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New palaeontological evidence suggests an early Middle Pleistocene age for the lower levels of Sun Hole Cave, Cheddar, Somerset, UK

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ABSTRACT

Sun Hole, a small fissure cave on the north side of Cheddar Gorge, Somerset, is best known as the site where late Upper Palaeolithic artefacts are associated with human and other mammal remains that immediately pre-date the Lateglacial interstadial. These remains from the upper levels (Unit I) overlie sediments (Unit II) that are thought to have accumulated during a full glacial period, below which are sediments (Unit III) attributed to an interglacial stage. The extinct land snail *Retinella* (*Lyrodiscus*) sp., which in Britain was only known from the Hoxnian Stage, had previously been recovered from Unit III. The interglacial at the base of the sequence was therefore assigned to the Hoxnian Stage (Marine Isotope Stage (MIS) 11, 424–374 kyr). Here we provide additional analyses of samples from Unit III, which as well as containing further *Retinella* (*Lyrodiscus*), also yielded a specimen of *Monachoides incarnatus*, its first record from the British Pleistocene. An associated assemblage of small mammals included a few that are rare in the British Pleistocene, such as birch mouse (*Sicista* cf. *betulina*) and garden dormouse (*Eliomys quercinus*). The vole *Lasiopodomys gregaloides* and the shrew *Sorex* (*Drepanosorex*) *savini* do not occur as late as the Hoxnian and therefore suggest an older age in the early Middle Pleistocene. The record from Sun Hole therefore has parallels with the well-known sequence from the upper Calcareous Member in the nearby cavern system at Westbury-sub-Mendip.

1. Introduction

Cheddar Gorge in Somerset is the largest and most spectacular karst gorge in Britain. It is incised into the Carboniferous Limestone succession on the southern flank of the Mendips and extends about 2 km eastwards from the village of Cheddar, forming the downstream portion of an extensive dry valley network that once drained most of the Mendip plateau (Fig. 1). There is an extensive literature about its origin, the most commonly accepted view is that the incision occurred during the last million years by a subaerial meltwater river during periglacial periods, when underground drainage was restricted (Smith, 1975; Stanton, 1985). This chronology is based on the dating of speleothems that occur in caves at different elevations within the gorge, although the dating becomes far less secure with increasing age (Atkinson et al., 1978; Farrant, 1991, 1995). Several of the caves contain Upper Palaeolithic archaeology associated with human and other faunal remains, some of the few instances where this occurs in Britain. Analyses of these hominin remains have shed much light on the diet of these Upper Palaeolithic populations (Richards et al., 2000; Stevens et al., 2010), as well as on their recolonization history during the early Lateglacial (Jacobi and Higham, 2009, 2011). Moreover, isotopic studies have elucidated the nature of the climatic conditions that these populations had to endure (Reade et al., 2020). This paper is concerned with a small but important cave known as Sun Hole, from which some of this Upper Palaeolithic archaeology was obtained. Our focus here, however, is not on the Upper Palaeolithic horizons in the upper levels of the cave but on the much older sediments in the lower parts of the sequence. We report new evidence from land snails and small mammals confirming that these lower levels accumulated during an interglacial, but we suggest that they formed during the early Middle Pleistocene, rather older than previously supposed.

2. The site

Sun Hole (UK National Grid Reference ST 467541; Fig. 1) is a small fissure cave on the north side of Cheddar Gorge situated 46 m above its floor at an elevation of about 83 m OD (http://www.ubss.org.uk/resources/surveys/survex/SunHole.pdf). It is located opposite and just north of the better-known Gough's Cave from which similar but slightly later Upper Palaeolithic Magdalenian archaeology has been recovered

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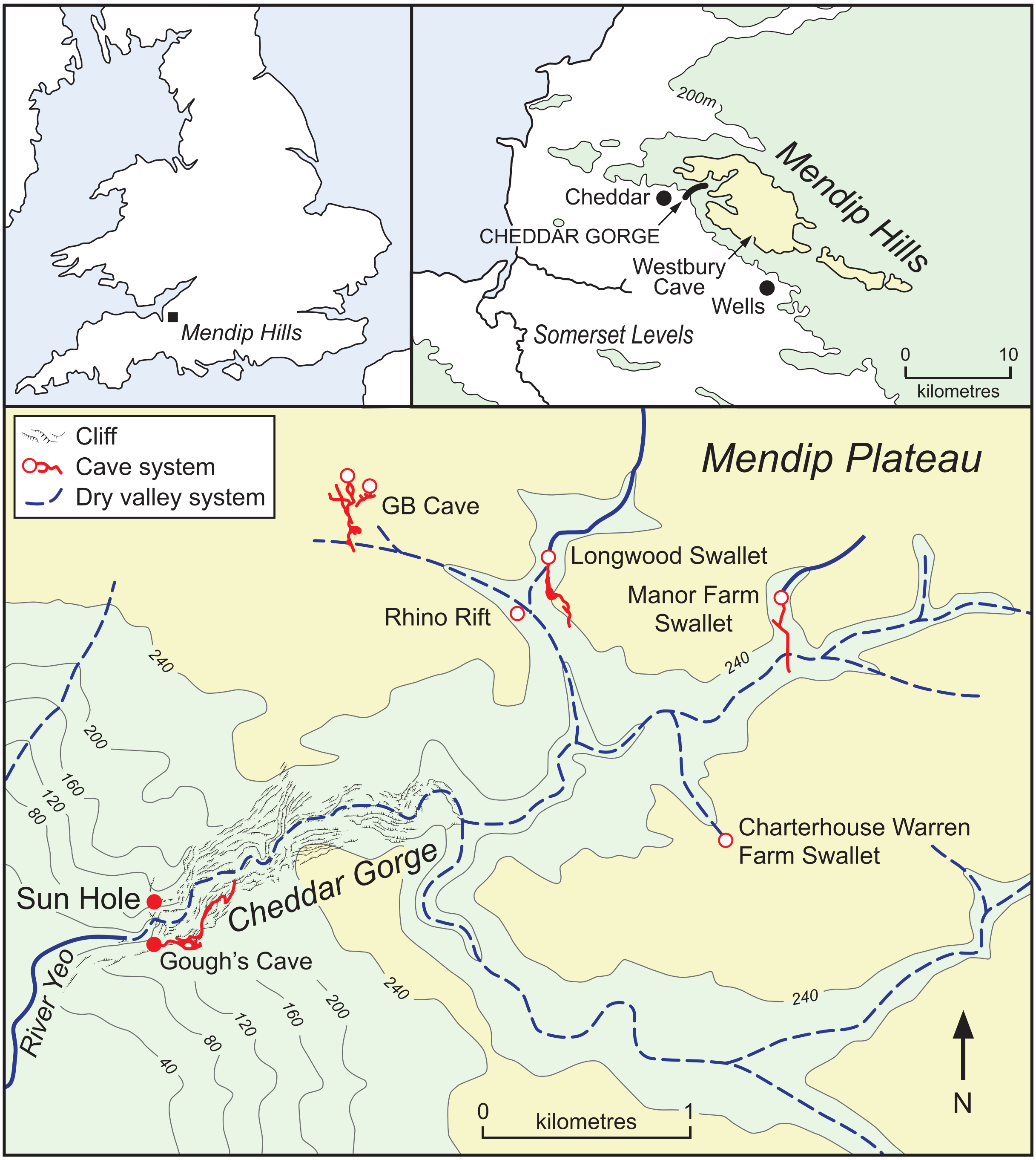


Fig. 1. Map showing the location of Sun Hole and Gough's Cave within Cheddar Gorge (modified from Waltham et al., 1997 and Cook, 1991). Contours in metres.

(Jacobi, 2004; Jacobi and Higham, 2011). The entrance to Sun Hole is about 4 m across and extends for just over 13 m in a northerly direction, narrowing towards the back, which is blocked by a boulder-choke. Extensive accumulations of cave sediment remain intact behind a standing section of the cave set 4 m in from the mouth. This has been the focus of a series of excavations at Sun Hole, firstly by Professor E.K. Tratman during the periods 1926–8 and 1951–3 and secondly by J.B. Campbell in 1968. This work gave rise to a number of publications on the cave sediments and stratigraphy (Tratman and Henderson, 1928; Tratman, 1955; Ollier, 1958), vertebrates (Jackson, 1955; Tratman, 1955; Bramwell, 1957), molluscs (Davis, 1955) and archaeology (Campbell, 1970, 1977).

New excavations were undertaken between 1977 and 1982 by S.N. Collcutt, A.P. Currant and C.J. Hawkes with the aim of resolving some outstanding stratigraphical issues and improving the site chronology (Collcutt et al., 1981; Collcutt, 1984). These new excavations were essentially of the same exposure figured by Tratman (1955) and Campbell (1977), but they extended the sequence for a further 3 m before conditions became too unsafe to continue. The cave sediments at Sun Hole are therefore at least 8 m thick and they have been divided into three main units, dating from the Holocene and Late Devensian (=Late Weichselian), from a full glacial episode (probably Devensian) and from an undated interglacial (Collcutt et al., 1981; Collcutt, 1984).

3. Stratigraphy

The stratigraphy of the cave sediments at Sun Hole is extremely complex (Collcutt et al., 1981; Collcutt, 1984; Fig. 2). The general slope of the deposits appears to be from north to south, down and out of the mouth of the cave, rather than into it. During the more recent excavations, 35 individual layers were identified and sampled to cover the full sequence exposed, although the base of the Pleistocene was not reached (Collcutt et al., 1981, fig. 6). The layers were assigned to three units separated by apparent breaks in the sequence as follows: Unit III (Layers 35–19), Unit II (Layers 18–14) and Unit I (Layers 13–1). This sampling provided the basis for the reconstruction of the sedimentary processes responsible for the formation of the deposits (Collcutt et al., 1981, fig. 7). We do not propose to review this complex history since our interest here only concerns the sediments towards the base of the newly exposed sequence assigned to Unit III. These sediments have a generally high clay content with extremely variable quantities of matrix carbonate. Crystalline concretions are abundant and surface growths on stones are frequent. Clastic material, which constitutes an important component throughout the deposits, includes material from a wide range of carbonate rocks. The dominant type is a dark grey calcite mudstone derived from the Clifton Down Facies of the Lower Carboniferous in which the cave is formed. Fractured stalactite and curtain formations, sometimes altered to a biscuity consistency, occur throughout. Some of the clasts reach the size of small boulders. Dolomitic sand, metallic (hydr)oxide aggregates, silicified crinoid ossicles and fragments of land snails are common components. There is extensive fissuring, especially of concretions and dolomitic conglomerates, coupled with staining, alteration and disintegration. Layer 34 at the base of the sampled sequence, which yielded the richest assemblage of land snails, has been described as a reddish brown (5YR 5/4 to 4/4 at top) compact clayey loam that became increasingly sandy and carbonate-rich upwards. Layer 23 is a reddish yellow (6YR 7/6) breccia with *in situ* flowstone and small stalagmites. This horizon appears to mark a significant change in the pattern of sedimentation. Figure 2 shows the stratigraphy of the cave sediments at Sun Hole based on Collcutt et al. (1981), who provided detailed descriptions of the individual layers.

Sun Hole was included as part of a programme to undertake new uranium-series dates from speleothems that could be related to associated mammal faunas (Hodge et al., 2016). The oldest age of ~400 ka, which is close to the limit of U-series dating, was obtained from a fragment of detrital speleothem within the cave breccia. Hodge et al. (2016) stated that this was sample SNH-15′ but this appears to be an error because according to Collcutt et al. (1981) this is a silty loam (Layer 5) that contains no speleothem clasts. Professor Peter Smart (*pers. comm.* to SAP) informs us that this sample came from the University of Bristol Spelaeological Society (UBSS) collection and was recovered from a depth of 15 ft (4.6 m) in Tratman's trench. Tratman (1955: 64) noted that "At a depth of 15ft. [4.6 m] fragments of a broken stalagmite floor begin to appear and continue right down to the bottom of the excavation [~5.5 m]". The thickness of the stalagmitic fragments varied from "less than 2 in. [51 mm] up to 1 ft. [0.3 m]" and occurred in various orientations, even upside down (Tratman, 1955: 64). Inspection of Tratman's section drawing (Tratman, 1955, fig. 8) shows that the 15 ft [4.6 m] level in his trench coincides with the flowstone Layer 23 of Collcutt et al. (1981). The provenance of sample SNH 2 is also problematic. According to Hodge et al. (2016) this related to a hanging flowstone of unit D, which yielded ages that were inverted but which agreed within error (344 +21/−17 ka and 311 +13/−12 ka), suggesting that this flowstone formed during MIS 9. The location of the sample is shown as an inset of figure 6 in Collcutt et al. (1981) but this does not match their descriptions as "Crystalline stalagmite blocks embedded within the granular stalagmite capping Layer 1. These are fragments of a floor which was once at least 15 cm thick." Inspection of the dated sample (Hodge et al., 2016, Supplementary material) shows that it has clear layering and appears to have formed within the cave interior. However, on the unsampled face there appears to be a thin coating of tufaceous material. SNH 2 might represent an early false floor that has collapsed and then been coated and incorporated into a much younger tufaceous granular speleothem deposit when the cave was open to the outside. Either way, it still demonstrates that the cave was relict by ~320 ka (Andrew Farrant, *pers. comm.*).

The provenance of the remaining samples dated by Hodge et al. (2016) is more straightforward. Three calcite sub-samples (SNH 44A-C) from cemented breccias of Layer 23 yielded concordant ages (128.6 ± 2.3 ka, 122.5 ± 2.7 ka and 117.5 ± 1.7 ka) consistent with an attribution to MIS 5e, although the youngest was affected by detrital contamination. Two further dates from a large broken, coarsely crystalline, stalagmitic boss (SNH 52B) from Layer 22, "but possibly referable to Layer 23" (Collcutt et al., 1981: 26), yielded late MIS 5e/MIS 5d ages (114.5 ± 1.5 ka and 110 ± 1.7 ka) but they appear to be inverted. The provenance of the dated samples is shown in Figure 2.

4. Material and methods

Shells and small mammal remains picked from the complete original series of small samples taken from successive stratigraphical levels within Unit III have now been analysed, together some from Unit II. These have been augmented by material from a previously unsorted residue (APC3) collected by A.P. Currant in 1982 from Layer 34 (Unit III), archived in the Department of Earth Sciences, The Natural History Museum, London (NHM). No record of original sample weights or the mesh size used to sieve the samples can be found. All fossils retained by a 0.5 mm sieve were picked under a binocular microscope using a wet paint brush. The scanning electron microscopy was undertaken using a Philips XL30 FEG-SEM in the Cambridge Advanced Imaging Centre at the University of Cambridge.

5. Results

5.1. Land snails

Eighteen samples from 12 individual layers were analysed through the lower levels of the sequence (Fig. 2). One of these samples came from Unit II, and the rest were from Unit III. Sample 38 was taken immediately above Unit III and is included because it contained a specimen of *Lyrodiscus*; other samples from Unit II contained very few indeterminate shell fragments or were completely barren. Few complete shells were recovered and the material consisted almost entirely of comminuted fragments that did not allow conventional shell counts. However, the surface detail of many of the fragments was well enough preserved to allow an assessment of the species present (*cf.*, Preece, 1981). All the fragments belonged to the shells of land snails. A total of 16 taxa was recovered, 15 of which occurred in Layer 34, the richest horizon in the sequence (Table 1). The species not recovered from Layer 34 was a juvenile specimen of *Oxychilus* sp. from Layer 19 (Sample 38), but the shell was more translucent than those of other species in the profile and, unlike these, it did not have orange sediment adhering to it. This specimen may therefore be intrusive, especially since *Oxychilus* is particularly common in rock-rubble habitats (Evans and Jones, 1973).

Amongst this limited fauna were three species that no longer live in the British Isles. The fragments of Clausiliidae included some that were coarsely ribbed. These have been tentatively attributed to *Clausilia pumila*, a central European species that extended into North-West Europe during interglacials of the Middle Pleistocene. The second non-British species is *Monachoides incarnatus*, represented by a single fragment of body-whorl from Layer 34. This species occurs in leaf-litter of relatively humid forests under shrubs and rock-rubble (Welter-Schultes, 2012). It is another species with a broad modern central European range, reaching eastern France and southernmost Sweden (Kerney et al., 1983; Welter-Schultes, 2012). The shell of this species has a distinctive fine reticulate microsculpture recognisable even on small fragments (Fig. 3a–c). There are no previous authenticated records of this species from the British Pleistocene. In France it is known from Middle and Late Pleistocene interglacials (MIS 11 and MIS 5) and there are two records from the late Holocene (N. Limondin-Lozouet, *pers. comm*., December 2021). The last non-

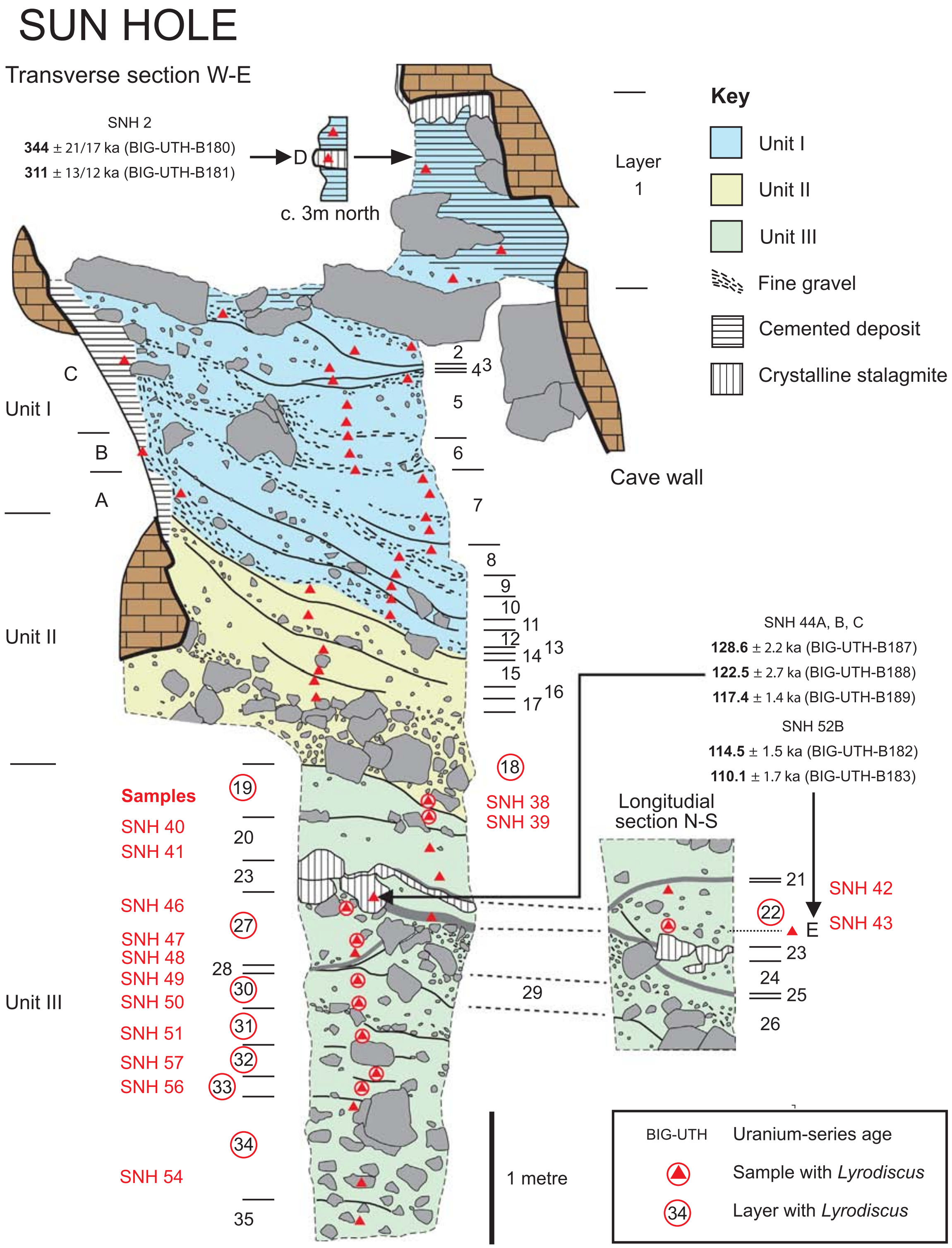


Fig. 2. The stratigraphy of the cave sediments in Sun Hole (adapted from Collcutt et al., 1981), showing the location of samples and the provenance of the material dated by Hodge et al. (2016). Layers A–D cannot yet be inserted into the main stratigraphy.

British species recovered from Sun Hole is *Retinella* (*Lyrodiscus*) *elephantium*, which is now completely extinct. This species, indeed the whole subgenus *Lyrodiscus*, can also be recognised by virtue of its distinctive microsculpture of raised spiral ridges irregularly interrupted by small breaks, again recognisable on minute shell fragments (Fig. 3d–f). On umbilical fragments the spiral microsculpture appears beaded. Living members of the subgenus *Lyrodiscus* are confined to the Canary Islands where they occur predominantly in woodland habitats (Rousseau and Puisségur, 1990; Alonso et al., 2013). From the late Neogene to the Middle Pleistocene *Lyrodiscus* had a much wider geographical range extending across large areas of NW Europe, where it has been recorded under a variety of generic and species names. The earliest available name for the Middle Pleistocene species is *elephantium* Bourguignat (Limondin-Lozouet and Antoine, 2006).

Table 1
Land snails recovered from the samples from Unit III at Sun Hole. Sample 38 came from the base of Unit II. $+^1$ = fragments with two bands; $+^2$ = possibly intrusive.

Unit	III																		II
Layer number	35	34			33	32	31	30		27			23	22		20		19	18
Sample number	53	APC 4	APC 3	54	56	57	51	50	49	48	47	46		43	42	41	40	39	38
Pupilla muscorum (Linnaeus)	-	+	+	-	-	-	-	-	-	-	-	-	FLOWSTONE (MIS 5)	-	-	-	-	-	-
Vallonia costata (Müller)	-	+	-	-	-	-	-	-	+	-	-	+		-	-	-	-	-	-
Vallonia cf. *pulchella* (Müller)	-	+	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-
Vallonia pulchella/excentrica	-	-	+	-	-	-	-	-	-	-	+	+		-	+	-	-	-	-
Ena montana (Draparnaud)	+	-	+	+	+	-	-	-	-	-	-	-		-	-	-	-	-	-
Discus rotundatus (Müller)	-	+	+	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-
Vitrinidae	-	+	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-
Vitrea cf. *crystallina* (Müller)	-	+	+	-	+	-	-	-	-	-	-	-		-	-	-	-	-	-
Aegopinella nitidula (Draparnaud)	-	+	-	+	-	-	-	-	-	-	-	-		-	-	-	-	-	-
Retinella (*Lyrodiscus*) *elephantium* (Bourguignat)	-	+	+	-	+	+	+	+	+	-	+	+		+	-	-	-	+	+
Oxychilus sp.	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	$+^2$
Clausiliidae (includes *Clausilia pumila* Pfeiffer)	-	+	+	-	+	+	-	-	-	-	-	-		-	-	-	-	-	-
Monachoides incarnatus (Müller)	-	+	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-
Trochulus cf. *hispidus* (Linnaeus)	-	+	+	+	+	+	-	-	+	+	+	-		+	-	+	+	+	-
Arianta arbustorum (Linnaeus)	-	+	+	+	-	+	-	-	-	+	-	+		-	+	?+	-	-	-
Helicigona lapicida (Linnaeus)	-	+	+	+	-	-	-	-	-	+	+	-		-	-	-	-	-	-
Cepaea sp.	-	+	$+^1$	-	-	?+	+	$+^1$	+	-	+	-		+	+	$+^1$	-	-	-
Helicidae indeterminate	+	-	-	-	-	+	-	-	-	-	-	-		-	-	-	-	-	-

The remaining species not only occur in the British Isles today but also still inhabit Cheddar Gorge itself (*cf.*, Kerney, 1999). The most frequent species was *Trochulus* cf. *hispidus* that lives in a broad range of habitats. This was identified by virtue of hair-pits clearly visible on many shell fragments. The identification is tentative because other taxa also have hair-pits on their shells. Some apertural fragments had a strong apertural rib and a thickened peristome that is not typical of this species, so other taxa may be present. A few additional catholic species were recovered but the other taxa come from two different habitats. Areas of open ground on the limestone slopes would provide the conditions necessary for *Pupilla muscorum* and the *Vallonia* species, whereas more shaded conditions are indicated by several of the other species including *Ena montana*, *Discus rotundatus*, *Aegopinella nitidula* and *Helicigona lapicida*. These are all species that typify temperate conditions and in Britain they are only known from interglacials (including the Holocene). The occurrence of *Ena montana* is particularly interesting because although widespread in central Europe, it has a far more restricted distribution in southern England (Kerney, 1999), where it is at the northern margin of its modern European range (Kerney et al., 1983; Welter-Schultes, 2012). It extends northwards into the Baltic States and European Russia and can clearly withstand cold winters. On the continental mainland *E. montana* tolerates disturbed habitats and is a common hedgerow species, whereas in Britain it is far more exacting in its requirements, occurring almost exclusively in old, undisturbed woodland, such as that within Cheddar Gorge. Kerney (1968) pointed out that all of its British sites occur in parts of the country with the highest summer temperatures, nearly all lying within the July isotherm for + 16.5 °C.

5.2. Vertebrates

Vertebrate remains from the sediment samples collected by Simon Collcutt and Andy Currant from Units II and III have now been re-examined. The small mammals from these levels were originally identified by Currant upon which his preliminary published description and discussion is based (Collcutt et al., 1981). A few misidentifications were corrected, and additional records were reported by Collcutt (1984), resulting from new analyses of larger bulk samples collected in 1982. Currant recognised two faunal groups in this new material from Unit III. One from Layers 19 and 20 immediately above the flowstone contained cold species, such as collared lemming (*Dicrostonyx torquatus*) and Norway lemming (*Lemmus lemmus*). Collcutt (1984: 943–4) noted that a further molar of *Dicrostonyx* was recovered from Layer 24, in an area where the overlying flowstone had been naturally disturbed. He suggested that this specimen is intrusive, a supposition supported by the distinctive dark staining of the lemming teeth from these two horizons. The second faunal group came from layers below the flowstone, which marks a significant break in the sequence. Vertebrate and molluscan faunas from beneath the flowstone form a coherent assemblage compatible with interglacial conditions, with no evidence for any obviously derived elements or for any major change in ecological conditions.

The vertebrate assemblage from Unit III can now be augmented by material from the previously unsorted sample (APC3) collected by Currant in 1982 from Layer 34. Finds from this sample and a re-examination of specimens in the NHM collection have provided several significant additions to the published list. Despite the fragmentary nature of

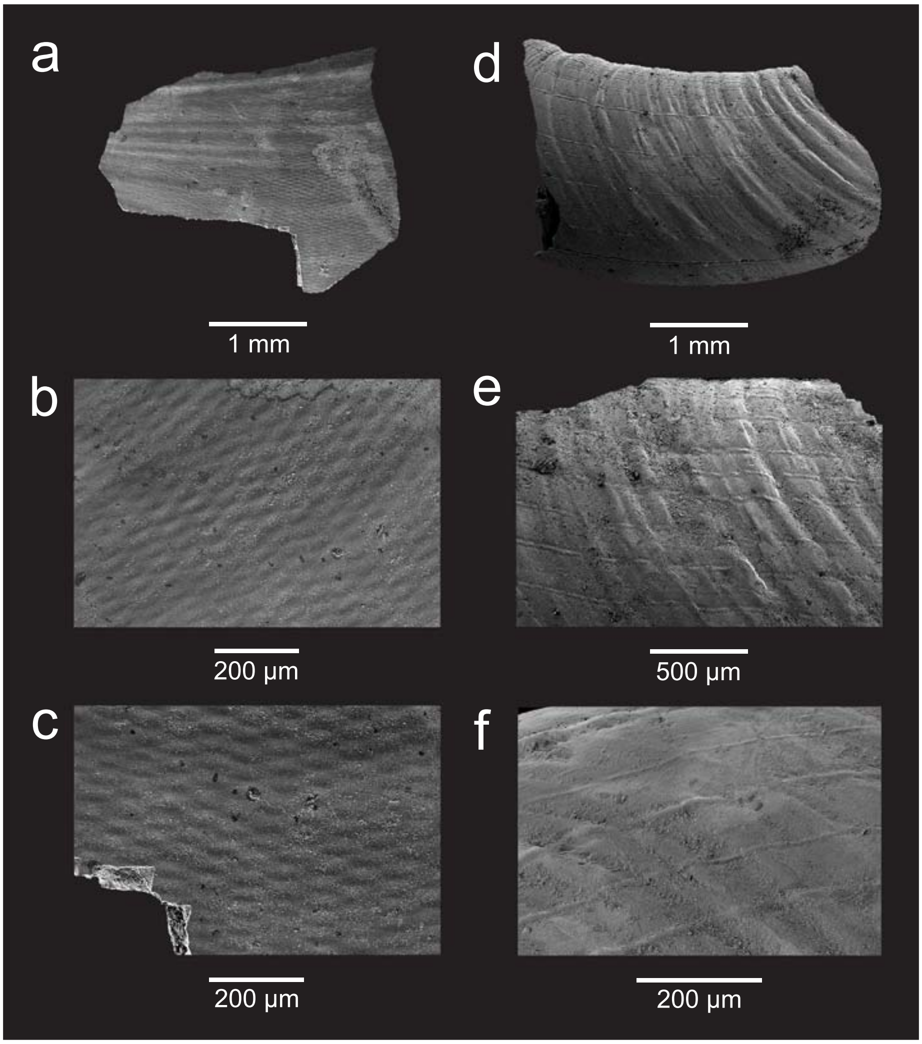


Fig. 3. Scanning electron micrographs of shell fragments from Layer 34: a–c, *Monachoides incarnatus* (Müller); d–f, *Retinella* (*Lyrodiscus*) *elephantium* (Bourguignat).

many of these specimens, it is now possible to recognise 17 microvertebrate taxa (Table 2), including several that are ecologically and biostratigraphically significant (Fig. 5). These records provide the basis for the radical shift in interpretation of Unit III from a possible Hoxnian age (MIS 11) to an older early Middle Pleistocene one.

The small mammals include some species that are now extinct in Britain. Of particular biostratigraphical significance is the vole *Lasiopodomys gregaloides*, which is unknown anywhere after the Anglian (= Elsterian/Oka, MIS 12, 478–424 ka) cold stage (Fig. 5a). One of the more significant elements of the Sun Hole fauna is the water vole *Arvicola*. Specimens from Sun Hole represent a transitional morphotype ('*cantianus*') between *Mimomys savini* (with rooted molars), described from the type Cromerian Stage at West Runton, Norfolk, and the modern species *Arvicola amphibius* (with continuously erupting cheek teeth) that extends from the Late Pleistocene (Fig. 5a–b). Another noteworthy addition is *Sorex* (*Drepanosorex*) *savini*, a distinctive extinct large shrew originally described from the type Cromerian at West Runton (Hinton, 1911). The Sun Hole record is based on an isolated upper antemolar from sample APC4 (Layer 34). The tooth is identical in size to Hinton's original material, and it displays the characteristically 'bulbous' morphology that is one of the defining features of *Drepanosorex* (Reumer, 1985). *Sorex* (*Drepanosorex*) *savini*, a common soricid in faunas from the later part of the 'Cromerian Complex' (*e.g.*, Boxgrove and Westbury Cave), does not appear to have survived into the Hoxnian, although a few fragmentary specimens of a large soricid from Southfleet Road, Ebbsfleet, Kent, may be a Hoxnian representative of the *Drepanosorex* lineage (Parfitt, 2013). Elsewhere in Western Europe, later representatives of this lineage are represented by the smaller species *S.* (*D.*) *postsavini* from Petersbuch 1, Germany (Horáček and Ložek, 1988), and by larger teeth of *Drepanosorex* from Neede, Netherlands, Erpfingen, Germany and Montousse 3, France (Rzebik-Kowalska, 1998). An almost complete cranium of a medium-sized shrew partly encased in calcitic mudstone was recovered from Layer 33 (sample SNH 56). This is identical in size and very similar in morphology to *S. runtonensis* from West Runton. The common medium-sized *Sorex* from British Hoxnian localities is indistinguishable from *S. runtonensis*, which according to Osipova et al. (2006) is closely related to the living tundra shrew *S. tundrensis* (but see Parfitt (1998), who suggested that it may be more closely related to the masked shrew *S. caecutiens*). *Sorex runtonensis* can therefore no longer be used as a biostratigraphical indicator for pre-Anglian sediments.

Another species that does have biostratigraphical significance is a pine vole *Microtus* (*Terricola*) sp. (assigned to *Pitymys arvaloides* by Currant, see Collcutt, 1984: 944). Pine voles do not occur in Britain today, but they were an important component of British early Middle Pleistocene and Hoxnian faunas (Schreve, 2001). Likewise, the small extinct mole *Talpa minor* has a similar stratigraphical range in Britain. Curiously, the larger, modern common mole *Talpa europaea* is absent from British Hoxnian sites, such as Southfleet Road (Parfitt, 2013), Barnham (Parfitt, 1998) and Beeches Pit, West Stow (Preece et al., 2007), which have

Table 2
Vertebrate remains recovered from the samples from Unit II and Unit III at Sun Hole. * denotes material identified and/or collected by A.P. Currant (AC) in 1982 and recorded in his notes with the Sun Hole collection at the NHM.

Unit	III																						II					
Layer	35	34			33	32	31		30			27			25	24	23	22		20	19		18	17	16	15	14	
Sample	53	APC4	APC3	54	56	57	51	AC	50	49	AC	48	47	AC	45	AC		43	42	40	39	AC	38	36	34	32	31	AC
AMPHIBIA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	FLOWSTONE (MIS 5)	-	-	-	-	-	-	-	-	-	-	-
Anura indet., frog or toad	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-		1	-	-	-	-	-	-	-	-	-	-
REPTILIA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Anguis fragilis Linnaeus, slow worm	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
MAMMALIA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Rodentia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Eliomys quercinus Linnaeus, garden dormouse	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Sicista cf. *betulina* Pallas, birch mouse	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Dicrostonyx sp., collared lemming	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*		-	2	1	-	*	-	-	-	1	-	*
Lemmus sp./*Myopus* sp., lemming	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*		-	-	-	-	-	1	-	-	-	-	-
Clethrionomys glareolus Schreber, bank vole	-	-	3	-	-	-	-	*	-	-	-	-	-	*	-	-		-	-	-	-	-	-	-	-	-	-	-
Clethrionomys, sp., vole	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Pliomys sp., extinct vole	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Arvicola cantianus (Hinton), water vole	-	-	-	-	-	-	1	*	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Microtus agrestis Pallas, field vole	-	1	-	-	1	-	-	-	-	-	*	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Lasiopodomys gregaloides (Hinton), extinct narrow-skulled vole	-	+[a]	1	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Microtus (*Terricola*) sp., pine vole	-	-	-	-	-	-	-	*	1[c]	-	?	1[c]	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Microtus sp., vole	-	3	6	-	10	4	-	-	1	2	*	1	-	*	-	*		1	-	-	1	*	-	-	-	-	1	-
Microtinae, vole	1	-	-	3	6	4	2	-	4	2	-	1	1	-	1	-		1	-	2	2	-	-	5	1	-	-	-
Apodemus sylvaticus Linnaeus, wood mouse	-	-	1	-	-	-	-	*	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Apodemus sp., mouse	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Eulipotyphla	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Sorex sp., shrew	-	-	4	-	1[b]	-	-	*	-	-	-	-	-	*	-	-		-	-	-	-	-	-	-	-	-	-	-
Sorex (*Drepanosorex*) *savini* Hinton, extinct shrew	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Soricidae indet, shrew	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Talpa europaea Linnaeus, European mole	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Talpa minor Freudenberg, extinct mole	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Talpa sp., mole	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Carnivora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
Mustela cf. *nivalis* Linnaeus, weasel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	1	-	-	-	-	-	-	-

[a] M_1 with anterior 'gregaloid' loop.
[b] identified as *Sorex araneus* by Currant (in Collcutt et al. 1981, Table 2).
[c] identified as *Microtus agrestis*/*arvalis* group by Currant (in Collcutt et al. 1981, Table 2).

yielded relatively large assemblages of *T. minor*. In the early Middle Pleistocene *T. europaea* occurs together with *T. minor* at Boxgrove (Parfitt, 1999) and they co-existed throughout the early Middle Pleistocene sequence at Westbury (Bishop, 1982; Andrews et al., 1999). The presence of both species of mole at Sun Hole strengthens the evidence for a pre-Hoxnian age for the lower deposits (Fig. 5a).

A molar of birch mouse, resembling that of *Sicista betulina*, from Layer 34 is also noteworthy as in Britain, birch mice are extremely rare as Pleistocene fossils hitherto only recovered from the Lower Palaeolithic land-surface (and associated deposits) at Boxgrove (Parfitt, 1999), and from earlier Cromer Forest-bed Formation deposits at Corton on the Suffolk coast (S.A. Parfitt, unpublished).

One other species found at Sun Hole deserves comment. This is field vole *Microtus agrestis*, identified on the basis of second upper molars with a diagnostic '*agrestis* loop', from three levels within Unit III. In Britain this species first appears during the late 'Cromerian Complex' but it is unknown from the type Cromerian at West Runton (Schreve et al., 1999: table 11). Its occurrence at Sun Hole, together with *Arvicola*, strongly points to an age post-dating the type Cromerian.

Some of the small vertebrates, especially the slow worm *Anguis fragilis* and the anurans may have lived or aestivated in the cave, but at least some of the bones and teeth were probably deposited either in the regurgitated pellets of birds of prey or in scats of mammalian predators. This conclusion is reinforced by the occurrence of a few teeth, some fragmentary and chipped, which bear traces of digestive acids indicative of the activity of predators. Significantly, none of the microvertebrate remains were rounded, abraded, or weathered in a way that would suggest extended periods of exposure or transport by flowing water, although other processes such as trampling or transport in a mudflow may have contributed to the fragmentation.

Ecologically, the range of small vertebrate taxa supports the molluscan evidence for a fully temperate environment that included woodland and dense vegetation suitable for bank vole *Clethrionomys glareolus*, garden dormouse *Eliomys quercinus* and wood mouse *Apodemus sylvaticus*, as well as open areas that favoured the *Microtus* voles.

6. Discussion

It is important first to consider the origin of the deposits containing the land snails and small mammal remains at Sun Hole. Collcutt et al. (1981) recorded extensive inwash of soil material during the early part of Unit III. This material consisted of sand-sized and smaller, irregular aggregates, containing oxides of iron, aluminium and manganese with colloidal silica, clay minerals and much organic material. They noted that the preservation of the shells, coupled with the closed fabric of the clay-rich sediments, militated against recent intrusion, a conclusion confirmed by the present study. They also noted that the modern soil outside the cave was rich in fragments of partially silicified oolites derived from the local bedrock, fragments of which are absent from the cave sediments, apart from rare occurrences in Unit I. Conversely, silicified crinoid ossicles are common in Unit III but absent in the modern soil and the immediately adjacent limestone bedrock. They consequently suggested that most of the ancient soil material entered the cave from some point further back in the system and not through the entrance of Sun Hole. This would also provide an explanation for the occurrence of a diversity of erratic lithologies recovered from Sun Hole.

Two lines of evidence suggested that the lowermost deposits (Unit III) of Sun Hole formed during an interglacial. First, Campbell (1977) recovered small quantities of pollen from his layer A1, equivalent to the top of Unit III, showing the presence of thermophilous tree pollen, which continued well into Unit II. Second, although microtine voles were well represented in Unit III, none of the remains belonged to species typical of cold stages. The interpretation of pollen from cave sediments is not straightforward because of uncertainties about its origin and taphonomy. The occurrence of *Abies*, *Tilia* and *Alnus* in Unit II in sediments reflecting the coldest part of the sequence clearly implies reworking or contamination. The presence of thermophilous trees, such as *Carpinus*, in Unit III, however, is less easy to dismiss and was used by Campbell (1977) to suggest a Last Interglacial (MIS 5e) age for the lower part of the sequence. Collcutt et al. (1981) were reluctant to assign an age to the interglacial but they tentatively agreed, not unreasonably, that it might be the Last interglacial. The subsequent discovery of *Retinella* (*Lyrodiscus*) sp. in the lowermost level led to a reappraisal of this age attribution (Ellis, 1983a, 1983b). Although known from earlier deposits, this extinct land snail is the index fossil of a rich forest assemblage (the '*Lyrodiscus* fauna') known from French calcareous tufas of MIS 11 age (Rousseau et al., 1992; Limondin-Lozouet and Preece, 2014; Limondin-Lozouet et al., 2015; Limondin-Lozouet, 2017; Limondin-Lozouet et al., 2020). The same distinctive assemblage with *Lyrodiscus* is known from two British Hoxnian interglacial tufa sites, namely Hitchin, Hertfordshire (Kerney, 1959; Holyoak et al., 1983) and Beeches Pit, West Stow, Suffolk (Kerney, 1976; Preece et al., 2007), where there is strong independent evidence for an MIS 11 age (Fig. 4). Since *Lyrodiscus* is unknown from later interglacial stages (post-MIS 11), the lowermost level (Layer 34) at Sun Hole was tentatively attributed to the Hoxnian (Ellis, 1983a, 1983b).

The new analyses presented here show that *Lyrodiscus* was not confined to Layer 34 but was present in eight of the overlying levels (Fig. 2; Table 1). The rather limited land snail assemblage recovered from these samples was ecologically consistent, suggesting that interglacial conditions may have extended up to Layer 18 (base of Unit II). Two things demonstrate that this interpretation is incorrect. First, the three samples from Layers 22, 19 and 18 occur above the flowstone (Layer 23) that has been dated to MIS 5. Second, these interglacial land snails were recovered from samples that had yielded small mammals including lemming (both *Lemmus* and *Dicrostonyx*), typical of cold stages. Unlike the assemblages from Layers 35–21, which yielded ecologically coherent assemblages of land snails and small mammals, those from Layers 22, 19 and 18 are obviously mixed. The land snails, including the *Lyrodiscus*, have clearly been reworked from lower levels and intermingled with a cold stage mammal fauna.

Leaving the mixed assemblages from the levels above the dated flowstone aside, there are features of the small mammal assemblage from beneath the flowstone (Layer 23) that suggest that the Hoxnian (MIS 11) age attribution may not be correct. Two species of vole, *Lasiopodomys gregaloides* and *Pliomys* sp., and the shrew *Sorex* (*Drepanosorex*) *savini* do not occur as late as the Hoxnian (Schreve, 2001; Parfitt, 2013) and therefore suggest an earlier age. Two other

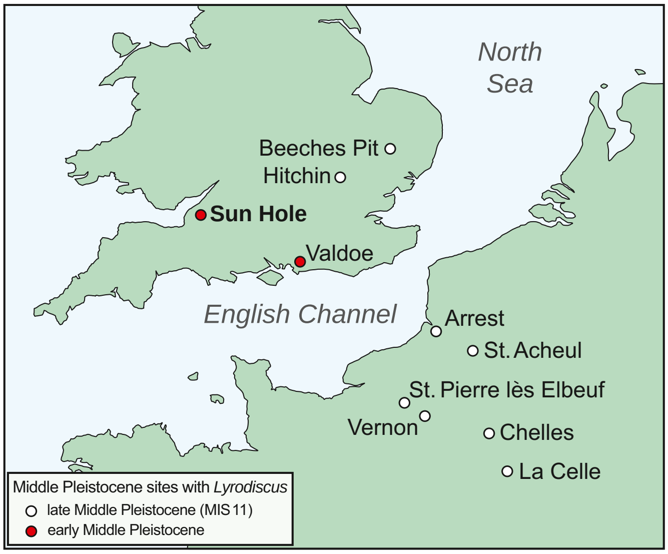
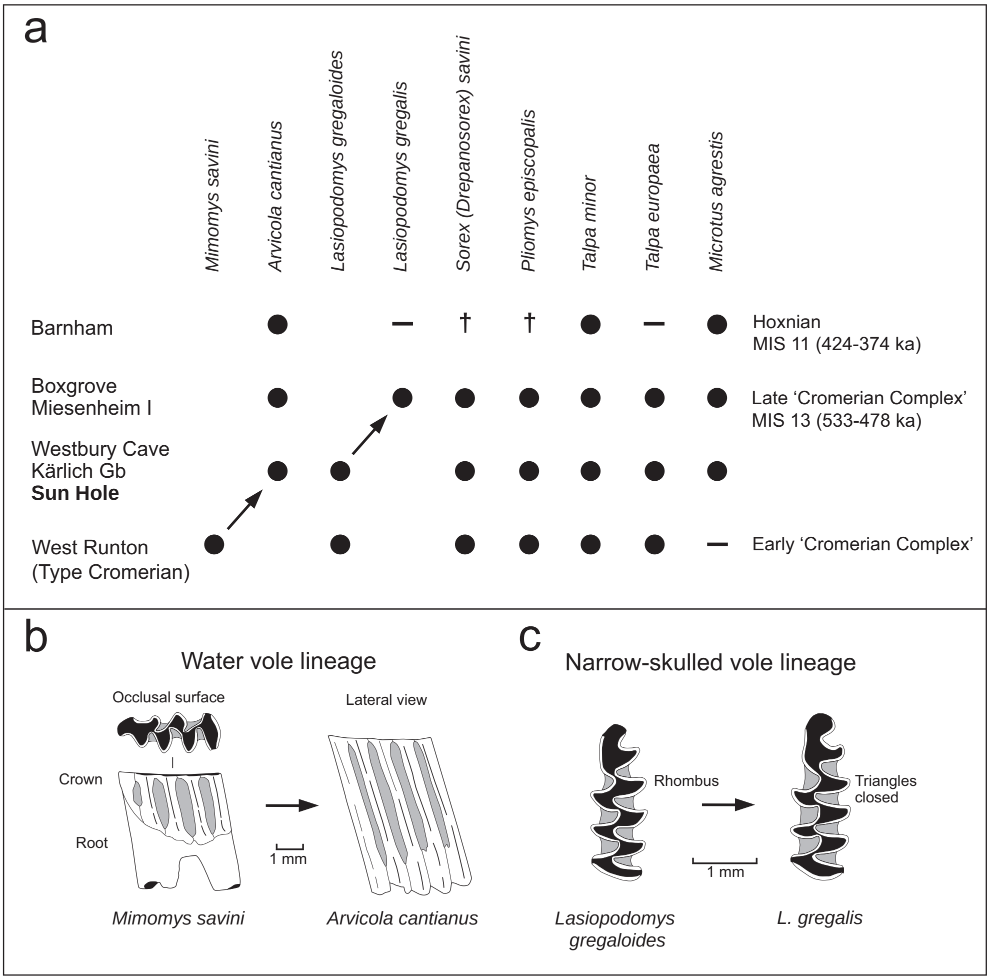


Fig. 4. Map showing Middle Pleistocene sites with *Retinella* (*Lyrodiscus*).

taxa help to constrain the dating further. The water vole at Sun Hole has unrooted molars (Fig. 5b) and is attributable to *Arvicola cantianus*, a Middle Pleistocene species that arose from *Mimomys savini* that occurs in the type Cromerian at West Runton. The field vole *Microtus agrestis* was also recovered from Sun Hole but this is also unknown from West Runton, despite the intensive sampling undertaken at that site (Schreve et al., 1999; Maul and Parfitt, 2010). The evidence from the mammalian biostratigraphy therefore suggests that the assemblage from Unit III existed after the type Cromerian but before the Hoxnian (Fig. 5a).

There is evidence from various sites across Europe that the *Mimomys*-*Arvicola* transition occurred during MIS 15 (Preece and Parfitt, 2008, 2012) and therefore early Middle Pleistocene interglacial sites with *Arvicola* are likely to fall within the later part of MIS 15 or in MIS 13. The morphological transition appears to have been a gradual process in which closure of the pulp cavity and root formation are progressively delayed until these are no longer achieved during the lifespan of the individual (von Koenigswald and van Kolfschoten, 1996). Successive stages in the transition between *M. savini* and *Arvicola* can be identified in Western Europe. An assemblage from Kärlich F (Germany), attributed to MIS 16, included a single upper molar of a water vole showing an early stage in the formation of roots, a character diagnostic of *Mimomys* (van Kolfschoten and Turner, 1996). Younger transitional populations, dating to MIS 15, are represented by water vole samples from Mosbach and Mauer, Germany and Isernia, Italy. These have a low percentage of molars exhibiting incipient root formation but none with well-developed roots and have been assigned to *A. mosbachensis* by Maul et al. (2000). The final stage in this transition is seen in water vole molars from sites correlated with MIS 13, which retain the *Mimomys*-like enamel differentiation found in earlier populations but lack even incipient traces of root formation. We contend that *A. cantianus* is the appropriate name for water voles of this evolutionary stage. Regardless of these taxonomic difficulties, the adaptive shift occurred during MIS 15, so that by the end of the 'Cromerian Complex' at sites such as Westbury Cave, Somerset (Bishop, 1982; Andrews et al., 1999), 5.5 km southeast of Sun Hole, and Boxgrove, Sussex (Parfitt, 1999), water voles had unrooted continuously-growing molars.

On the North Norfolk coast, the sites at Ostend (Stuart and West, 1976), Happisburgh 1 (Lewis et al., 2019) and the Sidestrand *Unio*-bed (Preece et al., 2009), all occur beneath the Middle Pleistocene glacial succession, now generally believed to have been emplaced during MIS 12 (Preece et al., 2009; Lee et al., 2016). At Waverley Wood in the English Midlands, fossiliferous channel infills also occur beneath Middle Pleistocene glacial sediments (Shotton et al., 1993). All these sites have yielded *Arvicola* rather than *Mimomys*, suggesting an age in the later part of the 'Cromerian Complex' (Preece and Parfitt, 2012). The other British sites assigned to the later part of MIS 15 or MIS 13 lie beyond the Anglian ice limit. Unlike those sites just mentioned, they do not come from fluvial contexts but are represented by two contrasting depositional environments. The first is represented by the cave



	Mimomys savini	*Arvicola cantianus*	*Lasiopodomys gregaloides*	*Lasiopodomys gregalis*	*Sorex (Drepanosorex) savini*	*Pliomys episcopalis*	*Talpa minor*	*Talpa europaea*	*Microtus agrestis*	
Barnham		●		–	†	†	●	–	●	Hoxnian MIS 11 (424-374 ka)
Boxgrove Miesenheim I		●		●	●	●	●	●	●	Late 'Cromerian Complex' MIS 13 (533-478 ka)
Westbury Cave Kärlich Gb **Sun Hole**		●	●		●	●	●	●	●	
West Runton (Type Cromerian)	●		●		●	●	●	●	–	Early 'Cromerian Complex'

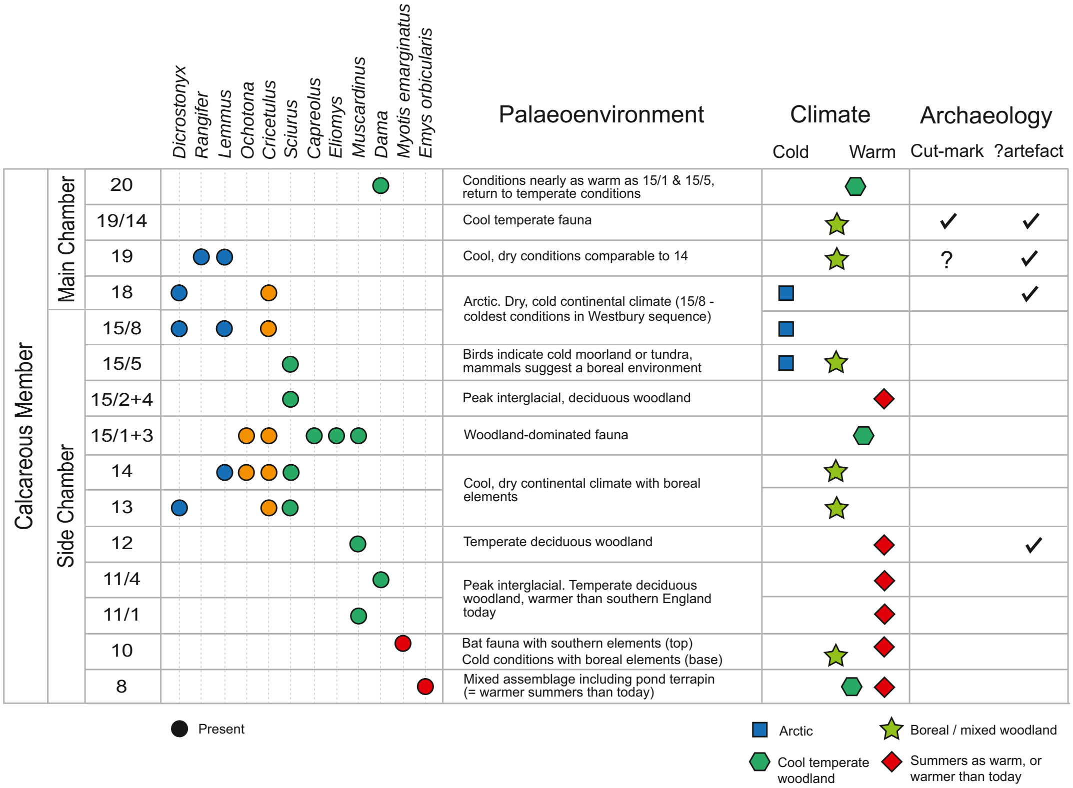
Fig. 5. a, Biostratigraphically important small mammals from Sun Hole shown alongside their occurrence at other critical British and German Middle Pleistocene sites. These occurrences reflect patterns of immigration, evolution, and extinction in successive faunal assemblages. • = Taxon present; – = absent; † = extinct. The identity of the *Pliomys* from Sun Hole is uncertain. Arrows depict evolutionary transitions reflecting (b) the loss of roots in the water vole *Mimomys*-*Arvicola* lineage; and (c) closure of triangles in the first lower molar in the narrow-skulled vole (*Lasiopodomys gregaloides*-*L. gregalis*) lineage.

sequence at Westbury-sub-Mendip (Bishop, 1982; Andrews et al., 1999) and the second by the Lower Palaeolithic land-surface and overlying colluvial deposits above the Goodwood–Slindon Raised Beach in Sussex (Roberts and Parfitt, 1999).

The cavern infills at Westbury are extraordinarily rich in small mammal remains that are believed to have accumulated from pellets regurgitated by various avian predators (Andrews, 1990). The infill of this cavern system can be divided into a basal Siliceous Member belonging to the Early Pleistocene (Bishop, 1982; Adams et al., 2019) and a Calcareous Member of early Middle Pleistocene age, the source of most of the vertebrates (Bishop, 1982; Andrews et al., 1999). Bishop (1982) recognised that the mammalian assemblages from the Calcareous Member contained several taxa that did not extend beyond the Anglian. However, *Arvicola* occurred throughout indicating that they must postdate those of West Runton, leading him to identify a previously unrecognised interglacial stage. This is the basis for assigning the Calcareous Member to the later part of the 'Cromerian Complex' (Preece and Parfitt, 2000, 2012). The sequence within the Calcareous Member revealed climatic oscillations reflected by changes in the composition of the vertebrate fauna (Andrews et al., 1999). The Calcareous Member occurred as two discrete sequences in different parts of the cave system (Fig. 6), namely the Main (eastern) and Side Chambers (western). The two sequences could not be linked but were correlated on the faunal similarity between Unit 15/8 in the Side Chamber and Unit 18 in the Main Chamber, which were both deposited during a period of extreme cold (Andrews et al., 1999). The mammalian assemblages from the Side Chamber provided clear evidence for two temperate phases (Units 11 and 15/2 + 15/4) during which pine vole, assigned to *Microtus* (*Terricola*) *subterraneus*, was dominant, separated by periods of drier, more continental climates, when *Lasiopodomys gregaloides* predominated (Andrews et al., 1999). Additional temperate phases may be represented because thermophilous elements occurred in the mixed assemblage from Unit 8 at the base of the sequence, and there is evidence of warming from the assemblage in Unit 20 at the top of the sequence above Unit 18 in the Main Chamber (Fig. 6).

Rich small mammal assemblages have also been recovered from the Lower Palaeolithic land-surface (Unit 4c) and overlying sediments (Units 5 and 6) that occur above the Goodwood–Slindon Raised beach at Boxgrove in Sussex. In common with the sites discussed above, these assemblages contain species that did not survive after the Anglian Stage, but *Arvicola* likewise occurred throughout (Parfitt, 1999). These assemblages from Boxgrove were consequently correlated with those from Westbury (Currant, 1989; Schreve et al., 1999). Reappraisal of the narrow-skulled voles from these sites, however, revealed marked differences. At Westbury *L. gregaloides* a species originally described from West Runton (Hinton, 1923), occurred throughout, apart from some of the levels representing the warmest phases. No remains of narrow-skulled voles were recovered from Unit 4c at Boxgrove but in Unit 5 *L. gregalis* appeared (Parfitt, 1999). This species is thought to have arisen from *L. gregaloides*, the ancestral species present at Westbury, suggesting that Boxgrove (Unit 5) post-dates the entire sequence at Westbury (Preece and Parfitt, 2000, 2012).

It is difficult to attribute the occurrence of different narrow-skulled vole species to regional variation and it seems far more likely that they reflect differences in age with Westbury older than Boxgrove. Apart from this difference, the small mammal assemblages from Westbury and Boxgrove are otherwise remarkably similar. This led Candy et al. (2015) to suggest that the two assemblages represent different parts of the same interglacial, probably MIS 13. They acknowledged the palaeoclimatic complexity in the Westbury sequence but claim that this does not indicate "glacial/interglacial-scale variability". This poses a problem because there are *at least* three temperate phases, two in the Side



Calcareous Member		Unit	*Dicrostonyx*	*Rangifer*	*Lemmus*	*Ochotona*	*Cricetulus*	*Sciurus*	*Capreolus*	*Eliomys*	*Muscardinus*	*Dama*	*Myotis emarginatus*	*Emys orbicularis*	Palaeoenvironment	Climate (Cold – Warm)	Archaeology: Cut-mark	Archaeology: ?artefact
Calcareous Member	Main Chamber	20										●			Conditions nearly as warm as 15/1 & 15/5, return to temperate conditions	⬢		
		19/14													Cool temperate fauna	★	✓	✓
		19		●	●										Cool, dry conditions comparable to 14	★	?	✓
		18	●				●								Arctic. Dry, cold continental climate (15/8 - coldest conditions in Westbury sequence)	■		✓
	Side Chamber	15/8	●		●		●									■		
		15/5						●							Birds indicate cold moorland or tundra, mammals suggest a boreal environment	■ ★		
		15/2+4						●							Peak interglacial, deciduous woodland	◆		
		15/1+3				●	●		●	●	●				Woodland-dominated fauna	⬢		
		14			●	●	●	●							Cool, dry continental climate with boreal elements	★		
		13	●				●	●								★		
		12									●				Temperate deciduous woodland	◆		✓
		11/4										●			Peak interglacial. Temperate deciduous woodland, warmer than southern England today	◆		
		11/1									●					◆		
		10											●		Bat fauna with southern elements (top) Cold conditions with boreal elements (base)	★ ◆		
		8												●	Mixed assemblage including pond terrapin (= warmer summers than today)	⬢ ◆		

● Present

■ Arctic
★ Boreal / mixed woodland
⬢ Cool temperate woodland
◆ Summers as warm, or warmer than today

Fig. 6. Summary of the stratigraphy and palaeoenvironmental evidence from the Calcareous Member of the cavern infill at Westbury-sub-Mendip (data from Andrews et al., 1999). A complex sequence of alternating cold/cool to fully temperate conditions is inferred from changes in the vertebrate assemblages. These climatic changes are seen in the pattern of faunal changes that reflects both climate and habitat. The lemmings (*Dicrostonyx* and *Lemmus*) and reindeer (*Rangifer*) indicate arctic conditions, the steppe pika (*Ochotona*) and hamster (*Cricetulus*) suggest a dry continental climate and open grasslands, squirrel (*Sciurus*) is found in humid coniferous or deciduous woodland, and roe deer (*Capreolus*), garden dormouse (*Eliomys*), hazel dormouse (*Muscardinus*) and fallow deer (*Dama*) indicate a temperate climate and woodland. Geoffroy's bat (*Myotis emarginatus*) and pond terrapin (*Emys orbicularis*) suggest warmer summers than experienced by southern England today. The occurrence of cut-marked bones and possible artefacts is also shown.

Chamber at Westbury (Units 11 and 15/2 + 15/4), and then Boxgrove (Unit 5), with *L. gregalis*, which must be later again. The intervening cold phases were each cold enough for the temperate elements to be replaced by lemming (*Dicrostonyx* and *Lemmus*), and in the case of Unit 19 by an assemblage with reindeer (*Rangifer tarandus*). This suggests a degree of faunal turnover unprecedented in other Middle Pleistocene interglacials, prompting a consideration of other scenarios, including whether the sequences under discussion all fall within MIS 13.

Grain-size records from Chinese loess have been used to interpret the extent of ice sheets in the Northern Hemisphere during MIS 15–

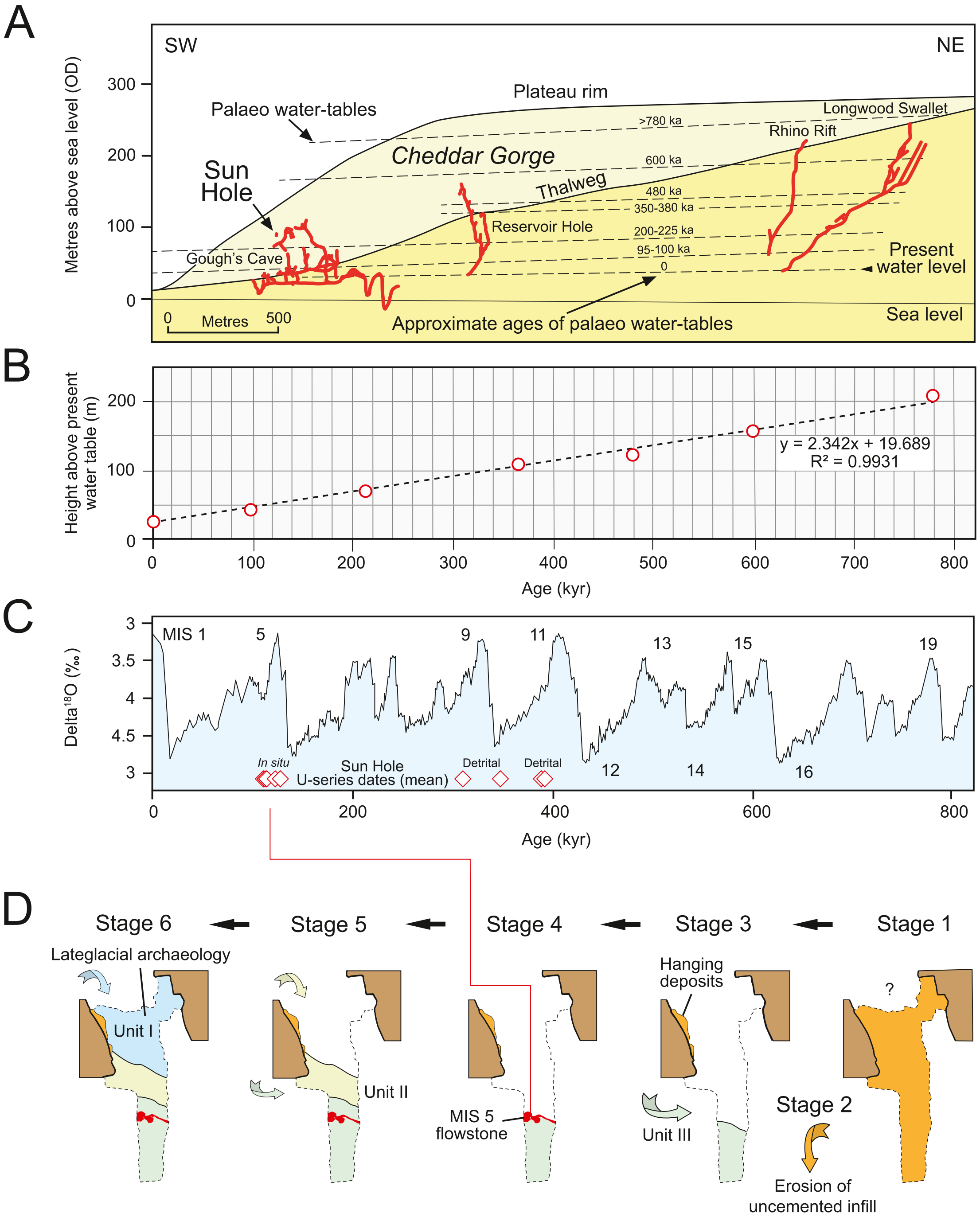


Fig. 7. Geomorphological history of Cheddar Gorge and the sedimentary infill of Sun Hole Cave. A. Long-profile of Cheddar Gorge, with caves superimposed. Palaeo water-tables are dated from speleothems in associated cave passages at both swallet and resurgence ends of the system (modified from Waltham et al., 1997, fig. 10); B. graph showing the height of palaeo water-tables in Cheddar Gorge over the past 800,000 years. The lowering of the palaeo water-tables at the mouth of the Gorge suggests downcutting of Cheddar Gorge at a rate of about 0.23 m/ka. New dates from Reservoir Hole (Farrant et al., 2016) suggest an incision rate of 0.20 ± 0.01 m/ka, which is consistent with the base-level lowering rate calculated from other sites in Cheddar Gorge; C. Sun Hole uranium-series dates (*in situ* and detrital speleothems) plotted on the marine oxygen isotope record (Lisiecki and Raymo, 2005). Numbered marine isotope stages (MIS) denote major cold periods (even numbers) separated by shorter warm stages (odd numbers), which include brief episodes of cold climate; D. schematic sections showing stages in the formation of the Sun Hole cave deposits. Stage 1 shows the cave filled with unconsolidated sediment capped by a granular stalagmite. During stage 2, a major erosional event removed unlithified deposits but left cemented sediments attached to the roof of the cave. In Stage 3, early Middle Pleistocene sediments (Unit III) entered Sun Hole from some point further back in the system. The cave entrance was sealed during Stage 4 (Last Interglacial, MIS 5e) and a flowstone formed over the pre-existing sediments. The cave mouth re-opened during Stage 5 and debris, including soil, rocks and bones, accumulated in the cave (Unit II). The base of Unit II includes a minor component of early Middle Pleistocene shell and microvertebrate material indicating that this source continued to provide sediment. The final episode (Stage 6) of deposition incorporates a Lateglacial occupation horizon and Holocene archaeological levels at the top of Unit I.

13. These demonstrate that an extra-long interglacial of over 100 kyr arose as a result of limited ice sheet extent during MIS 14, which is characterized by a climate in the Northern Hemisphere that was comparable to that prevailing during mild stadials within interglacials (Hao et al., 2015). This interval is much longer than expected from marine oxygen isotope records and might provide an explanation for the complexity of the terrestrial records from this period.

The early Middle Pleistocene sites at Kärlich and Miesenheim I, located 4 km apart, near Koblenz in the central Rhineland of Germany have an important bearing on these discussions because dated volcanic material occurs within stratified sequences of mammalian and molluscan assemblages (Bosinski, 1995). The heavy mineralogy of early Middle Pleistocene sediments shows a marked change from hornblende-dominated to those rich in augite, a feature that reflects volcanic activity in the Eifel region (Schmincke, 2007). This transition is also detectable in the sequences at Kärlich and Miesenheim I. In the upper part of the hornblende-rich sediments at Kärlich, the interglacial small mammal assemblage (unit Gb) includes *Arvicola* and *L. gregaloides*. This was recovered beneath a loess horizon rich in augite, containing pumice dated to 466 ± 3 ka (Gallant et al., 2014). The same pumice horizon can be observed at Miesenheim I, where it has been similarly dated at 464 ± 4 ka (Turner, 2000). The sediments immediately beneath the dated horizon are augite-rich and have yielded a small mammal assemblage with *L. gregalis* and interglacial land snails (Turner, 2000). Rare morphotypes resembling *L. gregalis* have been found at Westbury and in the Kärlich Gb assemblages (van Kolfschoten and Turner, 1996), but these appear to be extreme forms within the range of *L. gregaloides*, which dominates (S.A. Parfitt, personal observation).

At these two German sequences, two interglacial horizons occur between the *Mimomys-Arvicola* transition (~MIS 15) and the dated pumice within the early part of MIS 12. The oldest represented by unit Gb at Kärlich had *L. gregaloides* and pre-dated the influx of augite, whereas the later one had the dominant *L. gregalis* morphotype and occurred within augite-rich sediments. This evidence provides tight age constraints on these faunas, which are consistent with an MIS 13 attribution. These German sequences have parallels with those at Westbury and Boxgrove. It is likely that the fauna from Miesenheim I correlates with the assemblage from unit 5 at Boxgrove but it is harder to correlate the fauna from unit Gb at Kärlich with any specific temperate assemblage from Westbury because of the complexity of that record. Consequently, it is unclear how the Westbury sequence relates to the marine isotope record, although it would seem probable that it covers more than one substage. Similarly, it is not possible to match the small mammals from Sun Hole with any specific temperate horizon at Westbury, although it is noteworthy that *Eliomys quercinus* was only recovered from one unit (15/1) at that site (Andrews et al., 1999).

The latest occurrence of *L. gregaloides* on the continent is thought to date from MIS 15 at sites such as Hundsheim, Austria (Maul and Markova, 2007). The occurrence of this species with *Arvicola* at Westbury, Sidestrand (*Unio*-Bed) and Sun Hole, might therefore indicate an age earlier than MIS 13. However, assigning these deposits to MIS 15 is not without its problems because well-dated continental sites of this age have water voles with molars exhibiting early stages of root formation, which have yet to be found at these British sites. This might result from the sequences representing different substages of MIS 15 but the issue is complicated by small sample size and at Westbury by a bias towards younger individuals of *Arvicola* that often form the prey of avian predators.

Land snail assemblages have been recovered from Boxgrove (Preece and Bates, 1999) and from an identical stratigraphical sequence at Valdoe, 4.8 km to the west (Preece and Parfitt, 2022). The assemblages from Boxgrove and Valdoe are similar but show differences that reflect the environmental heterogeneity of the Lower Palaeolithic land-surface. Of particular relevance to our discussion here is the occurrence of *Retinella* (*Lyrodiscus*) *elephantium* at Valdoe in a context securely attributed to MIS 13 (Preece and Parfitt, 2022). This would remove any difficulty assigning Unit III at Sun Hole to the early Middle Pleistocene on the basis of the malacological data (but see below for caveats expressed by Collcutt et al. (1981) as to the possibility that Unit III may have been deposited by mass flow of older sediment from an unknown but presumably higher part of the cave). Unlike Sun Hole, no shells were recovered at Westbury, so it remains to be seen whether *Lyrodiscus* occurs in other temperate phases of the early Middle Pleistocene.

The dating of the sediments in Sun Hole has a bearing on the geomorphological history of Cheddar Gorge (Fig. 7A–C). Although some speleothems date from MIS 9 and MIS 5 and other dates towards the limit of the technique at ~400 ka were from a fragment of detrital speleothem, none of the surviving cave sediment can be reliably attributed to the late Middle Pleistocene. It is also interesting to note that 'Cromerian Complex' ages have been obtained from a stalagmite from Holcombe Cave in the Mendips (Baker et al., 1997). Unconsolidated sediments appear to have been periodically flushed from the cave system leaving hanging breccias as the only sedimentary evidence for its early history (Fig. 7D). Collcutt et al. (1981) suggested that Layers 31–35 in Sun Hole may represent a major mass flow deposit that incorporated faunal material significantly older than the solution cavity in which it was deposited. If so, this would explain the anomalously low elevation for sediments of this proposed age (~500 ka) in relation to the downcutting of Cheddar Gorge (Waltham et al., 1997, fig. 5.10; Fig. 7A–B). It is noteworthy that the revised age of the fossils from Unit III at Sun Hole now aligns with the record from the Calcareous Member at the nearby Westbury Cave, although how they relate to each other in detail and indeed to the marine isotope record for the early Middle Pleistocene remains to be seen.

Declaration of competing interest

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

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