalvo, Y. & Whittle, A. Dates, diet, and dismemberment: Evidence from the Coldrum megalithic monument, Kent. *Proc Prehist Soc* Vol. 79, 61-90 (2013).

[22]Henshall, A.S. & Wallace, J, C. The excavation of a chambered cairn at Embo, Sutherland. *Proc Soc Antiq Scot*, **96**, 9-36 (1965).

[23]Henshall, A. S. Embo. *Discovery and Excavation in Scotland,* **29** (1956).

[24]Boyd Dawkins, W. On the Cairn and Sepulchral Cave at Gop, Near Prestatyn. *Archaeol J,* **58**, 322-341 (1901).

[25]Schulting, R. J. and Gonzalez, S. 'Prestatyn Woman' reconsidered. In Bell, M. (ed.) Prehistorical Coastal Communities: The Mesolithic in Western Britain. Council for British Archaeology Research Report **149**, York, 303-305 (2008).

[26]Tratman, E.K. Problems of " The Cheddar Man", Gough's Cave, Somerset. *Proc U Bristol Spelaeol Soc* **14**, 7-23 (1975).

[27]Meiklejohn, C., Chamberlain, A.T. & Schulting, R.J. Radiocarbon dating of Mesolithic human remains in Great Britain. *Mesolithic Miscellany* **21**, 20-58 (2011).

[28]Schulting, R.J., Bello, S.M., Chandler, B. and Higham, T.F.G. A cut-marked and fractured Mesolithic human bone from Kent's Cavern, Devon, UK. *Int J Osteoarch* **25**, 31-44 (2015).

[29]Vulliamy, C.E. 1929. Excavation of an unrecorded long barrow in Wales. *Man* **29**, 34-6 (1929).

[30]van Nedervelde, B.J., Davies, M. & John, B.S. Radiocarbon dating from Ogof-yr-Ychen, a new Pleistocene site in west Wales. *Nature* **245**, 453 (1973)

[31]Piggott, S. *The West Kennet Long Barrow Excavations, 1955-56*. HM Stationary Office, London (1962).

[32]Bayliss, A., Whittle, A. and Wysocki, M. Talking about my generation: the date of the West Kennet long barrow. *Cam Archaeol J* **17**(S1), 85-101 (2007).

[33]Russell, M. & Rudling, D. Excavations at Whitehawk Neolithic enclosure, Brighton, East Sussex, 1991–1993. *Sussex Archaeol Collect* **134**, 39-61 (1996).

[34]Drewett, P., Cartwright, C.R., James, B., Thomas, K.D. & O'Connor, T.P. The excavation of a Neolithic causewayed enclosure on Offham Hill, East Sussex, 1976. *Proc Prehist Soc* **43**, 201-242 (1977).

[35]Whittle, A.W.R., Healy, F.M.A. & Bayliss, A. *Gathering time: dating the early Neolithic enclosures of southern Britain and Ireland*. Oxbow Books, Oxford (2011).

[36]Ralf A, Montiel González D, Zhong K, Kayser M. Yleaf: software for human Y-chromosomal haplogroup inference from next generation sequencing data. *Mol Biol Evol*, **35**, 1291-1294 (2018).

[37]Martiniano R, et al. The population genomics of archaeological transition in west Iberia: Investigation of ancient substructure using imputation and haplotype-based methods. *PLoS Genet*, **13**:e1006852 (2017).

[38]Hofmanová Z, et al. Early farmers from across Europe directly descended from Neolithic Aegeans. *Proc Natl Acad Sci USA* ,**113**, 6886–6891 (2016).

[39]Mathieson I, et al. Genome-wide patterns of selection in 230 ancient Eurasians. *Nature* **528**, 499–503 (2015) .

[40]Walsh S, Liu F, Wollstein A, et al. The HIrisPlex system for simultaneous prediction of hair and eye colour from DNA. *Forensic Sci Int Genet*, **7**, 98–115 (2013). doi:10.1016/j.fsigen.2012.07.005

[41]Walsh S, Chaitanya L, Breslin K, et al. Global skin colour prediction from DNA. *Hum Genet*, **136**, 847–863 (2017).

[42]Chaitanya L, Breslin K, Zuñiga S, et al. The HIrisPlex-S system for eye, hair and skin colour prediction from DNA: Introduction and forensic developmental validation. *Forensic Sci Int Genet*. **35**, 1–42 (2018).

[43]Olalde, I. et al. Derived immune and ancestral pigmentation alleles in a 7,000-year-old Mesolithic European. *Nature* **507**, 225–228 (2014).

[44]Lazaridis, I. et al. Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature* **513**, 409–413 (2014).

[45]1000 Genomes Project Consortium, Auton A, Brooks LD, et al. A global reference for human genetic variation. *Nature* **2015**, 526, 68–74 (2015).

[46]Li H. A statistical framework for SNP calling, mutation discovery, association mapping and population genetical parameter estimation from sequencing data. *Bioinformatics* **27**, 2987–2993 (2011).

[47]Loh P-R, Lipson M, Patterson N, et al. Inferring admixture histories of human populations using linkage disequilibrium. *Genetics* **193**, 1233–1254 (2013).

[48]Brown, T.A. Nelson, D.E. Vogel, J.S. and Southon, J.R. Improved collagen extraction by modified longin method. *Radiocarbon* **30**, 171-177 (1988).

[49]Richards, M.P. and Hedges, R.E.M. Stable isotope Evidence for similarities in the types of marine foods used by Late Mesolithic humans at sites along the Atlantic coast of Europe, *J Archaeol Sci*, **26**, 717-722 (1999).

[50]Reimer, P. Hoper, S. McDonald, J. Reimer, R. Svyatko, S and Thompson, M. Laboratory Protocols used for AMS Radiocarbon Dating at the 14Chrono Centre. *English Heritage Research Report Series No.5* (2015).

[51]DeNiro, M.J. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction. *Nature*, **317**, 806-809 (1985).

[52]van Klinken, G.J. Bone Collagen Quality Indicators for Palaeodietary and Radiocarbon Measurements. *J Archaeol Sci,* **26**, 687-695 (1999).

[53]Hedges, R. Saville, A. and O'Connell, T. Characterizing the diet of individuals at the Neolithic chambered tomb of Hazleton North, Gloucestershire, England, using stable isotopic analysis. *Archaeometry* **50**, 114-128 (2008).

[54]Richards, M.P. Hambledon Hill stable isotope values. In Mercer, R. and Healy, F. (eds) Hambledon Hill, Dorset, England: Excavation and survey of a Neolithic monument complex and its surrounding landscape. Swindon: English Heritage, 522-527 (2008).

[55]Whittle, A. W. R., Healy, F., Bayliss, A. & Allen, M. J. *Gathering time: dating the early Neolithic enclosures of southern Britain and Ireland*. Oxford, Oxbow Books (2011).

[56]Collard, M., Edinborough, K., Shennan, S. & Thomas, M. G. Radiocarbon evidence indicates that migrants introduced farming to Britain. *J Archaeol Sci,* **37,** 866–870 (2010).

[57]Jones ER, Gonzalez-Fortes G, Connell S, Siska V, Eriksson A, Martiniano R, et al. Upper Palaeolithic genomes reveal deep roots of modern Eurasians. *Nat Commun*, **6**, 8912 (2015).

[58]Broushaki F, Thomas MG, Link V, López S, van Dorp L, Kirsanow K, et al. Early Neolithic genomes from the eastern Fertile Crescent. *Science*, **353**, 499–503 (2016).

[59]Gamba C, Jones ER, Teasdale MD, McLaughlin RL, Gonzalez-Fortes G, Mattiangeli V, *et al*. Genome flux and stasis in a five millennium transect of European prehistory. *Nat Commun*, **5,** 5257 (2014).

[60]Haak, W., Lazaridis, I., Patterson, N., Rohland, N., Mallick, S., Llamas, B., *et al*. Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature,* **522**, 207–11 (2015).

[61]Cassidy LM, Martiniano R, Murphy EM, Teasdale MD, Mallory J, Hartwell B, et al. Neolithic and Bronze Age migration to Ireland and establishment of the insular Atlantic genome. *Proc Natl Acad Sci*, **113**, 368–73 (2016).

[62]de Barros Damgaard, P., Martiniano, R., Kamm, J., Moreno-Mayar, J.V., Kroonen, G., Peyrot, M., *et al*. The first horse herders and the impact of early Bronze Age steppe expansions into Asia. *Science*, **360**, eaar7711 (2018).

[63]Llorente, M.G., Jones, E.R., Eriksson, A., Siska V., Arthur, K.W., Arthur, J.W., *et al*. Ancient Ethiopian genome reveals extensive Eurasian admixture throughout the African continent. *Science* **350**, 820–2 (2015).

[64]Link V, Kousathanas A, Veeramah K, Sell C, Scheu A, Wegmann D. ATLAS: Analysis Tools for Low-depth and Ancient Samples. *bioRxiv*, (2017).

[65]Hellenthal, G., Busby, G.B.J., Band, G., Wilson, J.F., Capelli, C., Falush, D., *et al*. A genetic atlas of human admixture history. *Science* **80**, 747–51 (2014).

[66]Busby, G.B.J., Hellenthal, G., Montinaro, F., Tofanelli, S., Bulayeva, K., Rudan, I., *et al*. The role of recent admixture in forming the contemporary West Eurasian genomic landscape. *Curr Biol*, **25**, 2518–26 (2015).

[67]Leslie, S., Winney, B., Hellenthal, G., Davison, D., Boumertit, A., Day, T., *et al*. The fine scale genetic structure of the British population. *Nature*, **519**, 309–14 (2015).

[68]Chang, C.C., Chow, C.C., Tellier, L.C., Vattikuti, S., Purcell, S.M., Lee, J.J. Second-generation PLINK: rising to the challenge of larger and richer datasets. *Gigascience*, **4**, 7 (2015).

[69]Delaneau, O., Marchini, J., Zagury. J.F. A linear complexity phasing method for thousands of genomes. *Nat Methods*, **9**,179–81 (2012).

[70]Lawson, D.J., Hellenthal, G., Myers, S., Falush, D. Inference of population structure using dense haplotype data. *PLoS Genet*, **8**, e1002453 (2012).

[71]Chacon-Duque, J.C. et al. Latin Americans show wide-spread Converso ancestry and the imprint of local Native ancestry on physical appearance. *Nature Commun* **9**, 5388 (2018).

[72]Richards, M.P. Human consumption of plant foods in the British Neolithic: Direct evidence from bone stable isotopes. In A.S. Fairburn (ed.) *Plants in Neolithic Britain and Beyond*. Oxbow Books, Oxford, 123-135 (2000).

[73]Schulting, R. On the Northwestern Fringes: Earlier Neolithic Subsistence in Britain and Ireland as Seen Through Faunal Remains and Stable Isotopes. In S. Colledge, J., Conolly, K., Dobney, K. Manning and S. Shennan (eds.) *The Origins and Spread of Domestic Animals in Southwest Asia and Europe*. Left Coast Press, Walnut Creek, 313-338 (2013).

[74]Stevens, R.E., Lightfoot, E., Allen, T. and Hedges, R.E.M. Palaeodiet at Eton College Rowing Course, Buckinghamshire: Isotopic changes in human diet in the Neolithic, Bronze Age, Iron Age and Roman periods throughout the British Isles', *Archaeol Anthropol Sci.* **4**, 167-184 (2012).