

AVELINE'S HOLE: AN UNEXPECTED TWIST IN THE TALE

by

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ABSTRACT

Aveline's Hole is the largest known Early Mesolithic cemetery in Britain, previously thought to have no evidence for subsequent burial activity. Thus, it came as some surprise when the results of a recent ancient human DNA study found that, of four individuals from the site yielding genomic data, two showed high levels of ancestry from Early Neolithic Aegean farmers. Radiocarbon dating confirmed that these two individuals were indeed British Early Neolithic in date, while the other two had the expected 'Western Hunter-Gatherer' ancestry genomic signatures, with the two groups separated in time by nearly five millennia. Moreover, the two Neolithic samples were both crania, while the two Mesolithic samples were long bones. Given the absence of Neolithic dates in the previous sizeable dating programme combined with the difficult history of the collection, i.e., the WWII bombing of its Bristol repository, this raised the question of whether the crania might in fact be from another site. As we show in this paper, a very strong case can be made that the crania do in fact originate from Aveline's Hole. Additional radiocarbon dating (14 in total, including the above mentioned four) suggests that about half the cranial elements from the site fall within the Early Neolithic, though there is still no evidence for the deposition of post-cranial remains at this time, nor is there any burial evidence in the long intervening period between the Early Mesolithic and the Early Neolithic. Intriguingly, craniometric analyses of legacy data including three crania lost in the bombing suggest that one, Aveline's Hole 'A', may be Upper Palaeolithic in date.

As part of this re-investigation of the human remains from the site, we present new stable carbon and nitrogen isotope analyses that differ significantly from those originally reported for the Early Mesolithic, with the new results more in keeping with other isotopic data for this period. We also present new stable carbon and nitrogen isotope results on human remains from the nearby Early Mesolithic sites of Badger Hole and Greylake, and report new Early Mesolithic radiocarbon dates and isotopic data from Cannington Park Quarry. Clear isotopic differences between the Early Mesolithic and the Neolithic remains can be seen, but these are argued to relate primarily to shifts in the underlying ecological baselines, rather than to differences in types of foods consumed (with the caveat that terrestrial wild and domesticated foods will be isotopically similar). The genetic data are summarised, giving evidence not only of the ancestry of Mesolithic and Neolithic individuals from Aveline's Hole, but also suggesting something of their physical appearance. The degree of population replacement now indicated by ancient DNA suggests that there was a substantial migration of farmers into Britain at the start of the Neolithic. This new information demonstrates the archaeological importance of Aveline's Hole for both the Mesolithic and Neolithic periods.

INTRODUCTION

Located near Burrington Combe on the northern edge of Somerset's Mendip Hills, Aveline's Hole (Figure 1) is Britain's largest and earliest known cemetery, previously shown to date to a relatively brief period within the Early Mesolithic, centring on ca. 8300 cal BC and spanning less than 200 years (Schulting, 2005). It thus has a position of some importance in British, and indeed European prehistory. The site is a natural cave in Carboniferous limestone. When first discovered in 1797, as many as 50 or more skeletons may have been present, but these were rapidly depleted as visitors removed specimens as souvenirs, leaving very few that can be attributed to nineteenth century collections, comprising a single calvarium ('O'), collected by Buckland before 1823, together with a mandible, three molars and an axis

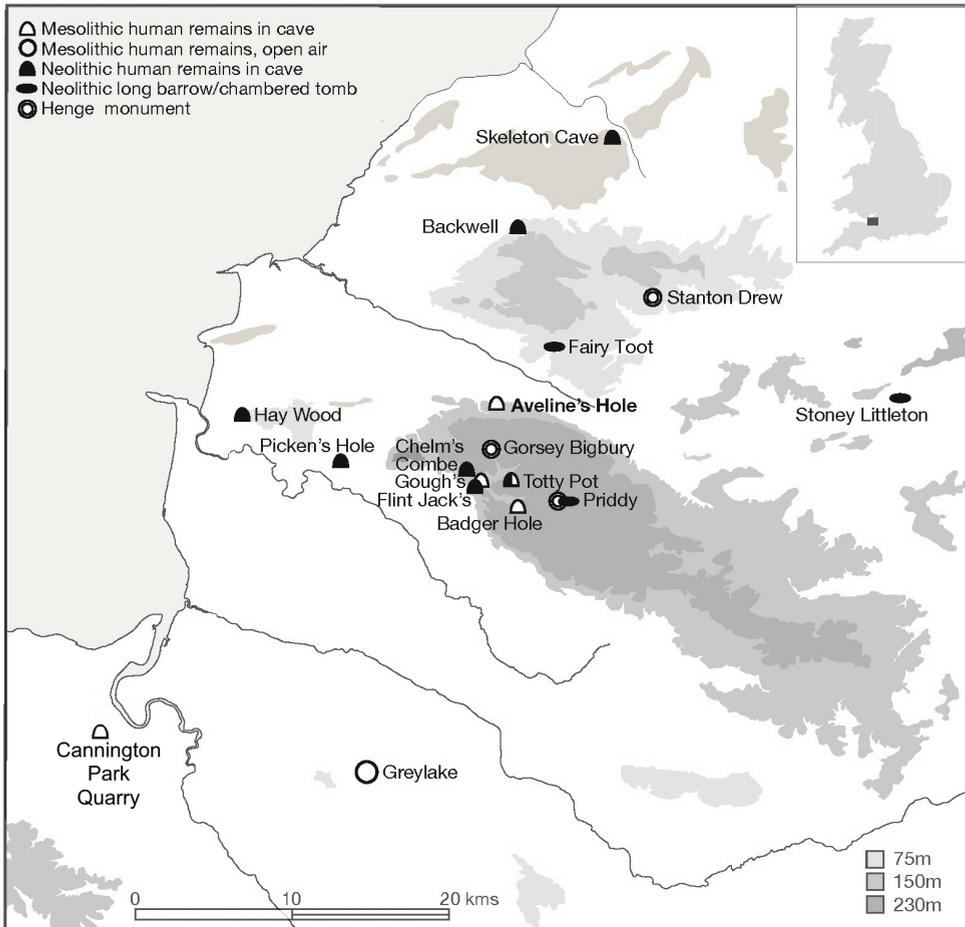


Figure 1. The study area showing locations of sites discussed in the text. Note that the location of the Early Mesolithic coastline would be substantially further away than shown here (cf. Schulting 2005, fig. 32).

collected by Richard Bright before 1840. A new series of excavations first by the Bristol Spelaeological Research Society and then by its successor the University of Bristol Spelaeological Society in the 1910s and 20s recovered a significant amount of incomplete and scattered human remains representing ca. 20 individuals, comprising material missed during antiquarian explorations.

Since the dating of the site plays a central role in the rationale for the present paper, we open with a brief synopsis. Aveline's Hole was long recognised as having evidence for Late Upper/Final Palaeolithic and Early Mesolithic occupation, based on recovered stone tools and reindeer remains (Jacobi, 2005). However, the human remains lacked clear association with diagnostic material culture that might indicate their age, although a Late Upper Palaeolithic date was posited on presumed association with the tools and fauna, together with the lack of pottery and metalwork (e.g. Fawcett, 1921, p. 82; Keith, 1924, p. 16). Two initial conventional

Table 1. *Previously published AMS dates and stable carbon and nitrogen data from Aveline's Hole (OxA- results from Hedges et al., 1987; GrA- results from Marshall and van der Plicht, 2005; recalibrated using OxCal 4.3 and IntCal13). Note that, as discussed below, the $\delta^{15}\text{N}$ measurements have been either replaced or retracted.*

Sample no.	Element	Lab code	^{14}C yr	\pm	cal BC (95%)		$\delta^{13}\text{C}\text{‰}$	$\delta^{15}\text{N}\text{‰}$
M1.14/99	L ulna	GrA-22558	9210	70	8606	8290	-19.6	6.9
M1.13/118	L ulna	GrA-22552	9200	50	8551	8296	-19.7	5.3
M1.13/301	L ulna	GrA-22548	9170	50	8543	8289	-19.8	7.8
M1.13/163	L ulna	GrA-22432	9155	45	8541	8284	-19.8	6.7
M1.13/302	L ulna	GrA-22621	9130	60	8541	8284	-19.7	6.2
M1.13/172	L ulna	GrA-22557	9120	50	8533	8281	-20.0	5.8
M1.13/160	L ulna	GrA-22429	9100	45	8537	8249	-19.8	7.1
M1.13/152	L ulna	GrA-22422	9095	45	8469	8248	-19.6	6.8
M1.13/164	L ulna	GrA-22433	9090	45	8444	8243	-19.1	6.5
M1.13/154	L ulna	GrA-22428	9075	45	8607	7982	-19.6	7.1
M1.13/166	L ulna	GrA-22546	9060	50	8436	8240	-21.6	7.7
M1.13/159	L ulna	GrA-22555	9020	50	8432	8236	-19.9	5.4
M1.13/144	L ulna	GrA-22605	8980	50	8423	8227	-21.0	5.7
M1.13/329	L ulna	GrA-22938	8960	50	8427	8208	-19.7	8.4
M1.13/161	L ulna	GrA-22431	8925	45	8307	7986	-19.4	7.8
M1.11/307	cranium, infant	GrA-22607	9180	50	8289	7970	-19.4	7.0
M1.13/300	L ulna	GrA-22547	9170	50	8280	7967	-20.2	6.1
M1.13/38	L ulna	GrA-22421	8890	45	8250	7960	-19.7	5.3
M1.13/23	R humerus	OxA-799	9100	100	8240	7842	-19.3	7.5
M1.13/24	R humerus	OxA-800	8860	100	8266	7678	-19.5	8.0
M1.13/146	R humerus	OxA-1070	8740	100	8203	7590	-18.7	8.7

radiocarbon dates were generated directly from human bone in the 1970s (Barker *et al.*, 1971; Burleigh, 1986; Tratman, 1977), followed by three AMS determinations on right humeri in the late 1980s (Hedges *et al.*, 1987). These confirmed an early Holocene assignment for between three and five individuals – the latter figure assuming no duplication of individuals in the dated elements. A more comprehensive dating programme was reported by Schulting and colleagues in 2005, with AMS determinations on 18 distinct individuals (Marshall and van der Plicht, 2005; Schulting, 2005), a figure close to the estimated minimum number of individuals surviving in the extant collection (there are an additional 1-2 infants, but these are represented by such small fragments that it was decided not to include them in the study). However, it is estimated that there were originally 50 or more individuals interred in the cave (Schulting, 2005). While it is likely that some of the five previous dates are on the same individuals as those in the 2005 study, it is nevertheless striking that all 23 dates on human bone from Aveline's Hole fall within a very restricted Early Mesolithic time period, modelled by Marshall and van der Plicht (2005, 228) as lying between 8460-8290 BC and 8260-8140 BC (95.4% probability) (Table 1). Furthermore, while there is evidence for earlier activity in the Final Upper Palaeolithic, the absence of evidence for any later activity suggests that access to the cave had been blocked, perhaps intentionally so (Jacobi, 1987; Schulting, 2005).

Thus, it was surprising when the initial results of an ancient DNA project focusing on Mesolithic and Neolithic Britain provided a clear indication not only of expected western European hunter-gatherer ancestry at Aveline's Hole, but also the presence of individuals with clear Early Neolithic farmer ancestry, no doubt from the adjacent mainland but ultimately of Aegean origin (Brace *et al.*, 2019). Initially only four samples yielded endogenous DNA, two long bones (a femur and tibia) and two cranial fragments (right temporal bones); intriguingly, the two long bones gave a hunter-gatherer ancestry while the two crania showed 'farmer' ancestry. The elements analysed were not the same as those that had been previously directly dated, so that the immediate course of action was to obtain AMS dates for these specimens. This confirmed an Early Mesolithic age for the long bones and an Early Neolithic date for the crania (Table 2), raising the question of whether the cranial fragments should be attributed to Aveline's Hole at all, or whether they could possibly derive from another collection held in the basement storage facility of the Bristol Spelaeological Research Society when the city was bombed in 1940.

Resolving the enigma

Two lines of inquiry then followed, the first a detailed examination of the collections held in the Society's museum at the time, and the second additional DNA analysis and AMS dating of temporal bones from distinct individuals. For the latter, at least some could be firmly attributed to the Bristol Spelaeological Research Society's excavations at Aveline's Hole in 1912-14, and those of the University of Bristol Spelaeological Society (UBSS), at various times between 1919 and 1931 (Buxton, 1925; Davies, 1921, 1922, 1923, 1925; Fawcett, 1921, 1925; Tratman, 1922, 1923, 1977). Attribution to these excavations derives from surviving catalogue numbers written directly on the elements, sometimes including context information in the form of Roman numerals (e.g., CXVII, see Schulting 2005, tab. 1). Importantly, the two temporal bones initially giving the 'farmer' ancestry lacked find numbers, though this was also the case for a significant proportion of the surviving collection, including four ulnae and a child's cranium previously dated directly to the Early Mesolithic (see Table 1). New find numbers, assigned during re-analysis of the collection published in Schulting 2005, are those starting at 300.

COLLECTION HISTORY

Linda Wilson and Graham Mullan

With the exception of a handful of specimens, detailed in Schulting (2005) and including the 'O' skull described below, the extant collection of human remains from Aveline's Hole derives from the excavations carried out in 1912-14 by the Bristol Speleological Research Society (BSRS) and in 1919-1931 by the UBSS (Donovan, 2017). This included three fairly complete adult specimens (discussed further below), along with fragments of perhaps eleven other crania. The lack of a final report after the cessation of work in 1930/1 means that we cannot now know the full extent of the collection. The collection suffered severe damage when the Society's museum was hit by a bomb during an air raid on Bristol in 1940. It is not known how much of the collection was destroyed, but it is certain that the three most complete crania, those described by Fawcett (1920, 1921) and Keith (1924), were on display and that all the display material was destroyed, along with all the relevant documentation. Davies (1923) mentions that Herbert Taylor was reconstructing skulls from 'the numerous fragments found in the area 65 to 85 feet from datum and excavated before and immediately after the War', adding that 'before long the measurements of five or six crania will be available.' No further mention of these reconstructions appears in the published record and it is not known whether this number includes the previously reported crania, but it is a reasonable presumption that if completed, the specimens would also have been on display before 1940 and thus destroyed. That said, it is possible that the partial reconstruction of 'Cranium 4' (M1.11.326) was one of those undertaken by Taylor, since old glue was noted along breaks during re-analysis in the early 2000s.

After 1945, it was found that, remarkably, the Society's museum store, located in a basement immediately beneath the destroyed museum, had survived relatively intact. It had been much affected by water, both in the immediate aftermath of the bombing and subsequently such that the cardboard storage boxes were in a very poor state, but most of the collection was still in much the same position as it had been before the bombing (D.T. Donovan, *pers comm*). This important fact meant that, despite the dearth of surviving documentation, it was possible to reconstruct the various parts of the collection. Much of the re-cataloguing of this material was undertaken by E.K. Tratman, with the help of various others, during the 1950s and 60s.

As noted above, the question arises as to whether any material from known Neolithic assemblages could have been intermixed during the recovery and re-cataloguing processes. The first thing to consider is what possible sources there might have been for Neolithic material. In the pre-1939 period, the Society had worked on a variety of sites, only three of which had yielded Neolithic human material. Of these, Kilgreany Cave, in Co. Waterford, Ireland, can be immediately discounted as the finds did not come to Bristol and are housed in the National Museum of Ireland in Dublin (M. Dowd, *pers comm*). Within Mendip itself, the excavation of Priddy Long Barrow was carried out in 1928 (Phillips and Taylor, 1972). The report describes only a few finds of human bone: two molars, part of the shaft of a humerus, part of either a radius or ulna and a fragment of a mandible. Lewis (2002) notes that, unlike a further 100 small fragments, these were not described as burnt. However, for the purposes of the current paper, it is sufficient to note that no cranial fragments were found. The third and potentially most significant site was Backwell Cave. This site was excavated in 1936-37 and reported on by Tratman and J.W. Jackson in 1938 (Tratman 1938). Significant quantities of human bone were recovered and a ^{14}C date of 4150 ± 40 BP (BM-3099) was obtained on a vertebra by Alison Roberts in 2003 (Ambers and Bowman, 2003). The material from this site was also re-catalogued post-1945 and the significant fact is that the catalogued material closely resembles that described by

Tratman in 1938, with the exception of two ‘fairly complete skulls’ which, as with those from Aveline’s, were on display in the museum and thus destroyed (Donovan, 1951).

It is a reasonable contention, therefore, that there was no admixture of Neolithic cranial material into the Aveline’s Hole collection after it was received into the UBSS Museum.

AMS RADIOCARBON DATING

Rick Schulting

The new programme of sampling for radiocarbon dating at Aveline’s Hole focussed on the temporal bone, since the associated petrous portion of the temporal has been shown to have particularly high yields of endogenous DNA (Pinhasi *et al.*, 2015), thus facilitating any future analyses. Sample preparation and measurement followed the standard protocols in place at the Oxford Radiocarbon Accelerator Unit, which include a 30kDa ultrafiltration step (Brock *et al.*, 2010). Ten new samples were selected (i.e., in addition to the four mentioned above), with all but two deriving from the right temporal and so representing distinct individuals. The remaining samples comprise what seemed to be a more heavily mineralised parietal bone fragment, and a left temporal, chosen as a specimen firmly attributed to the early twentieth century UBSS excavations, joining two right temporals that could be similarly attributed. Four of the right temporals had 300 numbers, the remainder having original UBSS numbers. All the latter should be attributable to the UBSS excavations, though the abovementioned three with specific context details provide the most secure associations.

The results confirm the presence of both Early Mesolithic and Early Neolithic individuals (Table 2), with no intervening or – with one exception – later individuals. The exception, right temporal M1.11.332, yielded a recent date of 355 ± 26 BP (OxA-35924), closely matching that previously obtained on the stalagmite-encrusted ‘AH9’ skull held in the Wells and Mendip Museum (307 ± 25 BP; OxA-19839). The two determinations can be successfully combined using OxCal’s *R_Combine* function (Bronk Ramsey, 2013), to AD 1488-1650 (330 ± 19 BP, χ^2 test, $T=1.8(5\%, 3.8)$). However, as discussed by Meiklejohn *et al.* (2012), the provenance of AH9 is unknown. What is certain is that the right temporal does belong to AH9, since a 1957 photograph clearly shows it in place (compare figs. 4 and 5 in Meiklejohn *et al.*, 2012). It must have subsequently become loose and then placed with the rest of the Aveline’s Hole collection to which it was assumed to belong. We do not deal with AH9 further here, as it has been treated in detail elsewhere (Meiklejohn *et al.*, 2012). The seemingly more heavily mineralised parietal bone sample yielded an Early Neolithic date.

Interestingly, the selected temporal bones with pre-300 numbers, including the three with more detailed context information, all yielded Early Mesolithic dates, while those with new 300 finds numbers gave Early Neolithic dates (Table 2). Nevertheless, as noted above, five previously dated samples with 300 numbers gave Early Mesolithic dates, so that the division seen in the new results is presumably a coincidence, albeit a statistically improbable one.

In the absence of any stratigraphic relationships, the Early Mesolithic and Early Neolithic dates are considered as separate, uniform, phases of activity for Bayesian modelling (Buck *et al.*, 1996; Bronk Ramsey, 2009). Agreement indices are used firstly to assess the model overall, and secondly to assess the fit of individual dates within the proposed model. In both cases, their value should be above 60, though individual determinations may have indices slightly below this and still not invalidate the model as a whole (see discussion in Bayliss *et al.*, 2007). Such individual results are then treated on a case-by-case basis, depending on the degree to which they fall below 60. They may be retained or removed and the model re-run. All results

below are reported at 95.4% confidence unless otherwise noted. Following accepted convention, modelled dates are presented in italics and as ‘BC’ rather than ‘cal BC’, since the date ranges are no longer based entirely on the calibration curve.

Table 2. *New AMS determinations from Aveline’s Hole (excluding OxA-35924 – see text). Calibrated in OxCal 4.3 (Bronk Ramsey, 2013) using IntCal13 (Reimer et al., 2013).*

<i>Sample no.</i>	<i>Element</i>	<i>Lab code</i>	^{14}C yr	\pm	<i>cal BC (95%)</i>		$\delta^{13}\text{C}\%$	$\delta^{15}\text{N}\%$	<i>C:N</i>
M1.15.3	femur, R	OxA-34338	9340	50	8750	8459	-19.9	8.3	3.2
M1.14.55	tibia	OxA-34339	9230	50	8596	8302	-19.3	9.2	3.2
M1.11.111	temporal, R	OxA-35053	9220	40	8552	8309	-19.6	8.2	3.2
M1.11.220	temporal, R	OxA-35930	9185	40	8537	8295	-19.4	9.2	3.2
M1.11.141	petrous, L	OxA-35925	9185	45	8542	8293	-19.9	8.8	3.2
M1.11.141B	temporal, R	OxA-34972	9145	45	8351	8276	-19.1	9.8	3.2
M1.11.2	temporal, R	OxA-34971	9125	45	8462	8257	-18.3	10.7	3.2
M1.11.308	temporal, R	OxA-35922	4958	33	3797	3655	-21.3	9.0	3.2
M1.11.325	petrous, R	OxA-34336	4934	35	3780	3650	-21.5	8.9	3.2
M1.11.309	petrous, R	OxA-34337	4906	33	3763	3640	-20.9	9.9	3.2
M1.11.322	petrous, R	OxA-35923	4893	31	3759	3637	-21.0	8.8	3.2
M1.11.326	cranium	UBA-30800	4809	45	3695	3384	-21.0	9.0	3.2
M1.11.315	parietal	OxA-34973	4643	33	3517	3360	-21.0	11.0	3.2

The seven new Early Mesolithic results form a consistent series, except for the earliest result, 8750-8459 cal BC (OxA-34338: 9340 ± 50 BP), with a low index of agreement (33.8). This precedes the earliest of the remaining six determinations by approximately a century. That said, there is no clear reason to exclude it from the model, i.e., all quality control indicators (C to N ratios, collagen yield, %C and %N) were within accepted ranges for the dated collagen (DeNiro, 1985; van Klinken, 1999), and there is no indication of significant contribution of marine or freshwater fish, which might introduce an ‘old carbon’ reservoir offset. Thus, it is either simply a statistical outlier, or it does represent one of the earliest Mesolithic burials at the site. Based solely on the new results, and retaining the early outlier, the start date for deposition of human remains at Aveline’s Hole is modelled as the range *8660-8335 BC*, ending *8450-8205 BC*, spanning *0-425 years*, or *0-210 years* at 68.2% confidence (Figure 2). While the model includes the possibility of a single deposition episode (i.e., a span of ‘0’), the unmodelled results narrowly fail the R_combine test in OxCal v4.3 (χ^2 test, T=13.1(5%, 12.6)), suggesting that it is more likely that deposition occurred over a somewhat longer period, though one still

relatively tightly constrained (as opposed to deposition over half a millennium or more). However, this could be entirely due to the early outlier (OxA-34338), removal of which does allow the remaining five results to be successfully combined to 8455–8305 cal BC (9182 ± 18 BP, χ^2 test, $T=4.1(5\% 11.1)$).

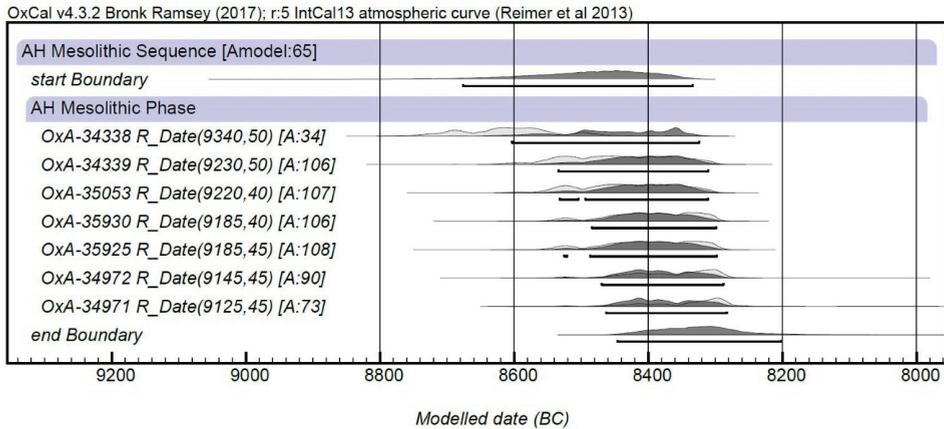


Figure 2. Bayesian model for the new Early Mesolithic AMS ^{14}C determinations. Note that the index of agreement for OxA-34338 is less than 60, suggesting that this determination does not fit well within the same phase of activity as the others, i.e., it is either a statistical outlier or an earlier burial.

It is noteworthy that the seven new Early Mesolithic determinations – two on postcrania, the remaining five on cranial elements – are, as a group, earlier by ca. 120 ^{14}C years than those previously published (Marshall and van der Plicht 2005). Specifically, the new results average 9204 ± 71 compared to 9085 ± 96 ^{14}C years, excluding the three dated humeri, which may duplicate individuals represented by the ulnae (Figure 3). This difference could be the result of the use of 30kDa ultrafilters at Oxford, which are intended to remove small molecular weight contaminants, generally of more recent age (Brock *et al.*, 2010; 2013). While suggestive, this comparison is not straightforward, since the new postcranial and cranial results may refer to some of the same individuals, and so should not be considered in a comparison with other results on distinct individuals. It is also possible that the dated temporal bones only represent four individuals, since a left temporal was selected alongside the four right temporals. Nevertheless, the new results raise the possibility that Early Mesolithic burial at Aveline’s Hole may be earlier by a century or so than previously proposed, centring on ca. 8400 rather than ca. 8300 cal BC (Figure 4).

The Neolithic dates span the period ca. 3750 to 3470 cal BC. A Bayesian model assuming a single uniform phase of activity places the start of Neolithic ‘burial’ in the cave in the range 3935–3665 BC, ending 3630–3275 BC (Figure 5). The model has an acceptable index of agreement ($A_{\text{model}} = 89$), and all individual dates have indices above 60. The range is exaggerated by the relatively small number (six) of determinations in the model, such that the 68.2% confidence interval may be more realistic, placing the start of activity at 3800–3690 BC, ending 3625–3395 BC, spanning 80–410 years. Thus, accepting the crania are indeed all from Aveline’s Hole, as argued above, the cave must have been entered on a number of occasions for

deposition of human remains, specifically crania (or skulls? – the important distinction being that the skull comprises mandible and cranium together, implying either a fleshed head, or intentional retention or recovery of both elements following disarticulation).

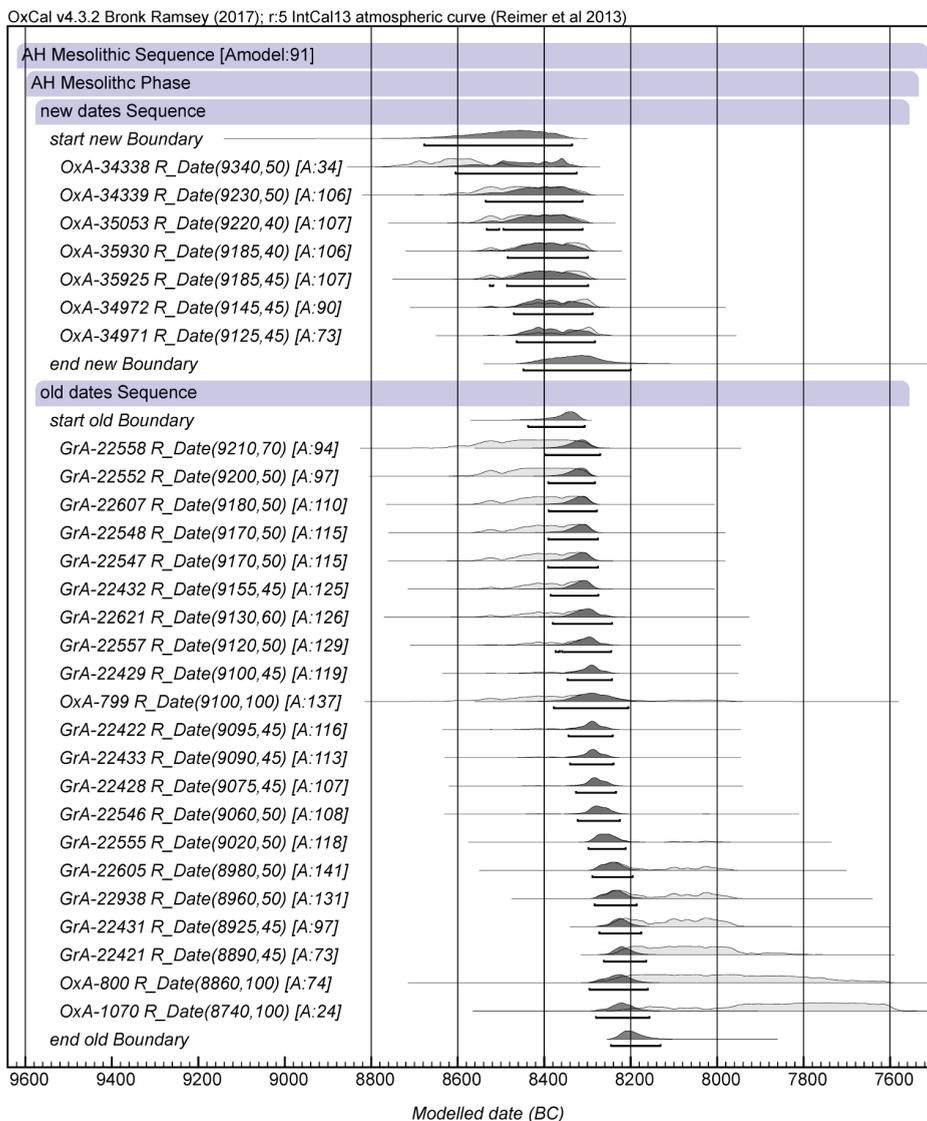


Figure 3. Bayesian model comparing the new and previous AMS ¹⁴C determinations from Aveline's Hole. Note that individual determinations OxA-34338 and OxA-1070 have low agreement indices but have been retained in the model.

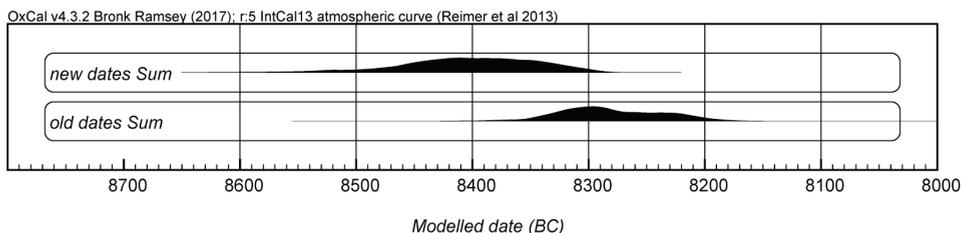


Figure 4. Summed probability distributions for the new and previously published Early Mesolithic dates from Aveline's Hole. Note that this is for heuristic purposes only, since the new dates may include repeat sampling of different elements from some individuals (invalidating the model, which assumes that determinations are independent of one another), though this is considered unlikely given the number of individuals represented.

With two exceptions, all the dated human remains from Aveline's Hole derive from the UBSS excavations. One exception has already been mentioned above – the temporal belonging to AH9 that was mistakenly incorporated into the UBSS collection, though the remainder of the skull is held at the Wells and Mendip Museum. The second exception is AH1, Skull 'O' (NHM PA SK 3107), recovered in the nineteenth century and currently held in the Natural History Museum, London (see below). Stalagmite inside the cranium yielded a date of 7305-6835 cal BC (GrN-5393: 8100 ± 50 BP), ostensibly providing a *terminus ante quem* for the specimen, which, following the remaining Early Mesolithic dates from the site, is likely to be a millennium earlier. However, there is the possibility of an unknown reservoir effect when radiocarbon dating calcium carbonate, so that in fact the date might be too old (Philippsen, 2013). While some uncertainty surrounds the provenance of skull 'O', including its date of recovery, its assignment to Aveline's Hole is probably correct (Buxton, 1925; Keith, 1924). The bone itself has not been radiocarbon dated, but is currently undergoing ancient DNA analysis.

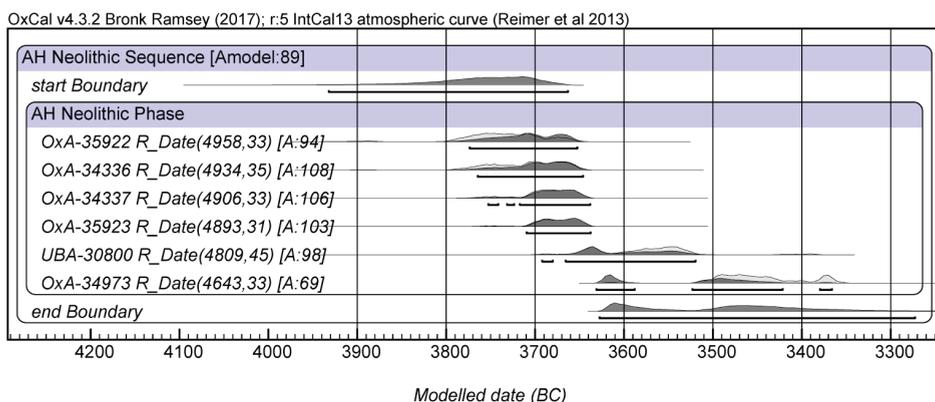


Figure 5. Bayesian model for the Early Neolithic results from Aveline's Hole..

By the time of the early twentieth century excavations, all human skeletal remains visible on the cave's surface had long been removed. Within 20 years of discovery, Reverend John Skinner noted the loss of skeletal material to visitors (Skinner 1820, p. 33). This is confirmed by an unpublished letter by Henry Thomas Aveline – the brother of William Talbot Aveline, after whom the cave was named by William Boyd Dawkins – dating to 1843, by which time no human remains were visible (Boycott and Wilson, 2012). Yet material excavated by the UBSS - which should have been stratigraphically lower than that removed in the nineteenth century - includes both Early Mesolithic and Early Neolithic human remains. How is this to be explained? Unfortunately, we have no radiocarbon determinations from material pre-dating the UBSS excavations; AH1, skull 'O', potentially fulfills this brief, but as noted above it has not yet been directly dated. Given the constrained date range of the Early Mesolithic human remains, it is unlikely that the cave was used for burial for more than a couple of centuries at most, until revisited in the Early Neolithic, when deposition again lasted over a few centuries. But it is unlikely that the human remains ever had significant stratigraphic integrity. Rather, they were probably originally horizontally distributed and became vertically displaced as disarticulated elements and fragments fell into small gaps between stones on the cave floor. There is some evidence for rodent and carnivore gnawing on human bones, so that this could be another contributing factor in the dispersal of the remains (Schulting 2005, p. 190). There is also the attested early nineteenth century attempt by a local rector to prevent the removal of skeletal remains, by having 'several cartfulls of earth thrown over the bones in order to bury them' (Skinner, 1824, p. 128). Between them, these processes are probably sufficient to account for the recovery of both Mesolithic and Neolithic human remains by the early twentieth century UBSS excavations.

STABLE CARBON AND NITROGEN ISOTOPE ANALYSIS

Rick Schulting, Chelsea Budd, Hans van der Plicht and Sophy Charlton

The main aims of this section are to address an issue that has arisen with the originally stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope measurements reported in Schulting (2005), and to discuss the new Mesolithic and Neolithic isotopic values from Aveline's Hole as well as on Early Mesolithic individuals from Badger Hole and Greylake.

Sample preparation in the Oxford stable isotope laboratory follows a modified Longin (1971) method (cf. Richards and Hedges, 1999) in which ca. 500mg of bone is demineralised in 0.5M HCl at 4°C followed by rinses in ultrapure MilliQ water. Unless there is a dark colouration in the sample at this point, suggesting the presence of humic contaminants, no NaOH step is applied. A pH3 solution is added and the samples are heated for ca. 48 hours at 75°C, then rinsed and filtered through an Ezee filter before being freeze-dried. Those samples subjected to the new round of radiocarbon dating at Oxford reported in this paper were subjected to an NaOH wash as standard practice, and underwent an additional 30kDa ultrafiltration step before freeze-drying (Brock *et al.* 2010), with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements made using the same collagen. IN both cases, approximately 1mg of the resulting 'collagen' was weighed into tin capsules along with alanine standards for measurement on a Sercon 20/22 continuous flow dual inlet mass spectrometer. Results are reported relative to the internationally defined standards of VPDB for $\delta^{13}\text{C}$ and AIR for $\delta^{15}\text{N}$. Shapiro-Wilk tests are used to assess whether or not the data depart significantly from a normal distribution, and parametric (Student's t-test; paired t-test) or

non-parametric (Mann-Whitney U test; Wilcoxon test for matched pairs) statistical tests are then applied as appropriate.

In a temperate C_3 environment, such as that of Britain, $\delta^{13}C$ distinguishes between use of marine and terrestrial foods, while $\delta^{15}N$ primarily reflects trophic level. As Aveline's Hole is located far from its contemporary coastline, we would not expect to see use of marine resources, as confirmed by previously published isotopic data, which clearly contrasted results from Aveline's Hole with those from Mesolithic sites nearer the coast in South Wales (Schulting, 2009). What is immediately apparent in the new dataset, however, is that Early Mesolithic $\delta^{13}C$ values are on average ($-19.4 \pm 0.6\text{‰}$, $n = 7$) slightly but significantly higher than Early Neolithic values ($-21.1 \pm 0.2\text{‰}$, $n = 6$; heteroscedastic t-test, $t = 7.61$, $p < 0.001$) (Figure 6). This remains the case even when the Early Mesolithic dataset is restricted to the four right temporals that must represent distinct individuals ($t = 6.74$, $p = 0.003$). There is no corresponding difference in $\delta^{15}N$ values between Early Mesolithic ($9.2 \pm 0.9\text{‰}$, $n = 7$) and Early Neolithic ($9.4 \pm 0.9\text{‰}$, $n = 6$) (homoscedastic t-test, $t = 0.54$, $p = 0.600$). The lack of positive correlation between the $\delta^{13}C$ and $\delta^{15}N$ values (cf. Richards and Hedges, 1999), together with the site's distance from the coast, means that greater consumption of marine foods cannot explain the higher $\delta^{13}C$ values seen in the Early Mesolithic group. Instead, their observed ^{13}C enrichment is in keeping with that documented for the Late Glacial Maximum, but also extending into the Early Holocene, interpreted as either a consequence of more open vegetation or of changing concentrations of atmospheric CO_2 , affecting ^{13}C discrimination in plants, or a combination of both (Drucker *et al.* 2003; Hare *et al.*, 2018; Hedges *et al.* 2004; Stevens and Hedges 2004).

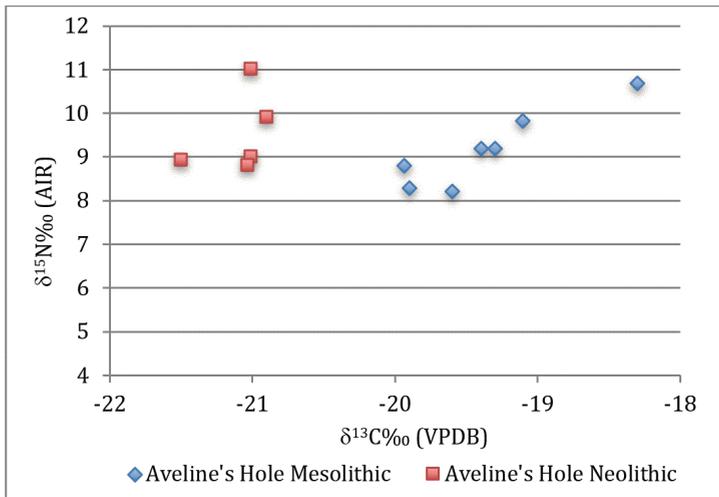


Figure 6. New stable carbon and nitrogen isotope results from Aveline's Hole.

While the new $\delta^{13}C$ results are broadly comparable ($-19.4 \pm 0.6\text{‰}$ vs. $-19.9 \pm 0.6\text{‰}$), there is a significant divergence between the new $\delta^{15}N$ results and those for the Early Mesolithic previously reported in Marshall and van der Plicht (2005) and discussed by Schulting (2005). These measurements were made at Groningen on the same collagen used for AMS dating. While it was noted at the time that the $\delta^{15}N$ mean of $6.6 \pm 0.9\text{‰}$ was unexpectedly low, it was

consistent with (i.e., significantly higher than) the small number of faunal measurements from the site, and with studies indicating that faunal $\delta^{15}\text{N}$ values in the Late Glacial and Early Holocene were lower compared to subsequent periods (Drucker *et al.* 2003; Hedges *et al.* 2004; Stevens and Hedges 2004). However, accumulating isotopic data across western Europe following this study raised questions concerning the published results for Aveline's Hole and led to reanalysis at Oxford in 2013 of a sub-set ($n = 12$) of the same ulnae originally measured (not all were re-analysed due to the small size of a number of the dated specimens). While the $\delta^{13}\text{C}$ results – measured in triplicate but without the two-point calibration that is now standard – were broadly comparable (old mean of $-19.8 \pm 0.6\text{‰}$ vs. new mean of $-19.5 \pm 0.3\text{‰}$), the $\delta^{15}\text{N}$ results were consistently higher than the previously reported $6.6 \pm 0.9\text{‰}$, averaging $8.3 \pm 0.7\text{‰}$ (paired t-test, $t = 5.01$, $p = <0.001$). This finding led to discussions with the Groningen laboratory where the original measurements were made, and to reanalysis there of a sub-set of 10 samples. Similar results were obtained, in that there was little difference in $\delta^{13}\text{C}$, while the new $\delta^{15}\text{N}$ average of $8.7 \pm 0.6\text{‰}$ was again substantially higher than that originally obtained (paired t-test, $t = 6.03$, $p < 0.001$). Eight of the same samples were successfully re-analysed at both laboratories, with no statistically significant differences seen in either $\delta^{13}\text{C}$ (Wilcoxon test for matched pairs, $Z = 1.12$, $p = 0.262$) or $\delta^{15}\text{N}$ (Student's paired t-test, $t = 1.96$, $p = 0.090$). This re-analysis highlights the fact that, despite being calibrated to international standards, differences in instrumentation and more importantly in sample preparation can lead to inter- and even intra-laboratory differences in stable isotope measurements (Jørkov *et al.* 2007; Pestle *et al.*, 2014).

Since both of the new datasets included some marginal C:N values (especially those above 3.4), the final isotopic dataset for the ulnae is based on measurements with C:N values closest to that expected for *in vivo* collagen, 3.1 (Matthew Collins, *pers comm*, 2017). The exception to this is the sample from specimen M1.13/144, analysed in triplicate at Groningen. Two of the runs gave unacceptably high C:N values of 4.6, combined with unusually low $\delta^{13}\text{C}$ values for this site, of less than -21‰ (though they were not atypical for $\delta^{15}\text{N}$). While the third run had an acceptable C:N value of 3.2, its $\delta^{13}\text{C}$ value was similarly unusually low at -21.9‰ . This is more than four standard deviations from the mean of the remaining 14 samples, and so has been excluded from the analysis. All the previously published $\delta^{15}\text{N}$ results for Aveline's Hole, including those on both humans and fauna, are hence retracted and replaced with the new results (Table 3). There are no grounds to discount the originally published $\delta^{13}\text{C}$ values, and so they are still considered as acceptable, although the new averaged results are preferred where available. Finally, it is worth noting that the seven new Early Mesolithic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements do not differ significantly as a group from the re-analysed results reported here for the postcrania ($\delta^{13}\text{C}$: Mann=Whitney U test, $Z = 0.746$, $p = 0.456$; $\delta^{15}\text{N}$: Student's t-test, $t = 1.27$, $p = 0.218$). However, they cannot be assumed to be distinct individuals as some cranial and postcranial remains may refer to the same individuals (note that this would invalidate the statistical test, which assumes that the measurements are independent).

In addition to re-running previously analysed samples from Aveline's Hole, stable isotope measurements were also made on three samples, representing at least two individuals, from an open-air Early Mesolithic site at Greylake (Brunning and Firth, 2012; Bulleid and Jackson, 1937; Gray, 1928). Two of the three specimens already had associated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the Waikato laboratory where they had been radiocarbon dated (Brunning, 2013). These were re-analysed at Oxford to ensure a robust comparison with the Aveline's Hole dataset. The results are similar, with the exception of a 1‰ difference between the $\delta^{13}\text{C}$ values for cranium E23 (Table 4). For consistency, the Oxford values are used in the discussion section below.

Table 3. Comparison of stable carbon and nitrogen isotope on a subset of the 2005 dataset ($n = 14$; all are adult or adolescent left ulnae), highlighting the difference in $\delta^{15}\text{N}$ values. The 'Laboratory' column refers to which laboratory's measurements yielded C:N values closest to 3.1 and hence are preferred. Values in italics indicate samples only measured at the laboratory indicated.

Specimen no.	Groningen 2005			new results			Laboratory
	$\delta^{13}\text{C}\text{‰}$	$\delta^{15}\text{N}\text{‰}$	C:N	$\delta^{13}\text{C}\text{‰}$	$\delta^{15}\text{N}\text{‰}$	C:N	
M1.14/99	-19.6	6.9	3.4	-20.0	9.0	3.5	Groningen
M1.13/118	-19.7	5.3	2.9	-19.3	9.2	3.0	Groningen
M1.13/301	-19.8	7.8	3.2	-20.0	7.7	3.4	Oxford
M1.13/163	-19.8	6.7	3.2	-19.9	8.4	3.4	Groningen
M1.13/302	-19.7	6.2	3.3	-19.0	10.3	3.0	Groningen
M1.13/172	-20.0	5.8	2.9	-19.8	8.1	3.4	Groningen
M1.13/160	-19.8	7.1	3.2	<i>-19.5</i>	8.8	3.4	Oxford
M1.13/152	-19.6	6.8	2.9	-19.3	9.0	3.3	Groningen
M1.13/164	-19.1	6.5	3.2	-19.1	8.2	3.4	Oxford
M1.13/154	-19.6	7.1	3.1	-19.6	9.3	3.5	Groningen
M1.13/166	-21.6	7.7	3.8	<i>-21.0</i>	8.5	3.1	Groningen
M1.13/159	-19.9	5.4	3.0	<i>-19.3</i>	8.4	3.3	Oxford
M1.13/329	-19.7	8.4	3.1	<i>-19.4</i>	8.7	3.3	Oxford
M1.13/161	-19.4	7.8	2.9	<i>-19.4</i>	9.0	3.4	Oxford
average =	-19.9	6.7	3.2	-19.6	8.7	3.3	
standard dev =	0.6	0.9	0.3	0.5	0.6	0.2	

As part of the wider DNA study in which Aveline's Hole featured (Brace *et al.*, 2018), new stable isotope analyses were undertaken on the two children's mandibles from Badger Hole, located on the slopes above Wookey Hole and ca. 10 km south of Aveline's Hole. The partial remains of two children, aged ca. 9 years (BH1) and ca. 5 years (BH2), and the frontal bone of what might be a third individual, were recovered from the site during excavations in the 1930s and 1940s (Balch, 1947, 80; Oakley *et al.*, 1971, p. 19-20), with their mandibles subsequently directly dated to approximately the same period as Aveline's Hole (Burleigh, 1986; Hedges *et al.*, 1989) (Table 5), making it one of the few Early Mesolithic British sites with human remains. The frontal bone, designated Badger Hole 3, has been lost but is assumed to also be Mesolithic in date (note that the published date of 1380 ± 70 BP (OxA-680) originally

attributed to BH3 is actually on cranial elements found in another location in the cave, and higher in the stratigraphy – Hedges *et al.*, 1991, p. 283). Stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was undertaken on the dated mandibles that were also sampled for aDNA analysis. Unfortunately, preservation of ancient DNA was poor and provided no useable information (see Table 6).

Table 4. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for Greylake. See Table 9 for associated ^{14}C dates.

Specimen	Element	Age	Waikato			Oxford		
			$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C:N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C:N
E22	cranium	adult	-19.4	9.1	3.4	-19.3	8.7	3.4
E23	cranium	adult	-20.4	9.6	3.4	-19.3	9.2	3.3
E22/23?	mandible	adult	–	–	–	-19.1	9.1	3.2

Badger Hole stable carbon and nitrogen isotope analysis (Sophy Charlton)

Stable isotope analysis followed a modified Longin collagen extraction protocol using ultrafiltration (Brown *et al.*, 1988; Charlton *et al.*, 2016). Briefly, ca. 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) 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‰ (1 σ) for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Both individuals yielded sufficient amounts of collagen for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis, and collagen quality fell within the prescribed range (DeNiro, 1985; van Klinken, 1999). Stable isotope values are presented here relative to the internationally defined standards of VPDB for $\delta^{13}\text{C}$ and AIR for $\delta^{15}\text{N}$ (Table 5). Collagen yields were calculated from retentate samples only, following ultrafiltration.

Table 5. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for Badger Hole. See Table 9 for associated ^{14}C dates.

Specimen	Element	Age	% collagen	$\delta^{13}\text{C}$ ‰	$\delta^{15}\text{N}$ ‰	C:N
BH1	mandible	child, ca. 9 yr	6.9	-20.3	8.5	3.5
BH2	mandible	child, ca. 5 yr	2.9	-20.5	9.6	3.4

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the Badger Hole individuals are similar to those from Aveline’s Hole, both being consistent with a diet based on C_3 plants and terrestrial resources, with no detectable contribution of marine protein to the diet, in keeping with distance from the contemporaneous shoreline, which was more distant than nowadays. The two Badger Hole individuals are slightly less ^{13}C -enriched than Aveline’s Hole, averaging -20.4‰ versus

-19.6‰. Unfortunately, no faunal material was available for analysis from Badger Hole, precluding a more detailed interpretation of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data.

ANCIENT DNA

Tom Booth, Selina Brace, Yoan Diekmann, Mark G. Thomas and Ian Barnes

Over the last decade, the application of Next Generation Sequencing (NGS) technology to ancient human remains has enabled the recovery of genomic data (DNA sequences distributed across all 23 pairs of chromosome and the mitochondrial genome) typically consisting of thousands to millions of short DNA sequences (Skoglund *et al.*, 2014). While these data can be used to determine sex, and close familial relationships, they have been perhaps most important in enabling inference of an individual's ancestry, as well as population affinities and population history including admixture events. These data can be used to make robust assessments of longer-term population history, by considering a single genome to be a sample of diversity within the broader population (Li and Durbin, 2011).

Analysis of ancient human genomes from Mesolithic western Europe has identified that all belong to a specific genetic cluster termed 'Western European Hunter-Gatherers' (WHGs; Fu *et al.*, 2016; Gamba *et al.*, 2014; Haak *et al.*, 2015; Lazaridis *et al.*, 2014; Olalde *et al.*, 2015; Skoglund and Mathieson, 2018; Skoglund *et al.*, 2014). This WHG genetic cluster lies outside the range of modern European genetic diversity due to a series of subsequent prehistoric demographic transformations. WHGs arrive in Europe ~12500 BC and largely replace the local hunter-gatherers that had occupied Europe since the retreat of the northern glaciers ca. 18000 BC (the so-called 'El Miron' cluster – Fu *et al.*, 2016). The geographic origin of this movement of WHGs is still uncertain, but is likely to have been southeast Europe, or possibly the Near East. Analysis of genetic variants in WHG individuals that are associated with pigmentation in modern human populations has indicated that WHGs lack two major alleles associated with lighter skin pigmentation in Europe, suggesting that they are likely to have had relatively dark skin (Brace *et al.*, 2019; Mathieson *et al.*, 2015; Olalde *et al.*, 2014; Skoglund and Mathieson, 2018). Two (Cheddar Man from Gough's Cave, and a skeleton from La Braña, northern Spain) are predicted to have had 'dark'-'dark to black skin', while a third (from Loschbour, Luxembourg) is predicted to have had 'intermediate' skin pigmentation (colloquially 'olive-skinned') (Brace *et al.*, 2019). However, perhaps surprisingly, most WHGs carry a genetic variant associated with lighter eye pigmentation, meaning their eye colour probably varied from blue, green or hazel (Mathieson *et al.*, 2015; Olalde *et al.*, 2014).

In most areas of Europe that have been studied, the genetic signatures of local populations changes considerably with the arrival of Neolithic farming cultures, suggesting that the Neolithic transition across Europe was largely driven by human migration rather than by the spread of ideas (Cassidy *et al.*, 2015; Gamba *et al.*, 2014; Haak *et al.*, 2015; Lazaridis *et al.*, 2014; Mathieson *et al.*, 2018; Olalde *et al.*, 2014; Olalde *et al.*, 2015; Skoglund *et al.*, 2014; Skoglund and Mathieson, 2018). The new ancestry accompanying the spread of the European Neolithic originated around the Aegean from a genetic cluster termed 'Aegean Neolithic Farmers' (ANF; Broushaki *et al.*, 2016; Hofmanová *et al.*, 2016; Kilinç *et al.*, 2016; Lazaridis *et al.*, 2016). ANF and WHG populations are likely to have been isolated from one another for tens of thousands of years, and subsequently are genetically highly divergent. There are similar levels of genetic divergence between ANF and WHG populations as there are between modern populations living in Europe and East Asia (Günther and Jakobsson, 2016). Thus, the change in ancestry across Europe that accompanied the spread of Neolithic cultures was substantial and,

importantly, identifiable from even relatively poor coverage ancient genomes. Populations carrying ANF ancestry took two routes through Europe; one along the Mediterranean, and another travelling northwest into Central Europe (the ‘Danubian route’), seeding geographically and genetically distinct groups of European Neolithic populations (Haak *et al.*, 2015; Olalde *et al.*, 2015).

Admixture between Neolithic farmers and local hunter-gatherer occurred in all areas of Europe that have been studied, meaning that Neolithic farmers have variable levels of WHG ancestry (González-Fortes *et al.*, 2017; Lipson *et al.*, 2017; Mathieson *et al.*, 2018). Sometimes significant admixture between the two groups does not occur until a few centuries to millennia after Neolithic farmers first arrive, possibly because they initially maintained cultural and genetic boundaries (Bollongino, *et al.*, 2013). But even after mixing, the genetic ancestry component of local hunter-gatherers is substantially smaller than that of the incoming groups, possibly because of disparities in population sizes. Episodic local admixture events are cumulative with respect to WHG ancestry, meaning that, as might be expected, Neolithic European populations farthest from the Aegean source of migrating farmers show the highest levels of WHG ancestry (Cassidy *et al.*, 2015; Olalde *et al.*, 2015). One of the two main genetic variants associated with lighter skin pigmentation in modern Europeans is fixed in ANF populations, while the other is at low frequency (Mathieson *et al.* 2015). Therefore, while skin pigmentation in ANF populations is likely to have been variable, broadly it would have been ‘intermediate’. ANF populations also carry genetic variants linked to brown eyes and dark hair in relatively high frequencies.

Human remains from Aveline’s Hole and surrounding sites were sampled for DNA as part of a Wellcome-funded project investigating adaptation and migration in Britain over the last ca.10000 years. Most of the Mesolithic and Neolithic results, including some from Aveline’s Hole and other Mendip sites have been published in Brace *et al.* (2019). This study concluded that populations living in Britain during the Mesolithic belonged to the WHG group, with no remnant of the preceding Palaeolithic El Miron cluster, confirming that the population movements from southeast Europe and/or the Near East ca.12500 BC extended to the north-western periphery of Europe. Thus far, all individuals from Britain who lived after ca. 4000 BC (the beginning of the British Neolithic) show substantial ANF ancestry, indicating that the appearance of Neolithic cultures in Britain is associated with the movement of people from mainland Europe and a large-scale replacement of the local population (Brace *et al.*, 2018). In addition, it seems that the British Neolithic population derives mainly from the Mediterranean population dispersal, with only a minor component of their ancestry coming from the Danubian route. This suggests that Neolithic British populations were descended from groups who had moved north from Iberia or southern France, mixed minimally with groups to the north carrying Danubian Neolithic ancestry before moving into Britain from of western Europe.

Aveline’s Hole aDNA results

DNA was extracted and NGS libraries were built from approximately 50 milligrams of powder sampled from thirteen human bones and teeth from Aveline’s Hole using the methods outlined in Brace *et al.* (2019) as part of a Wellcome Trust-funded project at the Natural History Museum. NGS technology involves sequencing a random selection of the DNA present in a sample (shotgun sequencing). However, the majority of DNA sequences found in ancient human bone tend to come from microorganisms which colonise the bone post-mortem. In samples with low percentages of ancient human DNA (endogenous DNA) it becomes very difficult to obtain the requisite amount of data from a sample through shotgun sequencing. The

petrous portion of the temporal bone consistently exhibits high endogenous content much more often than any other bone, which is why this bone has been targeted in recent genetic studies of ancient remains (Gamba *et al.*, 2014; Pinhasi *et al.*, 2015; Sirak *et al.*, 2017). The endogenous content of a sample can be improved through targeted in-solution capture array, which targets for pre-specified highly informative regions of the human genome and specifically removes these DNA fragments for ssequencing whiches and boosts the endogenous contentamount of useable human DNA The downside of targeted capture is that the data acquired are mostly limited to parts of the genome that have been predefined and included on the capture array. This means that the complexity of the data tends to be much reduced compared to shotgun sequencing, but in cases where endogenous content is low this may be the only way of obtaining sufficient amounts of ancient human DNA for analysis.

Each DNA library was put on an initial shotgun sequencing screening run to estimate the endogenous content and DNA complexity. All successful samples were sent to the Harvard University Medical School for targeted in-solution capture on their 1,420k single nucleotide polymorphism (SNP) capture array (Brace *et al.*, 2019; Olalde *et al.*, 2018). Samples showing particularly high levels of endogenous DNA were subject to deeper shotgun sequencing. The endogenous content of seven of the Aveline’s Hole samples was close to zero and therefore these samples could not be taken forward for further analysis. Four had endogenous contents of 1-3% and were put forward for capture. Two samples showed notably higher levels of endogenous DNA: M1.11.326 at 68% and M1.11.325 at 14%.

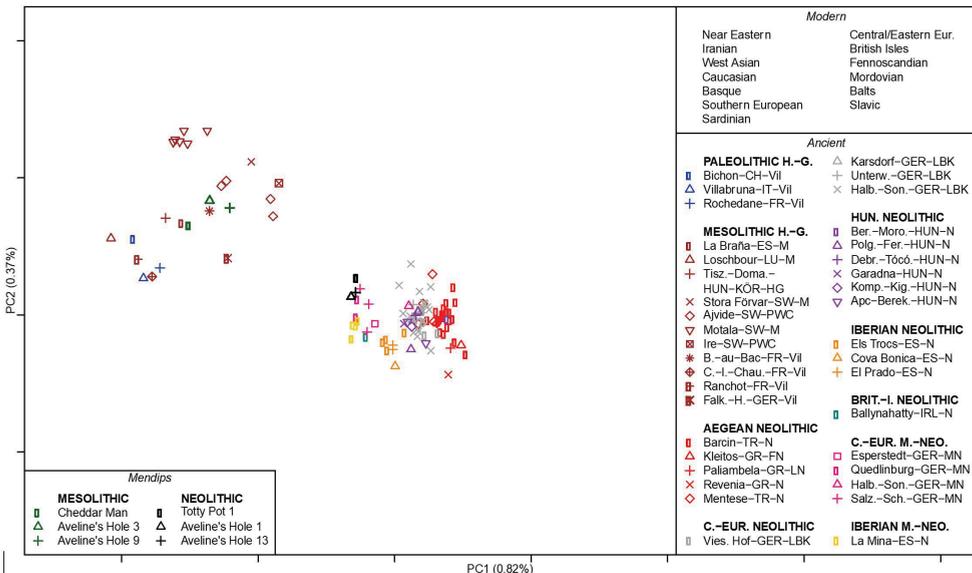


Figure 7. Principal components analysis of genome-wide SNP data of human remains from Mendip, plotted against ancient and modern samples from Europe (adapted from Brace *et al.*, 2019, fig. 2). Both samples dating to the 9th millennium BC plot outside of modern European variation with Mesolithic samples from other parts of Europe. Two samples that turned out to date to the beginning of the 4th millennium BC plot with Middle Neolithic populations from Iberian and Central Europe.

Screening is primarily intended to produce enough data to provide a rough measure of the DNA preservation. However, if a sample is particularly well preserved, there may be enough data available from a screening run to perform some rudimentary analysis. We plotted a Principal Components Analysis (PCA) of the two best-preserved Aveline's Hole samples against genetic data from both ancient and modern populations. Surprisingly, the two Aveline's Hole individuals plotted well away from WHGs (i.e. Mesolithic individuals from other parts of Europe), and clustered with Neolithic populations of Europe carrying ANF ancestry, close to modern populations from Sardinia. These unexpected results persisted following further sequencing and analysis (Figure 7).

Neolithic cultures arrive in Britain around 1000 years after they arrive in adjacent parts of mainland Europe (Sheridan, 2010). Some have argued that there was sustained cultural and biological interaction between Mesolithic populations of Britain and the Neolithic farmers occupying mainland Europe over this period (Thomas, 2013). However, the previous radiocarbon dating of individuals from Aveline's Hole fit all fall in the late ninth millennium BC, at least 1000 years before the first evidence of populations carrying ANF ancestry moving into Europe, let alone Britain (Broushaki *et al.*, 2016; Hofmanová *et al.*, 2016; Lazaridis *et al.*, 2016). Therefore, the presence of individuals carrying ANF ancestry in Early Mesolithic Britain was highly implausible. It was this paradox that led to us to organise the new radiocarbon dating programme reported above. Radiocarbon dates of these two samples placed them in the British Early Neolithic, which is entirely consistent with their high levels of ANF ancestry (Brace *et al.*, 2019).

It is probably no coincidence that the two best-preserved samples also happened to be Neolithic. Part of the explanation for this is that many of the Mesolithic samples were taken from long bones and not from the petrous bone, as were the two aforementioned Neolithic samples. However, as DNA damage increases with time it is likely that the Early Neolithic samples were better preserved precisely because they were almost half as old as the Early Mesolithic samples (Kistler *et al.*, 2017). Speculatively, the disparity in preservation may also reflect differences in early depositional histories, suggested by the observation that so far only cranial bones from Aveline's Hole have been dated to the Early Neolithic (see discussion above). Early depositional history affects preservation of the bone microstructure, which has been linked to DNA preservation (Booth, 2016; Hollund *et al.*, 2012; Hollund *et al.*, 2016; Jans *et al.*, 2004; Nielsen-Marsh *et al.*, 2007). The disparity in DNA preservation between the Neolithic and Mesolithic human remains from Aveline's Hole may tentatively support the idea that Neolithic bones originally formed parts of bodies that decomposed in a different environment which served to better preserve DNA, before disarticulated crania were retrieved and redeposited at Aveline's Hole.

Early Mesolithic DNA results

The results from the Aveline's Hole samples, as well as individuals recovered from other Mendip sites and the surrounding area are presented in Table 6. The two Early Mesolithic individuals from Aveline's Hole from which we were able to analyse genome-wide data plot on a PCA with WHGs, and are very distinct from the two samples dating to the Early Neolithic (Figure 8). The Early Mesolithic Cheddar Man skeleton from Gough's Cave, which is both geographically and temporally close to the Early Mesolithic Aveline's Hole human assemblage, plots in a similar position as the Early Mesolithic Aveline's Hole samples (Brace *et al.*, 2019). Further comparative tests suggest that the ancestry of the two Early Mesolithic Aveline's Hole individuals and Cheddar Man can be explained entirely by WHGs with no evidence for remnant ancestry from populations that had inhabited Europe prior to 12500 BC (the so-called

‘El Miron’ cluster; Brace *et al.*, 2019; Fu *et al.*, 2016). The Early Mesolithic Aveline’s Hole skeletons and Cheddar Man share more genetic drift with, meaning they descend from a population more closely related to a WHG from Luxembourg than one from northern Spain, suggesting that WHGs moved into Britain across Doggerland from the Low Countries, rather than up the Atlantic coast from Iberia.

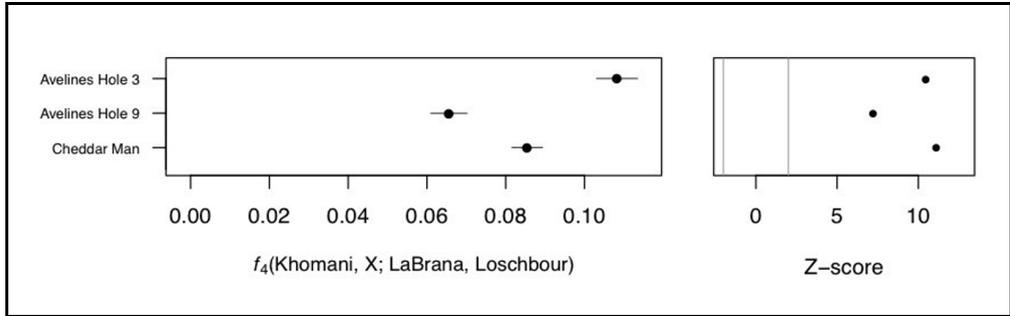


Figure 8. f_4 test investigating levels of shared drift between Mesolithic human remains from Mendip and different parts of mainland Europe. All three British Mesolithic samples share significantly ($Z\text{-score} > 2$) more drift with the Loschbour WHG from Luxembourg than the La Braña WHG from northern Spain, as indicated by their positive f_4 values. Full methods involved in the generation of this figure can be found in Brace *et al.* (2019).

There is insufficient coverage of variants related to pigmentation in the Early Mesolithic Aveline’s Hole individuals to predict physical characteristics. However, their temporal and geographical proximity to Cheddar Man, which did yield good coverage, suggests that they are likely to have had similar genetic profiles including relatively dark skin pigmentation (Brace *et al.*, 2019). This is consistent with the genetic profiles of other WHGs with respect to pigmentation, which would imply that they had variably dark skin, light (blue, green or hazel) eyes and black or dark brown hair (Brace *et al.*, 2019; Mathieson *et al.*, 2015; Olalde *et al.*, 2014).

All individuals included in genome-wide studies of ancient individuals are tested for kinship, as inclusion of close relatives can skew subsequent analyses (Brace *et al.*, 2019; Olalde *et al.*, 2018). The two Early Mesolithic Aveline’s Hole individuals were not close kin relatives. This is consistent with the results from their mitochondrial genomes indicating that they belong to different mitochondrial haplogroups (maternal lineages). It is difficult to reach any firm conclusions about the possibility that Aveline’s Hole was a familial burial place based on just two samples; however, these results suggest that Aveline’s Hole was certainly not reserved exclusively for the deposition of individuals belonging to particular families or maternal lineages in the Early Mesolithic. These results are more consistent with the view that disparate human groups from the surrounding region gathered here to inter their dead (Schulting, 2005).

Neolithic aDNA results

The two Early Neolithic Aveline’s Hole individuals show very different genome-wide ancestry profiles from those dating to the Early Mesolithic, with affinity to ANF rather than WHG populations (Figure 9). Furthermore, they show significantly greater similarity to Neolithic populations from Iberia than Neolithic populations from Central Europe, consistent with the results from Britain more broadly (Brace *et al.*, 2019; Figure 10). Levels of WHG

admixture in these two individuals are similar to those observed in Neolithic populations from Iberia and southern France, indicating that there was little admixture between their ancestors and WHGs living in Britain (Brace *et al.*, 2019). Further analysis of these two individuals using a programme which estimates the generational distance from the last admixture event between two populations indicates that there is no evidence of admixture with WHGs in the last 30 generations (Brace *et al.*, 2019). Thus, it is likely that the small amount of WHG ancestry we see in the Aveline's Hole Early Neolithic individuals reflects historic admixture between populations carrying ANF ancestry and WHGs on mainland Europe, rather than within Britain.

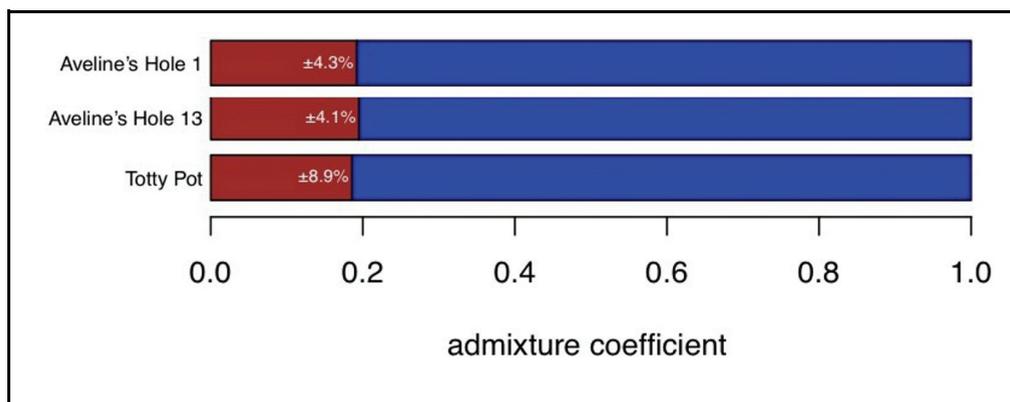


Figure 9. f_4 qpAdm test showing WHG (red) and ANF (blue) ancestry components of Early Neolithic samples from Mendip. Full methods involved in the generation of this figure can be found in Brace *et al.* (2019).

Adequate genomic data were also obtained from a femur (2004.9/257) recovered from Totty Pot. Despite dating to the Late Neolithic (Schulting *et al.* 2010), around a millennium later than the Early Neolithic individuals from Aveline's Hole, the results from Totty Pot are similar to those of the Early Neolithic Aveline's Hole individuals in showing predominantly ANF ancestry and sharing affinities with Iberian over Central European Neolithic populations. This result suggests that the ancestry of Neolithic populations around Mendip remained stable from the Early through to the Late Neolithic, unlike other parts of Europe where there was a later resurgence of WHG ancestry after the first populations carrying ANF ancestry had arrived (Brace *et al.*, 2019; González-Forbes *et al.*, 2017; Haak *et al.*, 2015; Lipson *et al.*, 2017; Mathieson *et al.*, 2017). The palaeogenetic results from Mendip reflect in microcosm the findings from the analysis of DNA from British Mesolithic and Neolithic human remains generally (Brace *et al.*, 2019).

The two Early Neolithic individuals from Aveline's Hole are not close relatives and belong to different maternal lineages. Two samples is too few to infer anything certain regarding the nature of Early Neolithic deposition at the site, although as in the Mesolithic, the results reject an interpretation of Aveline's Hole as being a place of deposition that was exclusively reserved for people from particular families or maternal lineages. This is consistent with palaeogenetic analyses of British Early Neolithic human remains from caves or tombs where no close relatives have yet been detected and where mitochondrial haplogroups tend to be variable (Brace *et al.*, 2019; Olalde *et al.*, 2018). The two Early Neolithic individuals are female (Table 6), although this is too small a sample to represent anything meaningful about Neolithic

depositional practices at the site. Genetic inference of sex for Neolithic individuals from British cave sites more generally suggests that there was approximately equal representation of males and females (Brace *et al.*, 2019; Olalde *et al.*, 2018).

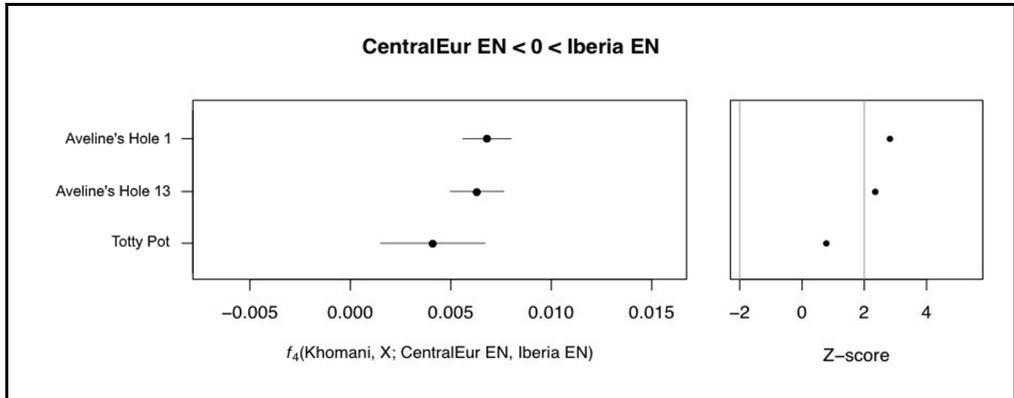


Figure 10. f_4 test investigating levels of shared drift between Early Neolithic human remains from Mendip and mainland Europe. Both Aveline's Hole samples share significantly ($Z\text{-score} > 2$) more drift with Neolithic populations from Iberia than Neolithic populations from Central Europe, as indicated by their positive f_4 values. The positive f_4 value from the Totty Pot individual suggests that they also share more drift with Neolithic populations from Iberia, although the Z-score is non-significant (< 2). Full methods involved in the generation of this figure can be found in Brace *et al.* (2018).

Pigmentation in Aveline's Hole M1.11.326

Coverage of genetic variants linked to pigmentation in the data from the Early Neolithic female from Aveline's Hole (M1.11.326) was adequate to predict pigmentation characteristics using the HIRISplex-S software (Chaitanya *et al.*, 2018; Walsh *et al.*, 2017). This program examines the state of 41 genetic variants linked to modern human pigmentation. Eight SNPs had no coverage and four were at low coverage (1x). Low coverage sites were assumed to be homozygous. Two predictions can be generated, one where the missing SNPs were assumed to be homozygous in the derived state, and one where they were assumed to be homozygous, in their ancestral state (Table 5). This strategy provides the extreme range of possible variation within the model, given the actual variation seen in the ancient sequences.

The output of HIRISplex-S is a probability vector over different pigmentation categories, the category scoring highest usually being the final prediction (Walsh *et al.*, 2017). However, when the highest probability falls below particular thresholds, the authors suggest to modify the final prediction and form mixtures of categories weighted by their probabilities (Chaitanya *et al.*, 2018). The probabilities for different eye pigmentation categories are the same for the three different strategies to deal with low coverage described above. Blue is the category with the highest probability, however, as no value is above 0.5, the predicted pigmentation would be a mixture of the three. This means that this female's eyes would probably have appeared hazel, although green cannot be ruled out. The probabilities for hair pigmentation are more variable across the three prediction types, although they consistently suggest that her hair was most probably dark. The ancestral SNP model is usually favoured, being most similar to the model where SNPs are missing (Brace *et al.*, 2018; Chaitanya *et al.*, 2018). Brown hair has

Table 5. Results of the analysis of genetic variants linked to pigmentation in M1.11.326 using the Hhrisplex-S software (Chaitanya et al., 2018; Walsh et al., 2017). Three scenarios were generated to produce a prediction of likely pigmentation characteristics, one where missing variants were left out, one where missing variants were assumed to be ancestral, and one where missing variants were assumed to be derived.

Scenario	Eyes			Hair						Skin				
	blue	intermed	brown	blonde	brown	red	black	light	dark	very pale	pale	intermed	dark	dark to black
Missing	0.459	0.155	0.387	0.027	0.617	0.001	0.355	0.062	0.938	0.012	0.008	0.693	0.171	0.116
Ancestral	0.459	0.155	0.387	0.023	0.598	0	0.379	0.045	0.955	0.077	0.006	0.649	0.051	0.216
Derived	0.459	0.155	0.387	0	0.003	1	0	0.08	0.92	0	0	0.519	0	0.481

the highest probability in both models, but is lower than 0.7 and therefore modified by the substantial probabilities associated with black hair, so that her hair would most likely have been perceived as dark brown or black. Probabilities for skin pigmentation categories are again variable, but broadly point to the same result. The ‘intermediate’ category is most probable in all three scenarios, but less than 0.7 in each case. This means that the prediction is influenced by the probabilities in the dark and dark-black categories. Therefore the overall prediction for her skin would be intermediate-dark pigmentation.

CRANIOMETRICS: THE A, B, C, AND ‘O’ CRANIA

Chris Meiklejohn and Jeff Babb

Introduction and background

This section examines whether data obtained from specimens destroyed in 1940 can add to information obtained from the new ¹⁴C and aDNA evidence that is central to this paper. The measurements from the now destroyed crania A, B and C recovered at Aveline’s Hole between 1912 and 1914 are the most complete of those excavated from the site, and could, in theory, allow comparison with the extant ‘O’ calvarium (NHM PA SK 3107), which has an indirect ¹⁴C date on adhering stalagmite placing it broadly in the Mesolithic. Other cranial material comprises fragments that survived the 1940 bomb raid, described by Schulting (2005); however, none of this material provides sufficient craniometric data for analysis. As the core of this paper indicates, we now know that Aveline’s Hole was used for burial at two disparate times, in the Early Mesolithic and in the Early Neolithic, though the latter period seems to be represented only by crania. One of the problems arising from this discovery concerns the available data from the destroyed cranial remains mentioned above. In other words, can we determine whether the three destroyed specimens belonged to the Mesolithic or Neolithic burial episodes?

The craniometric analysis presented here began with the four specimens introduced above. Before proceeding to the finds and the analysis, some comment is needed on the numbering systems used to identify the material. We begin with Buxton’s (1925) calvarium ‘O’ in the Oxford University Anatomy Department collection (Figure 11). Oakley (1953) identifies this as recovered by Buckland ‘before 1823’, referring to Buckland (1823) who, in turn, refers to material encrusted in stalactite at ‘Burrington’ (i.e., Burrington Combe). Later, Oakley *et al.* (1971) labelled this as Aveline’s Hole 1.¹ Available craniometric data for this specimen are from Buxton (1925) and Wells (1958). The twentieth-century material consists of three calvaria recovered in 1914. Initially identified as ‘skulls 1, 2 & 3’ by Fawcett (1920, 1921), this was changed to A, B and C by Keith (1924), noting that the first is dolichocephalic, the other two brachycephalic. A partial maxilla is also present. Subsequently, Oakley *et al.* (1971) re-labelled crania A-C as Aveline’s Hole 5 through 7.² The initial descriptions, by Fawcett, are general, directed most to individual 1/A, described as the most complete. No information is provided on

¹ Aveline’s Hole ‘O’ was apparently first mentioned by Buckland, but this contains no description other than that the find was encrusted in stalactite and parts of the material retained. The key description, by Buxton (1924), refers to the specimen as in the collections of the Department of Anatomy at Oxford, also noting that identification of the find rests on a piece of associated paper, identifying the skull as from Burrington Combe and referring to Buckland, an identification confirmed by E.K. Tratman. Some uncertainty exists in sourcing the calvarium to the site, as later work shows that Tratman’s identifications were not always fully secure, as seen in the saga of Aveline’s Hole 9 (Meiklejohn *et al.* (2012). No train of evidence links Buckland’s recovery of the piece and Tratman’s identification. According to Davies (1921, 62) this is only one of ‘many skeletons’ he removed.

² Aveline’s Hole 2 through 4 are the materials recovered by Bright.

archaeological context beyond general reference to the site. The approach, not surprisingly for the period, is typological. A full description is provided by Keith (1924), including diagrams of the three specimens and most of the craniometric data.

The analysis that follows began with the four specimens described above, all calvaria



Figure 11. *Aveline's Hole calvarium 'O' (NHM PA SK 3107, formerly E.11.6/257)*

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or crania without bases, though Aveline's Hole B is perhaps better seen as a calotte or skullcap. The motivation behind the craniometric analysis was to determine whether anything could be said about possible allocation of the specimens as Mesolithic or Neolithic, given the new ^{14}C results presented above. The methodology used below mirrors our work on the Aveline's Hole 9 and Skeleton Cave (Leigh Woods) material (Meiklejohn *et al.*, 2012; Mullan *et al.*, 2017). The database used for the comparison was initially compiled between 2007 and 2012 by one of us (CM) as part of a project with Ron Pinhasi and Winfried Henke on Upper Palaeolithic and Mesolithic material (Brewster

et al., 2014a; 2014b). For this project, we added Neolithic data collected for the earlier project, together with Neolithic data from Denmark (Bröste *et al.*, 1956) and Neolithic and post-Neolithic data from Great Britain (Brodie 1994). The primary limiting factor on the analysis was the availability of data from the material destroyed in 1940.

We initially put together a dataset that included all four of the Aveline's Hole specimens discussed above. However, it became immediately clear that calvaria B and C had very limited data; if all four specimens were to be included in the analysis only six variables would be available. We performed a principal component analysis on the resulting dataset but the results were not interpretable in any meaningful way, as the measurements were highly correlated, all effectively being measures of cranial length. The result was a clear separation of males and females on the first principal component, a simple measure of size, but with almost complete overlap of the four chronological groups on the next three components. No conclusions were possible. We therefore decided to concentrate on Aveline's Hole A (Figure 12), the individual with the most available variables, including those reflecting the three primary axes available in the measurement of crania: length, breadth and height.

The data were analyzed using two approaches, principal component analysis (PCA) and quadratic discriminant analysis (QDA). Our analyses were based on values for eight measurement variables, as defined below. We have identified them within the two primary

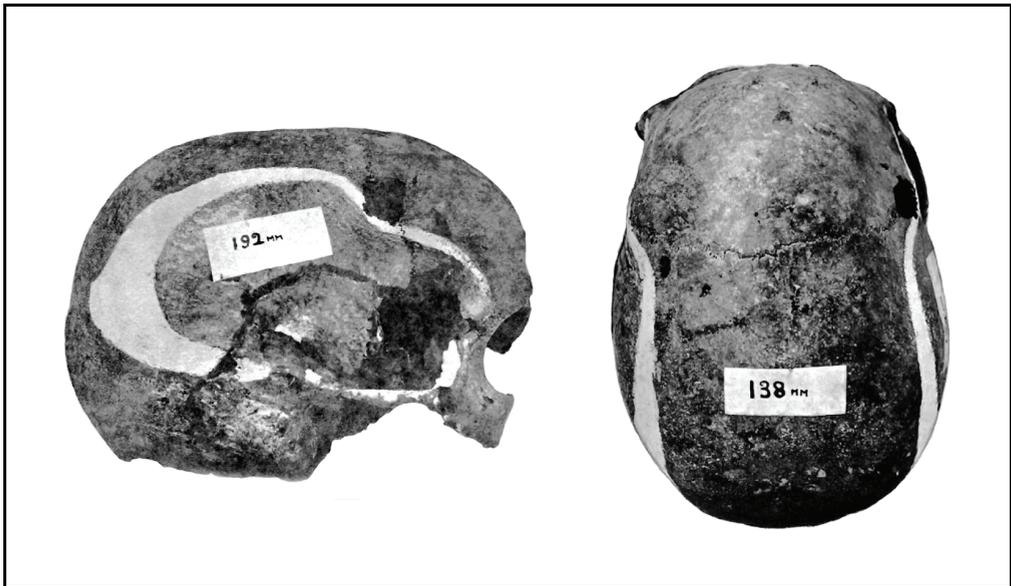


Figure 12. *Aveline's Hole 'A', right lateral and superior views (after Fawcett 1921, figs. 13 and 14).*

systems in general use in the field, those of Martin and Saller (1957) (the M numbers) and Howells (1973) (the letter abbreviation identifications). Two of the measurements, the frontal and parietal arcs, italicised in the list, are not defined in the Howells system. Note that there are five length, two breadth and one height measurement.

- M1 = GOL = Glabello-occipital length = Maximum cranial length
- M8 = XCB = Maximum cranial breadth
- M12 = ASB = Biasterionic breadth
- M26 = *Fr Arc* = Frontal arc
- M27 = *Par Arc* = Parietal arc
- M29 = FRC = Frontal chord
- M30 = PAC = Parietal chord
- M52 = OBH = Orbital height

The sample used comprised 177 individuals, distributed among four periods as follows: 17 Upper Palaeolithic, 37 Mesolithic, 82 Neolithic and 41 post-Neolithic. Geographic coverage was primarily restricted to Western Europe, though some Eastern European individuals were included in the Upper Palaeolithic sample to provide sufficient overall sample size in all four chronological groups.

Principal Component Analysis

Principal component analysis (PCA) was run on the covariance matrix of eight variables (M1, M8, M12, M26, M27, M29, M30 and M52) for 177 male specimens from

northwestern Europe (excluding Aveline Hole's A). The results are summarized in Table 8, with highlights as follows:

- The first three principal components (PC1, PC2 and PC3) collectively accounted for 82.6% of the total sample variation (TSV) for the dataset, with the three accounting for 43.7%, 26.1% and 12.8 %, respectively.
- The first PC is a weighted average of {M1, M27, M30, M26, M29, M12} with most of the weight on M1, M27, M30 and M26.
- The second PC is a weighted contrast between {M8, M26, M29} and {M27, M30}.
- The third PC is a weighted contrast between {M8, M12, M27, M30} with {M1, M26, M29}.

The PCA gives the most likely attribution of Aveline's Hole A as Upper Palaeolithic (Figure 13).

Table 8. Summary of PCA conducted on the covariance matrix for male crania (n = 177).

Eigenvalue	Proportion of TSV explained by corresponding PC	Cumulative proportion of TSV explained by corresponding TV
149.8520	0.4365	0.4365
89.6600	0.2612	0.6977
44.0210	0.1282	0.8259
30.4760	0.0888	0.9147
15.9230	0.0464	0.9610
5.8760	0.0171	0.9782
3.7680	0.0110	0.9891
3.7300	0.0109	1.0000
343.305		

NB: the above table suggests that the first three PCs are adequate to represent the data.

Variable	Coefficients of principal components		
	PC1	PC2	PC3
M1 = GOL	-0.5244	-0.0565	-0.3638
M8 = XCB	-0.0305	-0.4950	0.5830
M12 = ASB	-0.1796	-0.3534	0.4734
M26 = Fr Arc	-0.3772	-0.4805	-0.3159
M27 = Par Arc	-0.5205	0.4352	0.3290
M29 = FRC	-0.2646	-0.3169	-0.2256
M30 = PAC	-0.4567	0.3225	0.2100
M52 = OBH	-0.0106	-0.0472	-0.0253

NB: the first PC is a weighted average of M1, M27, M30, M26, M29, M12 with most of the weight on M1, M27, M30 and M26

The second PC is a weighted contrast between M8, M26, M29 and M27, M30

The third PC is a weighted contrast between M8, M12, M27, M30 with M1, M26, M29

Variable	Correlations of variables with principal components		
	PC1	PC2	PC3
M1 = GOL	-0.804	-0.067	-0.302
M8 = XCB	-0.056	-0.710	0.586
M12 = ASB	-0.359	-0.546	0.513
M26 = Fr Arc	-0.627	-0.618	-0.285
M27 = Par Arc	-0.783	0.507	0.268
M29 = FRC	-0.626	-0.580	-0.289
M30 = PAC	-0.831	0.454	0.207
M52 = OBH	-0.053	-0.182	-0.068

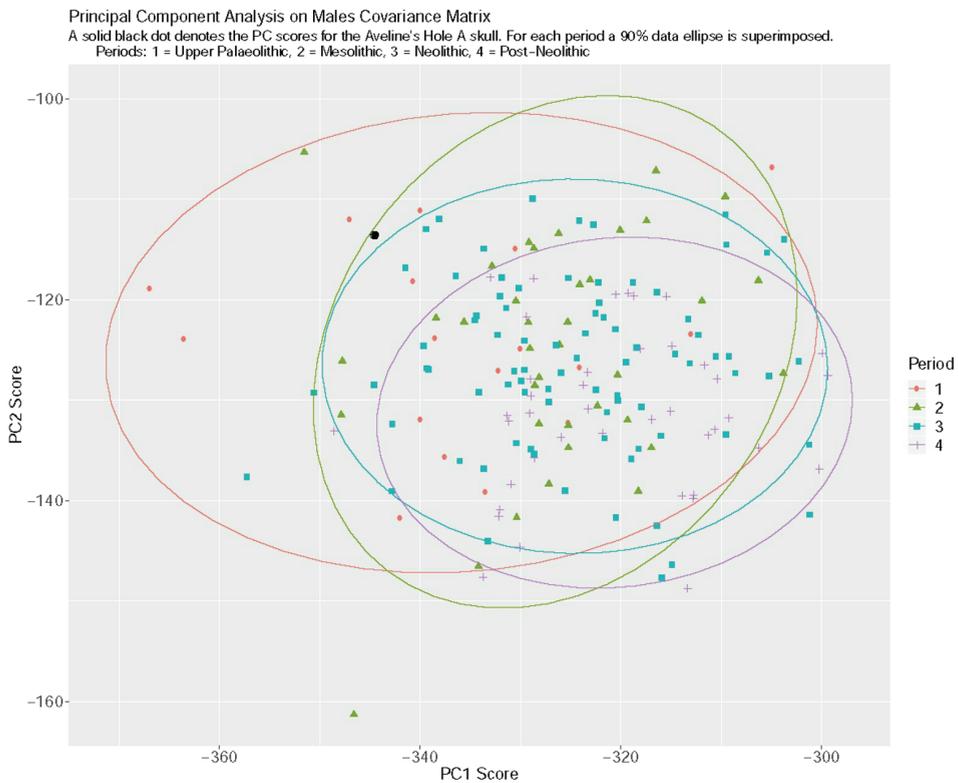


Figure 13. Scatterplot of PC1 and PC2 scores for each specimen with 90% data ellipses (i.e., containing 90% of the datapoints for that period): Upper Palaeolithic = 1; Mesolithic = 2; Neolithic = 3; post-Neolithic = 4. Aveline's Hole A is highlighted, with a most likely attribution to the Upper Palaeolithic. Created in R using ggplot2 (Wickham, 2016).

Quadratic Discrimination Analysis

A multivariate analysis of variance (MANOVA) indicated significant differences among the eight-variable mean vectors for the four time periods. As well, a separate analysis of variance was conducted on each of the variables. A quadratic discriminant analysis (QDA) was conducted to construct classification functions for separating the four time periods. Quadratic discriminant analyses were conducted using the quaDA function available in the R software package DiscrMiner (<https://cran.r-project.org/web/packages/DiscrMiner/>). It should be noted that, as discussed in Johnson and Wichern (2007), the apparent error rate in QDA tends to underestimate the actual error rate, since the apparent error rate evaluates the classification function using the same dataset from which it was developed.

The classification performance of the QDA algorithm on the dataset is summarized by the counts shown in the confusion matrix of Table 9a. A correct classification occurs each time an original classification matches the algorithm's predicted classification. Counts along the main diagonal (from top left to lower right) correspond to the number of correct classifications for each category; for example, 77 of 82 Neolithic crania were correctly classified as Neolithic by QDA. Counts that are listed in positions not along the main diagonal correspond to incorrect classifications. Of particular interest is the fact that only six of 123 Neolithic and Post-Neolithic crania were classified by the algorithm as Upper Palaeolithic or Mesolithic. The apparent error rate (APER) from this confusion matrix was $52/177 \approx 0.294$. When the QDA algorithm for the dataset with eight variables and four time periods was applied to the independent Aveline Hole 'A' cranium, it classified as Upper Palaeolithic.

Table 9a. *Quadratic discriminant analysis, confusion matrix with 4 eras and 8 variables.*

Actual Era	Predicted Era				Total
	UP	Meso	Neo	Post-Neo	
UP	7	2	8	0	17
Meso	1	18	18	0	37
Neo	1	1	77	3	82
Post-Neo	0	4	14	23	41
Total	9	25	117	26	177

APER = Apparent error rate: $52/177 \approx 0.294$

The apparent error rate should be compared to the error rate which would be obtained by simply classifying all the specimens as Neolithic = $95/177 \approx 0.537$.

Predicted classification for Aveline's Hole "A" specimen: Upper Palaeolithic.

Table 9b. *Quadratic discriminant analysis, confusion matrix with 3 eras and 8 variables.*

Actual Era	Predicted Era			Total
	UP	Meso	Neo or Post Neo	
UP	7	1	9	17
Meso	0	17	20	37
Neo	0	4	119	123
Total	7	22	148	177

APER = Apparent error rate: $34/177 \approx 0.192$

The apparent error rate should be compared to the error rate which would be obtained by simply classifying all the specimens as Neolithic or Post-Neolithic = $54/177 \approx 0.305$.

Predicted classification for Aveline Hole "A" specimen: Upper Palaeolithic

Following an initial analysis, the Neolithic and post-Neolithic crania were combined into a single sample and a quadratic discriminant analysis was undertaken using eight variables and three time periods. Classification performance is summarised by the confusion matrix in Table 9b; again, counts along the main diagonal (top left to lower right) correspond to correct classifications. Note that only four of the 123 Neolithic or post-Neolithic crania are now incorrectly classified by the algorithm as Upper Palaeolithic or Mesolithic, and the apparent error rate from this confusion matrix is $34/177 \approx 0.192$. As might be expected, the QDA algorithm developed for this second dataset also classified Aveline Hole 'A' as Upper Palaeolithic.

Summary of the craniometric analysis

The result of this analysis is to strongly suggest that the Aveline's Hole A calvarium comes from the earlier rather than the later set of burials at the site. This does not amount to an exclusion of the Neolithic or later periods, but it makes its probability very low. In fact, based on the available comparative datasets, the most likely allocation of the individual is to the Upper Palaeolithic. This is a distinct possibility, given the lithic and faunal evidence for Late Upper Palaeolithic activity in the cave (Jacobi, 2005), supported by a radiocarbon date of ca. 12950 cal BC (OxA-17722: 12565 ± 50 BP) on a red deer (*Cervus elaphus*) phalanx bearing a stone-tool cutmark (Jacobi and Higham, 2009; note that this is on the same specimen previously published as OxA-1121: 12380 ± 130 BP by Hedges *et al.*, 1987, where it is mistakenly identified as bovine). Comparable radiocarbon dates are available on a shed reindeer (*Rangifer tarandus*) antler (OxA-1122: 12480 ± 130 BP) and on an unshed red deer antler (OxA-801: 12100 ± 180 BP) (Gowlett *et al.*, 1986; Hedges *et al.*, 1987), contemporaneous with Late Upper Palaeolithic activity at nearby Gough's Cave (Burleigh, 1986; Jacobi and Higham, 2009).

Of interest may be the identity of specimens that lies close to Aveline's Hole A in the PCA chart (Figure 13). Three of the four 'closest neighbors' on the chart are Upper Palaeolithic: Predmosti 7, Arene Candide 1 (Gravettian) and Chancelade; the fourth is a post-Neolithic find from Tallington. At a greater distance but surrounding the placement of Aveline's Hole 'A' are also four Mesolithic finds: Braña 1, Cuzoul de Gramat, Hoëdic 6 and Ofnet 21. The outlier at the base of the figure, with the highest score on PC2, is Bøgebakken 10. The furthest removed Mesolithic crania, all much smaller as shown on PC1, are Döbritz 2, Moita do Sebastião 20 and Ofnet 24.

The possibility that cranium 'A' is of Upper Palaeolithic age is of considerable interest, though given the loss of the specimen it will never be possible to confirm this finding. It is unfortunate that individuals B, C and 'O' could not be included due to the limited measurements available. Equally unfortunate is that the almost total absence of archaeological records for the initial work by the Bristol Spelaeological Research Society between 1912 and 1914 means that the result obtained for the A individual cannot be transferred to B and C. A date on stalagmite adhering to Cranium 'O' suggests a Mesolithic age, though this should be confirmed with a direct ^{14}C determination on the bone. In addition, DNA analysis of this specimen is currently underway.

DISCUSSION

The new radiocarbon dating results significantly change our understanding of burial activity at Aveline's Hole, introducing a substantial, previously unknown Early Neolithic component. While initially raising a question, the collection history reported here fully supports the attribution of this material to the site. When combined with the previously obtained

determination on an infant cranial fragment (M1.11.307), seven of the 13 (54%) directly dated cranial elements yielded Early Mesolithic dates entirely in keeping with those on the postcrania, while the remaining six provided Early Neolithic dates. This is a sufficient sample of the crania represented at the site to infer an approximately 50:50 breakdown between the two periods. In both cases, evidence for deposition of human remains extends over a period of a few centuries. While Aveline's Hole forms something of a focus for burial in the Early Mesolithic, there are a number of other sites with human remains from this period in Mendip and the surrounding region, as well as a number of sites with Early Neolithic human remains. The following sections broaden out the discussion to consider this wider context.

Early Mesolithic

Beyond Aveline's Hole, Mesolithic human remains have been identified from the Mendip cave sites of Gough's New Cave, Badger Hole and Totty Pot (Table 9 and Figure 14). The adult male 'Cheddar Man' skeleton from Gough's Cave and two children from Badger Hole represented by mandibles date to approximately the same period as Aveline's Hole (Barker *et al.*, 1971; Burleigh, 1986; Gowlett *et al.*, 1986; Hedges *et al.*, 1989), while two adult long bones from Totty Pot, probably from the same individual, are directly dated to roughly a millennium later (7445–7080 cal BC) (Schulting *et al.*, 2010, table 1) and represent the most recent direct Mesolithic dates on human remains from Somerset. To the above cases can be added the human remains from Greylake, found in 1928. An unknown amount of material was removed before Harold St George Gray, curator of the Somerset County Museum, arrived on the scene, where he observed five 'skulls' in a shed, acquiring two of these and some postcranial fragments from the site for the museum (Gray, 1928). A number of long bones were reportedly removed before Gray arrived. The two crania together with a mandible, four damaged tibiae, a phalanx and a damaged metatarsal survive (Brunning, 2013; Brunning and Firth, 2012). The two crania and the mandible – which may belong to a third individual – have been directly dated to the Early Mesolithic, again contemporaneous with Aveline's Hole (Tables 1 and 2). The site is unusual in being an open-air cemetery, the only example from southwest Britain. The greater exposure to leaching by rainwater likely accounts for the lack of DNA preservation in any of the three samples analysed (see Table 6).

The most recent additions to this corpus derive from Cannington Park Quarry, better known for a large late Romano-British and Anglo-Saxon cemetery (Rahtz *et al.*, 2000) (Figure 1). A cave was discovered during quarrying in 1962 from which human and animal bones were recovered, with no reported associated artefacts (Rahtz *et al.*, 2000, p 17). At least four individuals were represented based on femora, of which two – a subadult and an adult – have been dated to the Early Mesolithic contemporary with those from Aveline's Hole, and with the majority of other dated Mesolithic human remains from Mendip (Table 1). The associated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, with means of -19.5‰ and 8.7‰, respectively (measured following a protocol similar to that in place at Oxford; Dunbar *et al.*, 2016), are closely comparable to those from Aveline's Hole and Greylake. The other human skeletal remains from the cave, including both cranial and postcranial elements, are currently being written up for publication (Sharon Clough, *pers comm*); they may also date to the Early Mesolithic.

The clustering of most of the Early Mesolithic dates (all those aside from Totty Pot) on human remains from Mendip and the surrounding area requires explanation. It was previously proposed that rapidly rising Early Holocene sea levels – resulting in the inundation of the Bristol Channel and concomitant loss of hunter-gatherer territories there – might be implicated (Schulting, 2005, p. 245-8; 2016), leading to a period of readjustment between these displaced hunter-gatherer communities and those living further to the east, including Mendip. Common

Table 9. Directly dated Mesolithic human remains from Somerset (see Figure 1 for locations).

Site/Specimen	Element	Lab code	^{14}C yr	±	cal BC (95%)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C:N	Reference
Badger Hole, BH2	mandible	OxA-1459	9360	100	9118	-20.5	9.6	3.5	Hedges et al., 1989; Charlton, this paper
Badger Hole, BH1	mandible	OxA-679	9060	130	8615	-20.3	8.5	3.4	Burleigh, 1986; Charlton, this paper
Gough's Cave ('Cheddar Man')	talus	OxA-814	9100	100	8607	-	-	-	Gowlett et al., 1986
Gough's Cave ('Cheddar Man')	tibia	BM-525	9080	150	8701	-	-	-	Barker et al., 1971
Gough's Cave ('Cheddar Man')	Talus, tibia	OxA-814, BM-525	9094	84	8562	-	-	-	combined in OxCal v4.3.2, this paper
Greylake, E22	cranium	Wk-30930	9118	37	8443	-19.3	8.7	3.4	Brunning, 2013; this paper
Greylake, E23	cranium	Wk-30931	9134	37	8453	-19.3	9.2	3.3	Brunning, 2013; this paper
Greylake, E22/23?	mandible	OxA-25666	9170	40	8533	-19.1	9.1	3.2	Brunning, 2013; this paper
Cannington Park Quarry, CPQ64-1	femur	SUERC-84330	9225	23	8545	-19.2	8.7	3.3	Sharon Clough, <i>pers comm</i>
Cannington Park Quarry, CAN65-2	femur	SUERC-84331	8925	21	8237	-19.7	8.6	3.4	Sharon Clough, <i>pers comm</i>
Totly Pot	humerus	BM-2973	8180	70	7451	-	-	-	Ambers and Bowman, 2003
Totly Pot, TP1	femur	OxA-16457	8245	45	7455	-19.7	10.3	3.2	Schulting et al., 2010
Totly Pot (combined)	humerus, femur	BM-2973, OxA-16457	8226	38	7418	-19.7	10.3	3.2	Schulting et al., 2010; combined in OxCal v4.3.2

burial places could have served to define group membership during this time (cf. Charles and Buikstra, 1983; Elder, 2010; Goldstein, 1981; Saxe, 1970), subsequently becoming unnecessary as new territorial boundaries became widely accepted and undisputed through habitual use. The new Early Mesolithic dates from Aveline's Hole, together with those from Greylake and Cannington Park Quarry, remain consistent with this scenario. What continues to be striking is the absence of directly dated Late Mesolithic human remains in southwest England, and their scarcity across Britain as a whole (Blockley, 2005; Chamberlain, 1996; Meiklejohn *et al.*, 2011; Schulting, 2016). Of course typologically Late Mesolithic lithic assemblages – supported by radiocarbon dates in a number of cases – are known from the region (Bond, 2009a; 2009b; Gardiner, 2001; Lewis 2011a), so that there is no suggestion it was abandoned, but clearly there was a major shift in burial practices (Blockley, 2005; Schulting, 2013a).

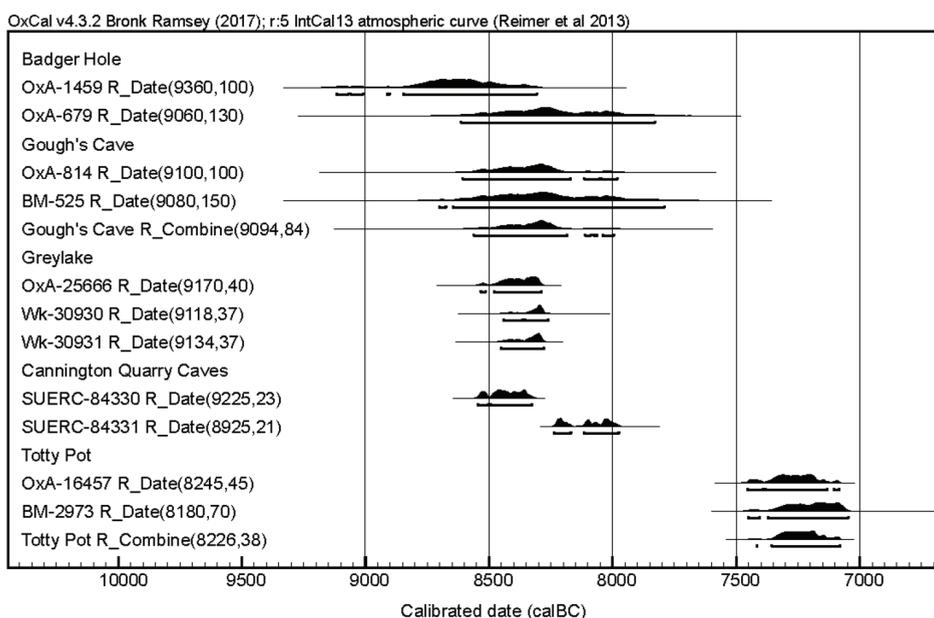


Figure 14. Mesolithic dates on human remains from Mendip and environs. Duplicate dates on Gough's Cave 'Cheddar Man' and on the presumed single individual from Totty Pot are plotted both individually and combined using the *R_combine* function in OxCal v4.3.

Early Neolithic

The use of caves in the Early Neolithic for deposition of human remains is well attested, both in Britain and on the Continent. Mendip itself has other examples of directly dated Early Neolithic human remains from caves (Table 10 and Figure 16). At Totty Pot, the postcranial remains of five individuals yielded radiocarbon dates spanning the Early, Middle and Late Neolithic, while two Mesolithic dates in the second half of the eighth millennium BC probably relate to a single adult (Schulting *et al.*, 2010). Other caves yielding Early/Middle Neolithic human remains on or near Mendip include Backwell, Chelm's Combe, Picken's Hole, Flint Jack's and Hay Wood Cave (Schulting *et al.*, 2010, table 3). Some 15 km to the north of Mendip is Skeleton Cave, Leigh Woods, with a directly dated Early Neolithic mandible,

3708–3639 cal BC (BRAMS-1258.2.2: 4889 ± 29 BP) (Mullan *et al.*, 2017). As two ulnae were also found in the minimal excavations at the site, deposition was not restricted to the skull. They cannot be assessed further as their current whereabouts are unknown, but they are reported as having been found with the mandible (Mullan *et al.*, 2017, fig. 2).

Table 10. Directly dated Neolithic human remains from Somerset (see Figure 1 for locations).

Site	Element	Lab code	^{14}C yr	\pm	Cal BC (95%)		Reference
Backwell	vertebra	BM-3099	4510	40	3361	3090	Ambers and Bowman, 2003
Chelm's Combe	longbone	BM-2974	4680	45	3630	3364	Ambers and Bowman, 2003
Flint Jack's	femur	BM-2839	4430	80	3343	2914	Ambers and Bowman, 2003
Picken's Hole	tooth	OxA-5865	4800	55	3695	3380	Hedges <i>et al.</i> , 1997
Skeleton Cave	mandible	BRAMS-1258.2.2	4889	29	3708	3639	Mullan <i>et al.</i> , 2017
Totty Pot, TP2	femur	OxA-16458	4706	35	3632	3372	Schulting <i>et al.</i> , 2010
Totty Pot, TP6	ulna	OxA-16462	4498	35	3354	3090	Schulting <i>et al.</i> , 2010
Totty Pot, TP3	femur	OxA-16459	4473	35	3341	3026	Schulting <i>et al.</i> , 2010
Totty Pot, TP5	femur	OxA-16461	4442	36	3334	2929	Schulting <i>et al.</i> , 2010
Totty Pot, TP4	femur	OxA-16460	4008	39	2831	2461	Schulting <i>et al.</i> , 2010
Hay Wood Cave	vertebra	OxA-5844	4860	65	3794	3385	Hedges <i>et al.</i> , 1997
HWC adolescent	tibia & tooth	OxA-19914-5	5044	23	3946	3781	Schulting <i>et al.</i> , 2013
HWC II	cranium	OxA-19768	4968	30	3889	3661	Schulting <i>et al.</i> , 2013
HWC 'Burial 1'	bone	OxA-19913	4851	31	3704	3536	Schulting <i>et al.</i> , 2013
HWC III	cranium	OxA-19906	4786	32	3645	3519	Schulting <i>et al.</i> , 2013
HWC VII	cranium	OxA-19910, 19917	4774	23	3639	3521	Schulting <i>et al.</i> , 2013
HWC V	cranium & tooth	OxA-19908, 19916, 19882	4765	20	3636	3521	Schulting <i>et al.</i> , 2013
HWC IV	cranium	OxA-19907	4762	31	3640	3384	Schulting <i>et al.</i> , 2013
HWC IX	cranium	OxA-19912, 19881	4744	24	3636	3382	Schulting <i>et al.</i> , 2013
HWC I	cranium	OxA19904-5	4741	23	3635	3381	Schulting <i>et al.</i> , 2013
HWC VI	cranium	OxA-19909	4723	32	3634	3376	Schulting <i>et al.</i> , 2013
HWC VIII	cranium	OxA-19911	4674	32	3622	3368	Schulting <i>et al.</i> , 2013

Hay Wood Cave provides by far the largest number of Neolithic human remains identified from a Mendip cave. While it has yet to be studied systematically, over 560 skeletal elements are present, representing at least 10 individuals, all directly dated to the earlier Neolithic. A Bayesian model places burial activity there between 3930-3715 BC and 3580-3350 BC (Schulting *et al.*, 2013).

Aveline's Hole presents a rather special case, since Early Mesolithic human skeletal remains would have been apparent to those entering the cave in the Neolithic. This is clear from

the earliest accounts of the cave's discovery in the late eighteenth century, when skeletons were observed on the surface (assuming that these were not all Neolithic, which seems highly improbable given the post-cranial dating results). While some other British caves contain both Mesolithic and Neolithic human remains (e.g., Totty Pot, Foxhole) (Schulting *et al.*, 2010; 2013), it is unlikely that these would have been visible to those entering millennia later. And while Aveline's Hole may have been known in the Late Mesolithic, there is little or no evidence for activity between the cessation of burial in the Early Mesolithic until its re-use in the Early Neolithic (there may be a single Late Mesolithic microlith – Jacobi, 2005). In both periods the term 'burial' is used guardedly, since in the former case at least some of the remains appear to have been simply left on the cave floor, while in the latter, the lack of Neolithic dates on postcranial remains (in a total of 22 determinations on bone) strongly suggests that only cranial remains were deposited. This would not be out of place for the Neolithic, since mortuary rites in long barrows and chambered tombs similarly involved placement of human remains on the ground surface within the monument, without interment.



Figure 15. John Skinner's (ca. 1820) sketches of: a) Aveline's Hole and b) Stony Littleton.
 (© British Library Board (Skinner, J. vol XXXV. Additional manuscripts 33,677, p 5, 8).

There are several Early Neolithic earthen long barrows on Mendip (Lewis, 2002; 2005; 2008; 2011b) with Cotswold-Severn chambered tombs in the surrounding landscape, most notably at Stony Littleton (Beddoe, 1886; Bulleid, 1941; Scarth, 1858; Thomas, 2002). While none have been radiocarbon dated, their construction and use is reasonably well constrained to ca. 3750–3400 cal BC by dating programmes undertaken on similar monuments in southern England and South Wales (e.g., Bayliss and Whittle, 2007; Smith and Brickley, 2006; Whittle and Wysocki, 1998). This is entirely consistent with modelled Early Neolithic dates from Aveline's Hole, indicating that these alternative burial locations were contemporaneous, raising the question of the rationale underlying the decision to place human remains in a cave rather than a monument (cf. Schulting, 2007; see also Fernández-Crespo and Schulting, 2017). While there is something a geological distinction, with caves dominating West Mendip, monuments could of course be placed anywhere, yet they do seem to be more abundant on East Mendip and to the north (Lewis, 2011b). Nevertheless, the two mortuary locations can be found in relatively close proximity. Located only ca. 5 km northeast of Aveline's Hole, Fairy Toot

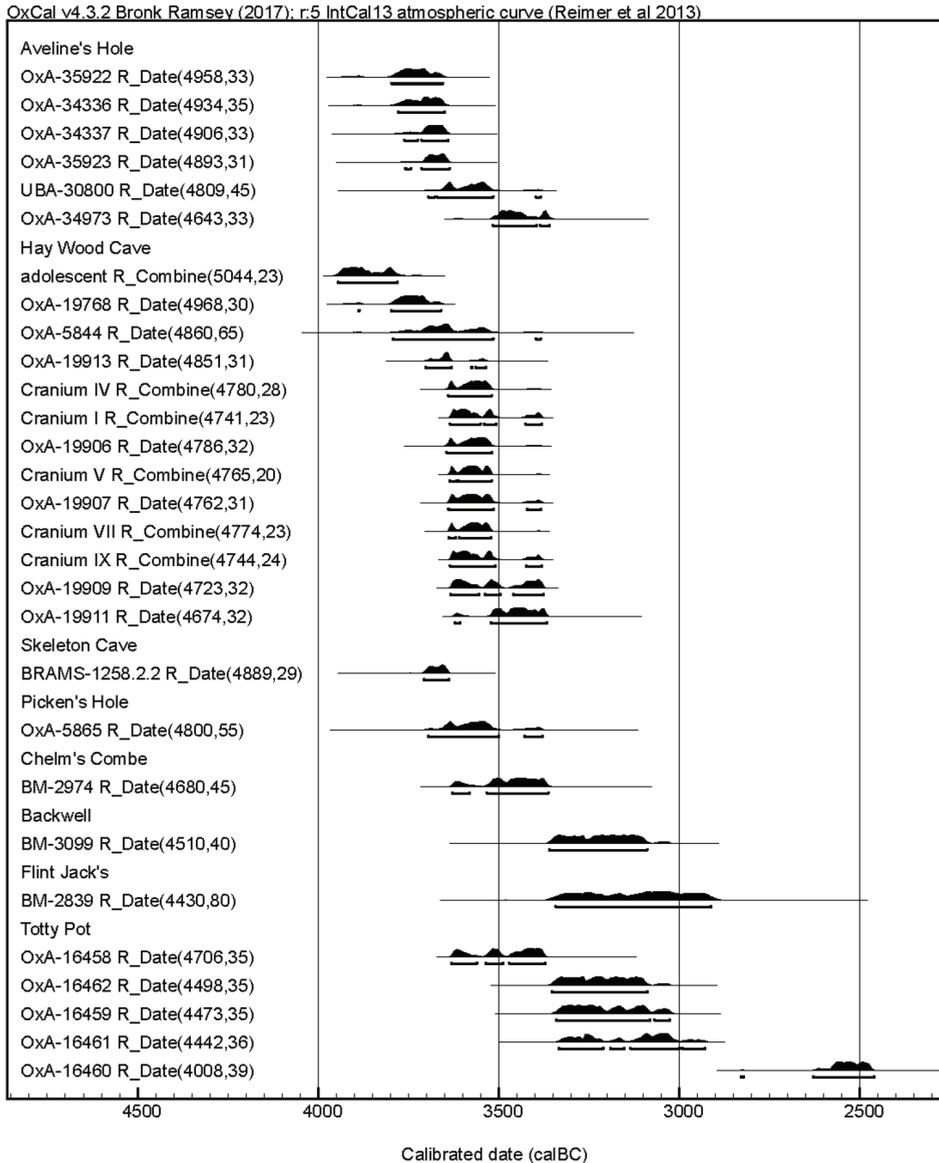


Figure 16. Neolithic dates on human remains from Mendip and environs.

chambered tomb was excavated in the late eighteenth century and never fully published (Boon and Donovan, 1954; Bore, 1789; 1792; Grinsell, 1965; Skinner, 1820). The Priddy long barrow is less than 10 km southeast of Aveline's Hole (Lewis, 2002), while the chambered tomb of Stoney Littleton is more distant, located some 25 km to the east. There are further possible long barrows on West Mendip, and still others have no doubt been destroyed (Lewis, 2008). But deposition in a cave or in a monument is not necessarily mutually exclusive, particularly if, as

current evidence indicates, only skulls or crania were placed in Aveline's Hole. If so, this suggests that these elements were taken from different primary burial locations. The death of crania has long been noted in Early Neolithic mortuary monuments, although causewayed enclosures are more often suggested as their final repository (e.g., Schulting, 2007; Smith 1965).

While those encountering human skeletal remains when entering Aveline's Hole in the Early Neolithic would not have had knowledge of their identity, they may nevertheless have appropriated them as 'ancestors', perhaps seeing the cave entrance in a hillside as an exaggerated entrance in a chambered tomb, blurring the distinction between found and built places (Barnatt and Edmonds, 2002; Bradley, 2000). A sense of their potential similarity is seen through the eyes of Rev. John Skinner in his early nineteenth-century watercolour sketches of both Aveline's Hole and Stony Littleton (Skinner ms. 33,677) (Figure 15).

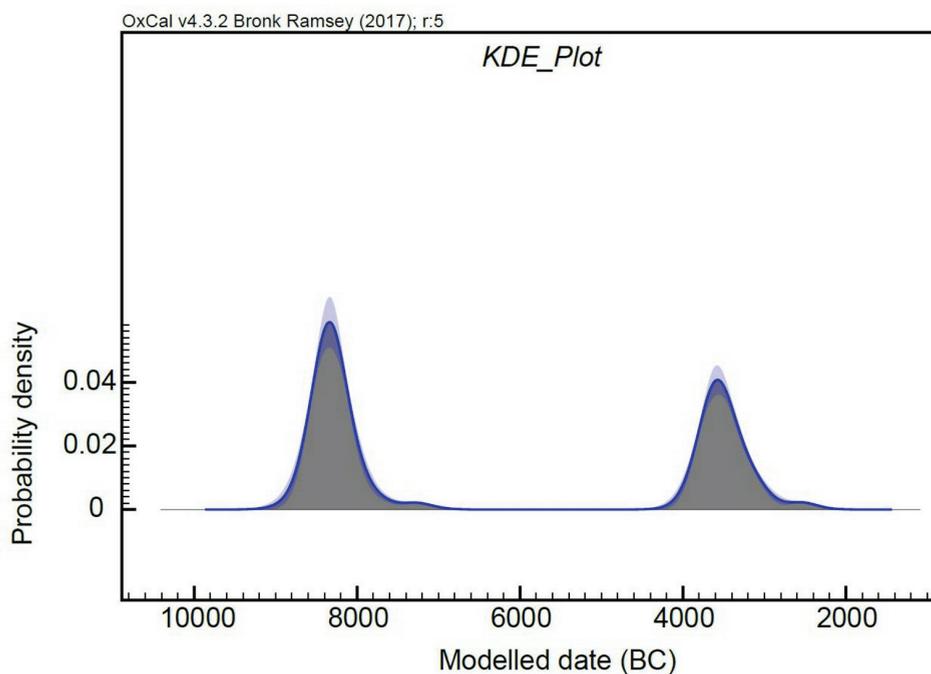


Figure 17. Kernel Density Estimate plot (Bronk Ramsey, 2017) for ^{14}C determinations on Mesolithic ($n = 37$) and Neolithic ($n = 28$) human remains from Somerset.

Despite such chance encounters, there is no indication of continuity between the Mesolithic and Neolithic in the practice of cave burial in Britain. Indeed, the latest directly dated Mesolithic human remains from caves precede the start of the Neolithic by over a millennium (Chamberlain, 1996; 2012; Schulting, 2007; 2016; Schulting, Fibiger *et al.*, 2013). Thus, the origin of cave burial in the Neolithic therefore appears to be an entirely separate phenomenon, one more plausibly connected with parallels drawn between chambered tombs and caves, as discussed above. This is dramatically reinforced by the results from Somerset (Figure 17).

As with the country more widely, it is clear that there must have been a major shift in burial practices in the Late Mesolithic.

Diet and ancestry in Somerset (Rick Schulting)

The $\delta^{13}\text{C}$ distinction noted above in relation to Early Mesolithic and Early Neolithic human remains from Aveline's Hole is upheld in the wider dataset of Mesolithic and Neolithic humans in Somerset (Mann-Whitney U-test, $Z = 5.177$, $p < 0.001$). While the $\delta^{15}\text{N}$ results for Aveline's Hole on its own did not differ significantly between the two periods, the mean $\delta^{15}\text{N}$ value for the Mesolithic in Somerset as a whole is lower by 1.3‰ compared to the Neolithic (Student's t -test, $t = 5.238$, $p < 0.001$, excluding two Neolithic infants subject to a nursing effect – Schurr, 1998) (Figure 18). Since, with the exception of Totty Pot, all of the Mesolithic dates fall very early in the period, the same explanation as given above for Aveline's Hole can be extended to this wider comparison, i.e., a shift in the underlying isotopic baselines affecting both ^{13}C and ^{15}N .

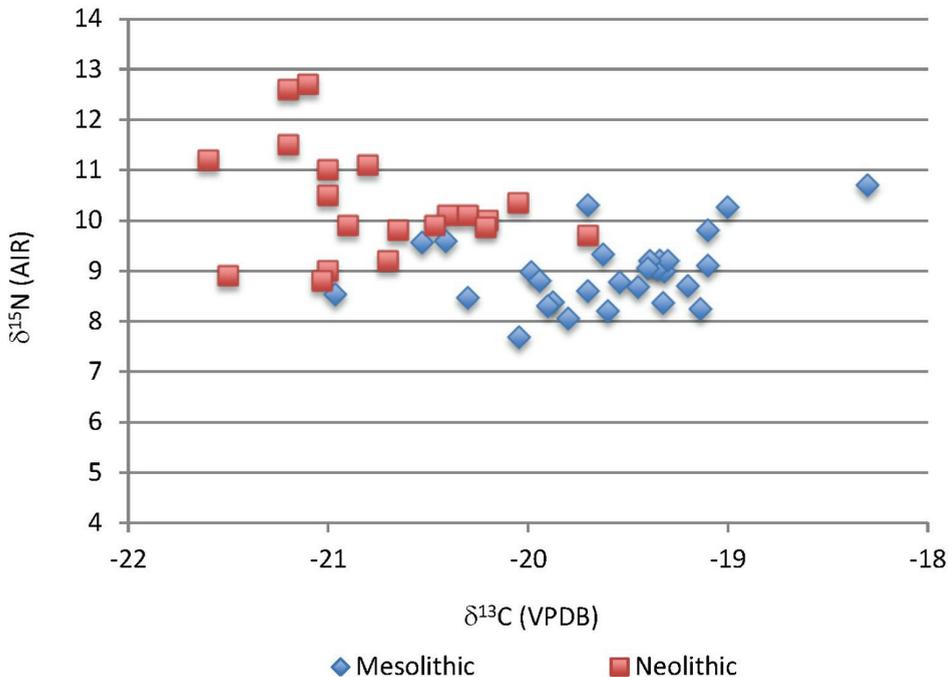


Figure 18. Stable carbon and nitrogen isotope values for human bone collagen for Mesolithic (Aveline's Hole, Totty Pot, Badger Hole, Greylake and Cannington Park Quarry) and Neolithic (Aveline's Hole, Totty Pot, Haywood Cave) sites. Other dated Neolithic humans lack $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements and cannot be plotted. The two Neolithic datapoints plotting above 12‰ in $\delta^{15}\text{N}$ are infants subject to a nursing effect (Schurr, 1998). Mesolithic datapoints from Aveline's Hole likely include some replication of measurements on different elements of the same individuals (i.e., ulnae and crania).

There is no indication of significant (i.e., detectable) consumption of marine foods in any of the Mesolithic and Neolithic individuals analysed from Somerset. This is perhaps more striking for the Neolithic, when the sea would have been considerably closer than in the Early Holocene, though this pattern is seen throughout Britain and Ireland and indeed much of the Continent (Schulting, 2011; 2013b; 2018; Schulting and Borić, 2017). At first glance it might be considered as surprising that Mesolithic individuals, particularly those from Greylake and Cannington Park Quarry, located in the midst of what would become the Somerset Levels, do not show stronger evidence for consumption of freshwater resources (depleted in ^{13}C but enriched in ^{15}N) (Schulting, 2015; 2018). However, given that sea levels were much lower in the early Holocene, this wetland would not yet be present (Campbell, 1998; Kidson and Heyworth, 1976), leaving the focus on terrestrial plant and animal resources.

A useful comparison can be made between the Somerset data and that from the cave site of Blätterhöhle, Germany, where both Early Mesolithic and, in this case, Late Neolithic individuals were recovered (Orschiedt *et al.*, 2012). As in Somerset, the Early Mesolithic hunter-gatherers at Blätterhöhle exhibited lower $\delta^{15}\text{N}$ values than seen in the Neolithic. What was more interesting, however, is that the Neolithic group at Blätterhöhle clearly divided into two isotopic clusters, with one showing greater reliance on freshwater aquatic resources seen in higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Moreover, these individuals were found to belong to the 'hunter-gatherer' mtDNA U5 haplogroup (cf. Pinhasi *et al.*, 2012), the same as seen in the Early Mesolithic individuals from Somerset, and while most of the others were placed in 'farmer' mitochondrial H and J haplogroups (Bollongino *et al.*, 2013). This resurgence of hunter-gatherer genetic influence is widespread in Continental Europe, but, as discussed above, is seen neither in Somerset nor across Britain more widely.

Rethinking ritual behaviour at Aveline's Hole

During the excavations of the site by the UBSS in the 1920s, a number of humanly modified objects were found that might be described as "grave goods" (Davies, 1924). These include teeth and shells that had been pierced, possibly to be strung as necklaces and also the modified ammonites later described by Donovan (1968). These would be unusual for the Neolithic but are common in both the Mesolithic and late Upper Palaeolithic. Donovan (1968) in his account of the ammonites lists several LUP analogues. A further intriguing point about this assemblage of humanly modified items is that, as far as we can tell, given the destruction of the original documentation, they were associated with two burials around the 60' from datum mark, that is deeper into the cave than the majority of the Mesolithic internments (Davies, 1924). It has been thought that these two burials, described as 'A' and 'B' in the early reports, would be earlier in date than the majority and the finding, by Meiklejohn and Babb reported here, that one of the crania destroyed in the blitz might have been Palaeolithic lends more weight to this possibility.

More problematic are the engraved lines found in 2003 and reported by Mullan and Wilson (2005). The Late Upper Palaeolithic or the Early Mesolithic was thought to be the most likely period of origin, based on comparisons with motifs across Europe and on the dating results for burials at the cave, with the latter favouring an Early Mesolithic assignment. However, similar motifs are also known from Neolithic contexts, including the flint mines in the chalk of southern Britain (see for example Teather, 2011, 2015), the Ness of Brodgar in Neolithic Orkney (Card and Thomson, 2011) and 'megalithic art' from a number of passage tombs in Ireland (Hensey, 2012; Shee Twohig, 2000). As it is impossible to describe these engravings as anything other than 'old' based on appearance, a Neolithic origin must now be considered.

Consequences for previous and future research

When first analysed, it was noted that Aveline's Hole showed considerably less evidence for dental microwear than might be expected for hunter-gatherers (McLaughlin, 2005). The new dating results reported here suggest that at least some of the molars analysed are likely to be of Neolithic rather than Mesolithic age, which could account for this anomaly. Similarly, it is now unknown whether the published strontium isotope measurements (Price and Schulting 2005) refer to Mesolithic or Early Neolithic individuals. Based on dated crania, the two periods are likely to be approximately equally represented, so that it is highly probable that this 50:50 ratio extends to teeth. Most teeth from the site are loose specimens, and no petrous bones analysed for DNA and AMS radiocarbon dating were associated with mandibles or maxillae. Unfortunately, then, any future work on the teeth from Aveline's Hole would need to be accompanied by DNA and/or radiocarbon dating directly on the specimens in order to distinguish between individuals of Early Mesolithic and Neolithic age. The cautionary tale provided by Aveline's Hole may be relevant for other sites as well.

More broadly, Aveline's Hole provides an extreme example of the potential biases that may be incurred when choosing samples for scientific analysis of the archaeological record. The use of the petrous portion of the temporal bone or tooth cementum in genetic analysis is well justified, as these provide the highest likelihood of recovering endogenous DNA from a specimen. However, it may impact on the representativeness of the resulting dataset. Not all cases will be as unexpected as at Aveline's Hole, where postcranial elements are from an entirely different time-point and culture, but one can easily imagine cases in which skulls or crania from a site might only be representative of a particular sex, kinship group or ethnicity, and not of the site (or the source community) as a whole.

CONCLUSIONS

The inclusion of a number of human bone samples from Aveline's Hole in a recent ancient DNA study revealed the completely unexpected presence of individuals with Neolithic 'farmer' ancestry. This led to a considerable re-analysis of aspects of the collection, including research into the history of the collection, combined with 14 new AMS ^{14}C dates and stable carbon and nitrogen isotope measurements, as well as a re-appraisal of the previously reported $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements. The results demonstrate renewed deposition of human remains, specifically crania, in the cave in the Early Neolithic, following a hiatus of nearly five millennia. It is possible that the visible presence of earlier (i.e., Mesolithic) skeletons on the cave floor, combined with perceived similarities between caves and chambered tombs, led to the re-use of the site in the Neolithic, by people with a very different ancestry. New analyses were also undertaken on the three more complete, but unfortunately now lost, crania from the site, leading to the suggestion that Aveline's Hole 'A' may be of Late Upper Palaeolithic date.

The results from Aveline's Hole were then placed into a broader comparative context of human remains from Mesolithic and Neolithic Somerset. While the site is still unmatched for the number of Early Mesolithic individuals represented, it is becoming increasingly evident that a number of both cave and open-air sites in Mendip and the surrounding area were used for burial at this time, including Gough's Cave, Badger Hole, Greylake and Cannington Park Quarry, while Totty Pot is later by approximately one millennium. What remains striking is the continued absence of any evidence for the deposition of human remains dating to the four millennia prior to the appearance of the Neolithic. Burial practices must have changed

significantly in the Late Mesolithic since, all else being equal, there would be expected to be more, rather than fewer remains from earlier than later periods, let alone none. While a definite difference in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can be seen between the Mesolithic and Neolithic, this is likely related to changes in the underlying isotopic baseline between the early and middle/late Holocene – in both periods terrestrial plant and animal resources dominated the diet, though these would be exclusively wild in the Mesolithic and predominantly domesticated in the Early Neolithic.

What perhaps emerges most strongly from the study is the ability of the archaeological record to continue to surprise, and hence the need to revisit previously accepted conclusions. While Aveline's Hole is in many ways a difficult collection, its importance to understanding the early Holocene prehistory of Britain and of western Europe is clear. The narrative of Aveline's Hole has been developed over the course of the last century, but with the previous extensive dating programme it seemed that the chronological element was complete. The decision to generate the additional radiocarbon dates reported here was driven by seemingly anomalous results from a newly applied method – palaeogenomics, or ancient DNA. Despite the previous seemingly comprehensive dating series, it is salutary to note that an entirely separate phase of activity at the site could be missed. While we cannot suggest that the history of this internationally important site has now been fully captured, the new results do take its story forward.

ACKNOWLEDGEMENTS

Funding for nine of the new radiocarbon dates from Aveline's Hole reported here was provided by NERC's NRCF programme (NF/2016/2/16). The ancient DNA study was funded by the Wellcome Trust (100713/Z/12/Z), as were three new radiocarbon dates from Aveline's Hole. The isotopic analysis of the Badger Hole human remains was funded as part of a NERC studentship (NE/K500987/1). Many thanks to Sharon Clough of Cotswold Archaeology for permitting us to cite the new dates and stable isotope data from Cannington Quarry, to Richard Brunning of the Somerset Heritage Centre for allowing sampling of the Greylake crania for stable isotope analysis, and to Andrew Chamberlain, University of Manchester, for directing us to the Brodie dataset, critical to the craniometric analysis. Thanks also to reviewers for their comments and suggestions.

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Site/Sample	Sample id.	Element	Lab No.	Nuclear Coverage	Mitochon. Coverage	% Endog	Radiocarbon date and period	Result	Y-haplogroup	mtDNA	Sex
Gough's Cave	Cheddar Man (GC1)	Petrous	SB524/I6767	2.31635x	85.02269x	46.64	9100±100 BP, OxA-814, EM	Pass	I2a2	U5b1	XY
Badger Hole, 1	BH2 (1783/30)	Tooth	SB404	0.00374x	1.23707x	0.93	9360±100 BP, OxA-1459, EM	Fail – preservation	-	-	-
Badger Hole, 2	BH1 (227, 2011.37)	Tooth	SB405	0.00262x	6.60016x	0.92	9060±130 BP, OxA-679, EM	Fail - contaminated	-	-	-
Aveline's Hole, 1	M1.11.326	Petrous	SB350/I6746	0.92596x	68.59835x	68.3	4809±45 BP, UBA-30800, EN	Pass	NA	U5b1	XX
Aveline's Hole, 2	M1.11.321	Petrous	SB349/I3009	0.00700x	0.22663x	1.43	Undated – period unknown	Fail – preservation	-	-	-
Aveline's Hole, 3	M1.15.3	Femur	SB343/I6745	0.00913x	1.63414x	2.15	9340±50 BP, OxA-34338, EM	Pass	NA	B5 / H13 / HV	XX
Aveline's Hole, 4	M1.11.309	Petrous	SB348/I3008	0.00722x	0.31535x	2.89	4906±33 BP, OxA-34337, EN	Fail – preservation	-	-	-
Aveline's Hole, 5	M1.14.130	Femur	SB342	0.00003x	0.00966x	0.04	Undated – presumed EM	Fail – preservation	-	-	-
Aveline's Hole, 6	M1.11.323	Petrous	SB344	0.00006x	0.00821x	0.07	Undated – period unknown	Fail – preservation	-	-	-
Aveline's Hole, 7	M1.11.374	Cranial fragment	SB345	0.00001x	0.00489x	0.02	Undated – period unknown	Fail – preservation	-	-	-
Aveline's Hole, 8	1A.1.10A	Tibia	SB346	0.00026x	0.04822x	0.22	Undated – presumed EM	Fail – preservation	-	-	-
Aveline's Hole, 9	M1.14.55	Tibia	SB337/I6744	0.00882x	6.22446x	1.42	9230±50 BP, OxA-34339, EM	Pass	IJK	U5b1	XY
Aveline's Hole, 10	M1.11.270	Petrous	SB339	0.00019x	0.02788x	0.39	Undated – period unknown	Fail – preservation	-	-	XY
Aveline's Hole, 11	M1.11.101	Tooth	SB351	0.00052x	0.17110x	0.84	Undated – period unknown	Fail – preservation	-	-	-
Aveline's Hole, 12	M1.11.241	Tooth	SB352	0.00005x	0.02939x	0.04	Undated – period unknown	Fail – preservation	NA	-	XX
Aveline's Hole, 13	M1.11.325	Petrous	SB338/I3005	0.11656x	6.97489x	13.97	4934±35 BP, OxA-34336, EN	Pass	NA	K1a4	XX
Greylake, 1	E22	Cranium	SB407	0.00071x	0.08099x	0.92	9118±37 BP, Wk-30930, EM	Fail – preservation	-	-	-
Greylake, 2	E22/23	Tooth	SB408	0.00011x	0.07297x	0.07	9170±40 BP, Wk-30931, EM	Fail – preservation	-	-	-
Greylake, 3	E23	Cranium	SB406	0.00017x	0.02221x	0.41	9134±37 BP, OxA-25666, EM	Fail – preservation	-	-	-
Hay Wood Cave, 1	HWC III	Petrous	SB432	0.01825x	1.28807x	7.82	4786±32 BP, OxA-19906, EN	Pass - low coverage	-	-	-
Hay Wood Cave, 2	HWC adolescent	Tibia	SB410/I3022	0.00593x	5.70487x	2.67	5044 ± 23 BP, OxA-19914-5, EN	Fail -contamination	-	-	-
Totty Pot, 1	2004.9/257	Femur	SB400/I5374	0.02941x	6.68357x	0.28	4008±39 BP, OxA-16460, LN	Pass	I	H1c	XY
Totty Pot, 2	2004.9/68	Femur	SB399	0.00139x	0.32730x	0.7	4473±35 BP, OxA-16459, MN	Fail -preservation	-	-	-

Table 6. Results of the palaeogenetic screening and analysis of Mesolithic and Neolithic human remains recovered from Mendip and the surrounding area.