

Environmental heterogeneity of the Lower Palaeolithic land surface on the Goodwood-Slindon Raised Beach: comparisons of the records from Boxgrove and Valdoe, Sussex, UK

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ABSTRACT: The buried soil above the Goodwood-Slindon Raised Beach running along the foot of the South Downs (Sussex) is one of the most extensive Lower Palaeolithic land surfaces known. It extends for 16 km but exposures are limited to Boxgrove, the focus of archaeological excavations since the 1980s, and Valdoe, 4.8 km to the west. The palaeosol yielded vertebrates suggesting attribution to Marine Isotope Stage (MIS) 13 and land snails important in the reconstruction of local environments. Important differences exist between the molluscan assemblages from Valdoe and Boxgrove. An extinct land snail *Retinella (Lyrodiscus) elephantium*, previously known in Britain only from MIS 11, occurred at Valdoe at unusually high frequencies in assemblages poor in woodland species, prompting a reappraisal of its stratigraphical and ecological significance. Conversely, *Spermodea lamellata*, a woodland species present at Boxgrove, was absent at Valdoe. This lateral variability results both from the original heterogeneity of the environment, and from differential preservation resulting from decalcification and erosion. Calcitic slug plates are over-represented (>50% of the molluscan fauna) in decalcified sediments where shells composed of aragonite are rare. These considerations, and comparisons with modern and fossil assemblages, have led to more nuanced reconstructions of the landscape occupied by early humans in southern England ~500 ka ago.

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KEYWORDS: Boxgrove; decalcification; land snail analysis; *Lyrodiscus*; MIS 13; Valdoe; vertebrates

Introduction

Spatial scale is an important consideration in environmental archaeology. In reconstructions of environments adjacent to, or beneath, archaeological features it is important to know just how large an area is reflected in the analyses. Do the records relate to the immediate area, pinpointing conditions at a precise location, or do they provide a more general indication of habitats in the local area? Such issues have been much discussed and sampling strategies devised to capture information at a variety of spatial scales. In calcareous regions, land snail assemblages from buried soils have often been used to shed light on environmental changes that occurred during their formation (e.g. Evans, 1972). Such records provide valuable information at extremely local scales (e.g. Whittle *et al.*, 1993; Davies, 1999) but increasingly it is what happens at the landscape scale that is of particular interest for archaeologists (Allen and Gardiner, 2009; Davies and Gardner, 2009; Allen, 2017). Consequently, laterally extensive buried soils have been studied from many late Holocene sequences to reconstruct the landscape archaeology but far less work has been undertaken on the lateral variation of land snail assemblages from pre-Holocene soils.

Little was known about British palaeosols that formed during the Middle Pleistocene until reddened horizons on the surface of certain terrace deposits, such as the Kesgrave Sands and Gravels,

were shown to be buried soils (Rose *et al.*, 1976). The most extensive of these, the Valley Farm Soil, which occurs over a relatively large part of southern East Anglia (Rose *et al.*, 1985: Fig. 18.4) is rubified, mottled and contains substantial quantities of translocated clay but no calcareous fossils. This was initially thought to have formed during temperate conditions of the 'Cromerian' (Kemp, 1985) but the frequent superimposition of cryogenic features of the later Barham Soil, indicated a more complex pedogenic history (Kemp and Rose, 1993). These observations have complicated the stratigraphical significance of the soils, but they remain important not only in allowing the recognition of former land surfaces but also in confirming that where they occur on terrace surfaces, the heights of the latter are original and have not been reduced through erosion.

Virtually no other pre-Anglian palaeosols are known from southern Britain with one notable exception. This is the palaeosol that has formed on the surface of the Goodwood-Slindon Raised Beach in West Sussex. Unlike the Middle Pleistocene palaeosols from East Anglia just described, the Sussex palaeosol is both laterally extensive and it has yielded land snails and other fossils. It occurs at an elevation of 40 m OD and extends for about 16 km (Roberts and Pope, 2018). Archaeology has been recorded from several sites associated with Goodwood-Slindon Raised Beach (Woodcock, 1981) but since the 1980s, the key locality has been Boxgrove, where excellent sections could be seen through the full sequence before backfilling and landscaping in 2007 rendered the sections inaccessible. This site has been the focus of major archaeological excavations, which recovered *in situ* Lower Palaeolithic archaeology (Roberts and Parfitt, 1999) and

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mammalian assemblages suggesting attribution to Marine Isotope Stage (MIS) 13 (Parfitt, 1999).

During the 1990s another quarry was opened at Valdoe, 4.8 km west of Boxgrove (Pope *et al.*, 2009). Sections exposed an almost identical stratigraphy to that seen at Boxgrove so that samples from the palaeosol were therefore expected to yield similar land snail assemblages to those recovered from the same horizon at Boxgrove. Although there were close similarities, there were some important differences; in particular the occurrence of the extinct land snail *Retinella (Lyrodiscus) elephantium* at frequencies far higher than those reported from any other Pleistocene sites in Britain or northern France. *Lyrodiscus* is a characteristic species of MIS 11 and the index fossil of the so-called 'Lyrodiscus fauna', a distinctive assemblage of land snails known from this period, but it also occurs in much older deposits on the continent. This unexpected discovery at Valdoe necessitated a reappraisal both of the stratigraphical significance of this extinct species as well as its ecology. It also prompted comparisons with the land snail assemblages from Boxgrove and other sites, especially those yielding the *Lyrodiscus* fauna. The lateral variation of the molluscan assemblages between Valdoe and Boxgrove is discussed as is the fine-scale spatial variability at each site. Some of this variability reflects environmental heterogeneity at different locations along this land surface but some results from differential decalcification and erosion that has caused the loss of certain faunal components and over-representation of others. Land snails from the palaeosol at Boxgrove contain some shade-demanding species that pose difficulties with respect to the short duration of subaerial exposure previously suggested from the pedology. These considerations, together with lessons learned from modern studies and from other fossil assemblages, have led to a more nuanced reconstruction of the Boxgrove landscape inhabited by early humans about 500 ka years ago.

Geomorphological context and stratigraphical framework

The West Sussex coastal plain, shaped by successive marine transgressions over the last half-million years, forms an area of relatively low relief between the chalk downland along its northern boundary and the English Channel to the south. It extends from Hampshire east to the River Adur in Sussex with an average width of 9 km, reaching 17 km at its widest point (Fig. 1). A staircase of marine terraces (Bates *et al.*, 1997, 2000, 2010) emplaced on the bedrock surface in this area has been affected by regional uplift

(Preece *et al.*, 1990; Westaway *et al.*, 2006). These deposits have been divided into a group forming the Upper Coastal Plain about 2 km wide that occurs between the 65 m and 20 m contours and a second group, below 20 m, forming the Lower Coastal Plain that covers the greater part of this low-lying area.

The Goodwood-Slindon Raised Beach is the highest of this series of marine terraces that occur along the foot of the south-facing dip slope of the South Downs, forming a component of the Upper Coastal Plain. It principally occurs between 35 and 40 m OD, but attains a maximum elevation of 43.5 m OD at Eartham, and was consequently formerly known as the 100 foot Raised Beach (e.g. Fowler, 1932). The Pleistocene sediments associated with this feature rest on a marine platform that has cut into the Cretaceous Upper Chalk to form a cliffline along its northern margin (Fig. 1). This cliffline, which is now 12 km from the present coast, is estimated to have been at least 60 m high but it is now buried with no surface expression (Fig. 2). The Goodwood-Slindon Raised Beach has been mapped between Steward's Copse, Arundel (TQ 003068) and Westbourne Common (SU 751087), a distance of 26 km (Roberts and Pope, 2018), although marine sediments representing a possible western limit extend as far as Fort Wallington on the western limb of the Portsdown anticline (ApSimon *et al.*, 1977). Estuarine sediments (the Steyne Wood Clay) that occur at the same elevation (38–40 m OD) in the grounds of Bembridge School (SZ 642865) on the Isle of Wight appear to have been deposited during the same marine event (Holyoak and Preece, 1983; Preece *et al.*, 1990; Whittaker and Parfitt, 2017).

Exposures of the Goodwood-Slindon Raised Beach have been created by quarrying at Waterbeach, Slindon and most recently at Eartham Quarry, Boxgrove (SU 923086), which has been the focus of intense interest since the discovery of *in situ* Lower Palaeolithic archaeology, including evidence of hunting and animal butchery, together with the remains of hominins themselves (Roberts *et al.*, 1997; Roberts and Parfitt, 1999; Pope *et al.*, 2020). The full sequence of Pleistocene sediments can be reconstructed from sections opened in the two main quarries at Boxgrove (Q1/B and Q2/B), which cover an area of 9.8 ha. The sections here have been designated as the type site for the Slindon and Eartham Formations (Roberts and Parfitt, 1999). The Slindon Formation consists of the gravels of the raised beach itself (Slindon Gravel Member), together with overlying beds of sand (Slindon Sand Member) and silt (Slindon Silt Member). A series of individual units has been recognised within each of these Members (Table 1); those relevant to the present study occur at the top of the Slindon Silt Member (Figs. 2 and 3). The sediments forming this Member

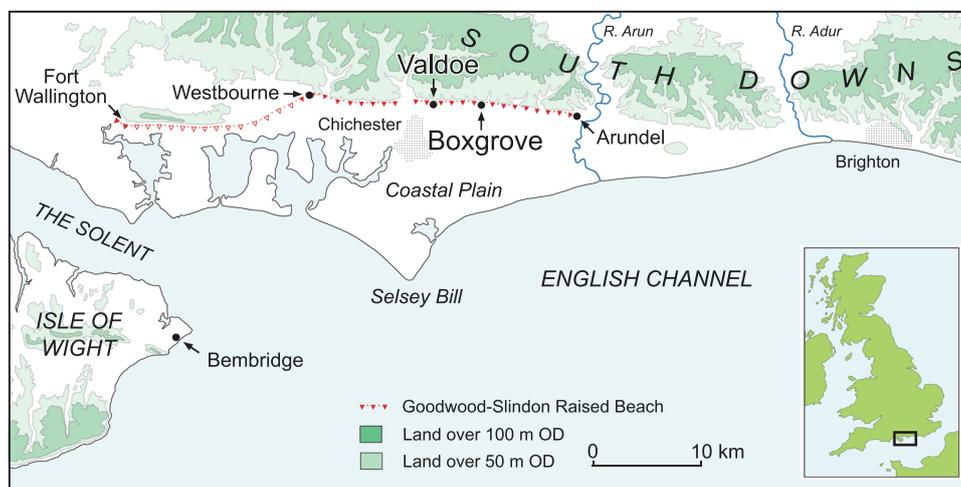


Figure 1. Map showing the location of Valdoe and Boxgrove in relation to the extent of the Goodwood-Slindon Raised Beach and the coastal plain. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

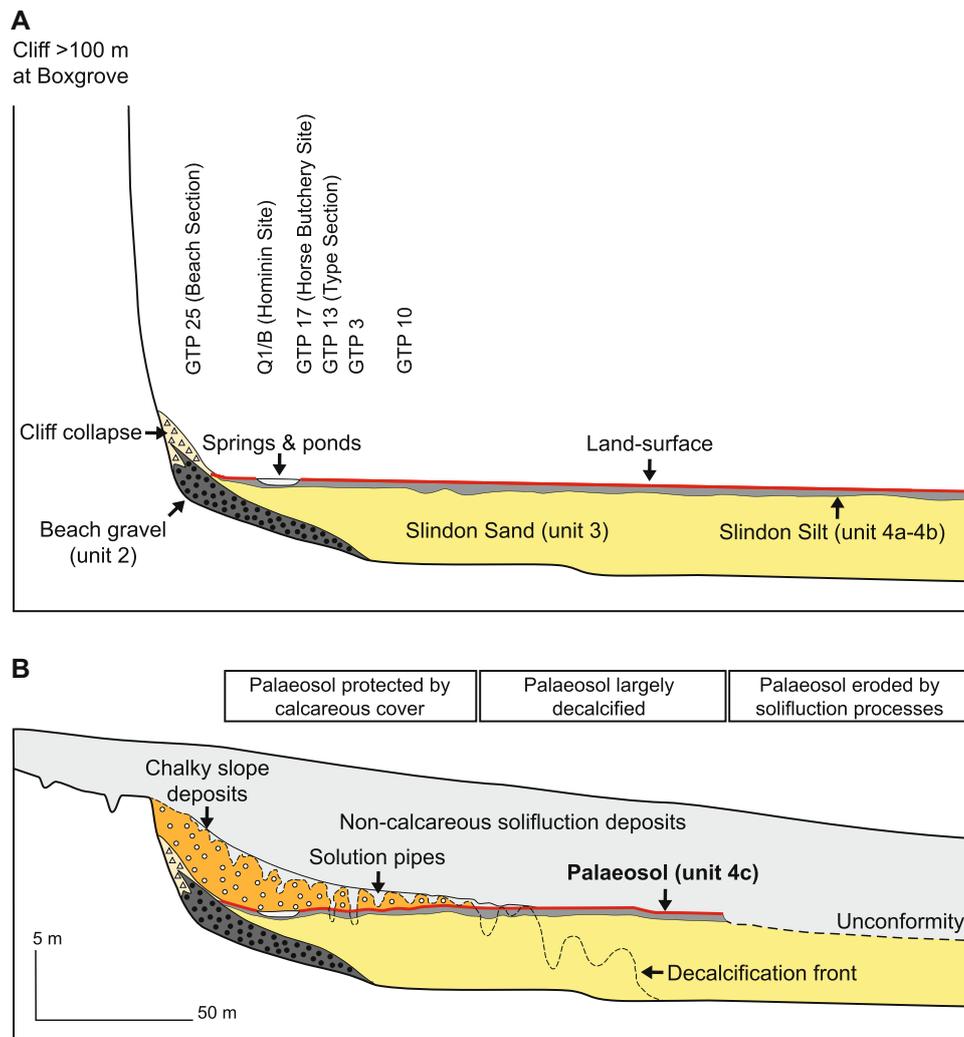


Figure 2. Schematic sections through the stratigraphical sequence at Boxgrove showing the context of the Palaeolithic land surface: A. In the Middle Pleistocene landscape; and B. After burial (unit 4c). [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1. Stratigraphy of the sequence at Boxgrove and Valdoe. The palaeosol (unit 4c), which yielded most of the archaeological and molluscan remains is highlighted

Formation & Member	Sediments	Environment	Climate	Stage
Eartham Formation Eartham Upper Gravel Mbr	Flint-rich gravel, silt (unit 11) and chalky solifluction gravel (unit 10) with interdigitating beds of laminated non-calcareous silt (upper brickearth, unit 6)	Bare unstable ground affected by solifluction and freeze-thaw	Arctic	Anglian MIS 12 478–423 kyr
	Sub-rounded flint gravel (unit 9) overlying chalk pellet gravel (unit 8) and calcareous silt (lower brickearth, unit 6)	Waterlain gravel, silt and colluvium affected by freeze-thaw		
Slindon Formation Eartham Lower Gravel Mbr Slindon Silt Mbr Slindon Sand Mbr	Chalk pellet gravel (LGC, unit 8) Calcareous silty clay (unit 5b, 6) Angular chalk gravel (unit 7)	Scree resulting from cliff collapse and colluviation. Ponding in a shaded environment beyond the foot of the cliff	Temperate ↑ Cooling	'Cromerian Complex' MIS 13 524–478 kyr
	Horizon of mineralized organic material (unit 5a) Palaeosol (unit 4c) and freshwater silts (unit 4d, 4u) Laminated mud/fine sand (unit 4b)	Fen/alder carr Land-surface with grassland becoming increasingly shaded. Shallow pools and mixed woodland Intertidal mudflat with channels; freshwater spring and seeps within grassland closer to the cliff		
	Beach gravel (unit 2), sand (unit 3) and angular chalk gravel (unit 7)	Near-shore marine beach with episodes of cliff collapse		

(A) Main archaeological horizon

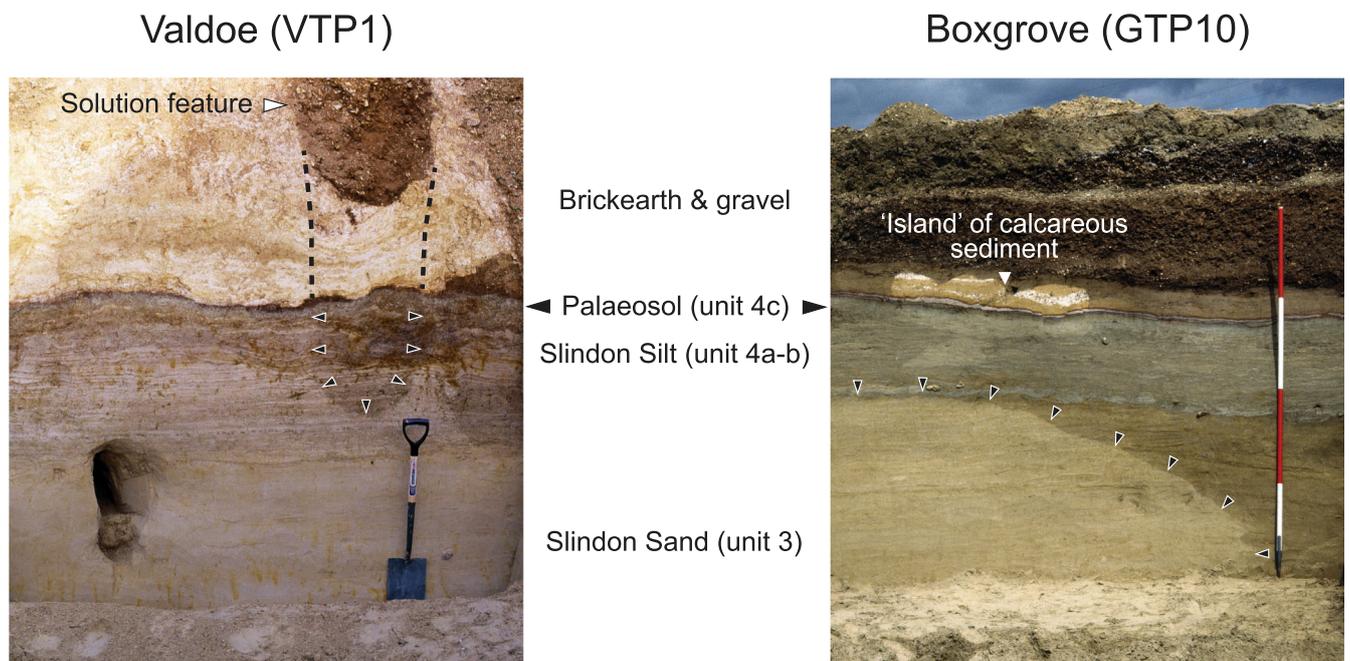


Figure 3. Sections at Valdoe (VTP1) and Boxgrove (Q2 TP 10) showing the palaeosol (unit 4c) and adjacent sediments. Note the stratigraphical similarity despite being 4.8 km apart. Evidence for decalcification can be seen in the form of solution hollows and decalcification fronts (arrowed). Ranging pole scale = 2 m. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

are marine silts with clay laminations that formed in a low-energy, euryhaline intertidal environment during a regressive phase. As the sea-level fell, a prominent soil horizon (unit 4c), visibly no more than about 10 cm thick, developed on the surface of the intertidal silts (unit 4b). This is overlain by a thin Fe/Mn horizon (unit 5a) of mineralised organic material thought to have accumulated in fen/alder carr. These terrestrial sediments, which contain temperate faunal assemblages, are overlain by periglacial sediments of the Eartham Formation (Table 1).

Whereas Pleistocene marine sediments between 35 and 40 m OD extend as far as 40 km (Fig. 1), the Palaeolithic land surface developed on them is much more limited in extent. A recent borehole survey (Roberts and Pope, 2018) has shown that the soil horizon (4c) developed at the top of the Slindon Silt Member, the source of most of the archaeology at Boxgrove, occurs within a 30–250 m wide area that can be traced for 16 km between Slindon Park (SU 95760824) and Adsdean Farm (SU 799088), north of Funtingdon. The palaeosol has been buried by sediments derived from the Chalk Downs to the north. At Boxgrove (GTP25) it is buried to a maximum depth of 13 m close to the fossil cliffline but the overlying sediments thin progressively southwards (Fig. 2). Close to the cliffline the overlying sediments include material resulting directly from cliff collapse, as well as a range of periglacial sediments that form the Eartham Formation. In places these overlying sediments have formed a protective covering but elsewhere they have eroded the palaeosol and the top of the marine sequence. The palaeosol therefore has a rather patchy occurrence further fragmented by subsequent stream channelling.

The micromorphology and mineralogy of the sedimentary sequence at Boxgrove has been studied in detail from various sections (Macphail, 1999; Catt, 1999). The palaeosol (4c) is essentially a non- or poorly calcareous silty clay with similar amounts of organic matter (0.1–0.2%) to the intertidal silts (unit 4b) but contains less calcium carbonate (0–1.7% CaCO_3) than that unit (19.9–23% CaCO_3). It appears to be the weathered, decalcified and partially homogenised upper part

of the Slindon Silts (unit 4b). The thickness of the soil varies, which in part may have been caused by decalcification leading in places to the loss of 20–30% of its volume, although loss of organic matter, structure and porosity would have been contributory factors, as well as compression (Macphail, 1999: 130). The palaeosol is also strongly oxidised, precluding the preservation of meaningful pollen.

In the western part of the Boxgrove site (Q1/B) the palaeosol horizon passes laterally into a 'pond facies' represented by calcareous silts, formed locally about 50–100 m south of the projected fossil cliffline (Fig. 2). Ostracods and fish remains were abundant in the calcareous silts indicating deposition in small lakes or ponds that were shallow but permanent and fed by groundwater and spring-water (Holmes *et al.*, 2010; Whitaker and Parfitt, 2017). It was in this vicinity that an extraordinary density of hand-axes and butchered large mammal bones was recovered, together with the remains of the hominin tibia (Roberts *et al.*, 1994) and incisors (Hillson *et al.*, 2010).

Valdoe Quarry

Good sections through the Goodwood-Slindon Raised Beach were exposed at Valdoe Quarry (SU 877086), located 3 km north-east of Chichester and 4.8 km to the west of Boxgrove (Fig. 1). The site was first visited in October 1996, when gravel extraction in the northern part of the quarry had largely ceased, leaving a series of silt ponds separated by 5 m baulks (Pope *et al.*, 2009, Fig. 3). A section in a small drainage ditch (VTP1) demonstrated that the main elements of the stratigraphical sequence at Boxgrove were replicated at Valdoe, which occurs at the same elevation and is essentially a lateral extension of that sequence (Fig. 3). The archaeological potential at Valdoe was therefore recognised but it was not until 2005 that plans to exploit this were initiated following proposals for renewed quarrying to remove an area of 250 × 100 m in the northern part of the quarry. In 2006 the site was surveyed and samples/monoliths taken from various sections, test pits and boreholes

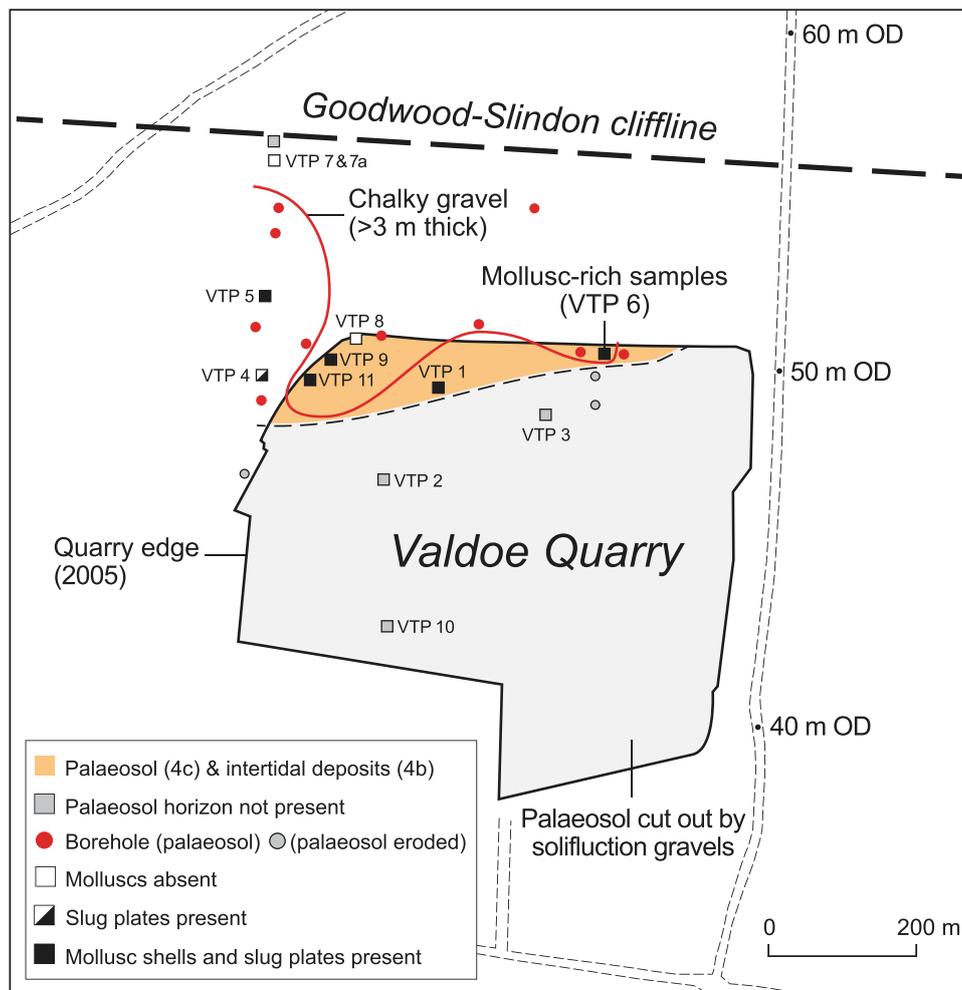


Figure 4. Map of Valdoe Quarry, showing the occurrence of the palaeosol in the trial pits and boreholes and the preservation of molluscan remains within it. [Colour figure can be viewed at wileyonlinelibrary.com]

both within the threatened area and adjacent to it (Fig. 4). This initial assessment was followed in 2007 by archaeological excavation of seven test pits in the north-western part of the quarry. A total of 115 flint artefacts (>20 mm) was recovered from six of the 11 test pits investigated during the assessment (Pope *et al.*, 2009). Most of the artefacts ($n = 80$) came from the palaeosol (4c). These were fresh and unabraded and in three test pits the artefacts showed weak clustering suggestive of *in situ* spreads of late-stage biface-thinning debitage (Pope *et al.*, 2009). Other artefacts were recovered from higher stratigraphical levels but there was no evidence of clustering and they were clearly not in primary context.

Methods

Experience from Boxgrove suggested that in order to recover reasonable yields of vertebrates and molluscs from the palaeosol and adjacent sediments at Valdoe, bulk sampling would be required. Consequently, 52 samples of between 2 and 34 kg (total 1065.1 kg) were analysed from the following units at Valdoe: 4b (11 samples, 241.3 kg), 4c (20 samples, 436.6 kg), 5a (7 samples, 116.8 kg), 5b (6 samples, 87.1 kg) and 6b (8 samples, 183.3 kg). These samples were taken from various trenches and trial pits in and around Valdoe Quarry (Fig. 4). Each sample was dried and sieved in water through a nest of sieves, the finest of which had a 0.5 mm mesh. The dried residues were systematically scanned under a binocular

microscope and all vertebrate remains and shells extracted with a fine paintbrush. Standard procedures were used to assess the minimum number of individual specimens (Evans, 1972; Parfitt, 1999). For environmental analyses, species of non-marine mollusc have been allocated to particular ecological groups following Evans (1972).

Results

Vertebrate fauna

Samples taken from various locations across the site yielded variable numbers of identifiable remains of small vertebrates, the highest concentration coming from unit 5a (Table 2). Unit 6 proved barren. Most of the remains were represented by isolated teeth and fragmentary post-cranial elements.

Several aquatic/wetland taxa were recovered from unit 4b. These included a dermal denticle of flounder *Platichthys flesus*, a flatfish that spends most of its life in brackish estuaries, coastal pools and bays but frequently penetrates the lower reaches of rivers, where it inhabits freshwater. The occurrence of newt (*Triturus* sp.) and an anuran (frog or toad) also indicates the presence of still or slow-flowing water. Amongst the mammals, the most common species was water vole (*Arvicola*), which occurs predominantly in damp grassland and marsh bordering lakes and rivers. Similar open habitats are also inhabited by

Table 2. Vertebrates from Valdoe Quarry. Counts indicate the number of identified specimens

Unit	4b	4c	5a	5b
Pisces				
<i>Platichthys flesus</i> (Linnaeus), flounder	1	-	-	-
Indeterminate fish	-	1	1	-
Amphibia				
<i>Triturus</i> sp., newt	2	-	-	-
Anuran indet.	1	-	-	-
Mammalia				
Eulipotyphla				
<i>Sorex</i> cf. <i>minutus</i> Linnaeus, pygmy shrew	+ ^a	-	-	-
<i>Sorex</i> cf. <i>runtonensis</i> Hinton, extinct shrew	1	1	-	-
<i>Sorex</i> (<i>Drepanosorex</i>) <i>savini</i> Hinton, extinct shrew	1	-	-	-
Soricidae indet., shrew	1	-	-	-
<i>Talpa minor</i> Freudenberg, extinct mole	-	1	3	-
Rodentia				
<i>Clethrionomys glareolus</i> (Schreber), bank vole	1	1	2	13
<i>Pliomys episcopolis</i> Méhely, extinct vole	-	-	1	-
<i>Arvicola cantianus</i> Hinton, water vole	24	8	12	-
<i>Microtus agrestis</i> (Linnaeus), field vole	1	-	-	-
<i>Microtus agrestis</i> (Linnaeus) or <i>M. arvalis</i> , (Pallas), field or common vole	-	1	-	-
<i>Microtus</i> sp., vole	5	11	3	-
<i>Apodemus sylvaticus</i> (Linnaeus), wood mouse	2	-	1	-
<i>Muscardinus avellanarius</i> Kaup, hazel dormouse	-	-	-	1

+^a Fragmentary teeth probably from same individual (micropalaeontology sample Borehole 3ii, depth 4.45–4.65 m).

the field vole *Microtus agrestis*, which is also common in rank grassland. Minor components included wood mouse *Apodemus sylvaticus*, at least two species of extinct shrew, *Sorex* cf. *runtonensis* and *S. (Drepanosorex) savini*, and bank vole *Clethrionomys glareolus*.

Grassland voles (*Arvicola*, *Microtus* sp. and *M. agrestis/arvalis*) were the dominant small mammals recovered from the soil horizon (4c). The decrease in the relative abundance of water vole may indicate drier conditions, a conclusion supported by the occurrence of the mole *Talpa minor*.

A return to wetter conditions is suggested by the relative increase in water vole abundance recovered from unit 5a. At Boxgrove, this unit showed a similar increase in *Arvicola*, and sedimentological evidence suggests periodic flooding of an extensive marshland. Although the number of identifiable specimens was small, the occasional *Clethrionomys glareolus* and *Pliomys episcopolis* suggests thick vegetation.

The abundance of bank vole (*Clethrionomys glareolus*) in unit 5b suggests dense vegetation. This species has a wide western Palaearctic distribution where it occurs in woodland with a dense shrub layer, woodland-edge habitats and even dense grassland providing that there is good cover. Hazel dormouse *Muscardinus avellanarius*, represented by a first lower molar from VTO 5 (BS 18), has more specific requirements that include dense cover combined with a source of berries, nuts, flowers and highly nutritious foliage. Favoured habitats include forest-edge and woodland glades but also scrub where there is an understory of shrubs, often with bramble and honeysuckle. Today, hazel dormouse extends into the mixed woodland of southern Scandinavia and as far north as the Gulf of Finland (to 60° N), broadly coinciding with the 17°C July isotherm. Hazel dormouse is generally rare in the British Pleistocene but was abundant at Boxgrove (Parfitt, 1999). Small mammals

from open grassland habitats were rare in unit 5b at Valdoe.

The small vertebrate fauna from Valdoe is extremely similar to that from equivalent deposits at Boxgrove (Parfitt, 1999), and includes several species of biostratigraphical significance, such as *Pliomys episcopolis*, *Talpa minor*, *Sorex (Drepanosorex) savini* and *Arvicola*. Despite these close similarities, there are nevertheless some important differences, first with regard to the inferior preservation, and second regarding faunal composition. At Boxgrove, units 4b, 5a and 4d yielded abundant fish remains, supporting other evidence that the sediments accumulated in nearshore marine environments, freshwater marsh and spring-fed ponds, respectively (Roberts and Parfitt, 1999; Whittaker and Parfitt, 2017). Fish remains were also found in the palaeosol horizon (4c) at Boxgrove, especially at the margins of the Q1/B waterhole. The occurrence of fish in the palaeosol may reflect periodic inundation or the activities of predators, assuming that they have not been reworked from earlier deposits. Few of the deposits sampled at Valdoe contained fish remains, possibly because of diagenetic loss, but more probably due to the generally drier conditions at the sampled locations.

Further evidence for spatial heterogeneity at Valdoe is suggested by the relatively abundant small vertebrates from unit 4b in VTP 6 as well as the apparently more open environment indicated by the rodents from unit 5a. The sediments at Valdoe and Boxgrove both record the transition from vegetated intertidal mudflats through a grassland phase towards closed habitats, probably of woodland or scrub before a reversion to open, cold environments with onset of the ensuing cold stage. At Boxgrove, open grassland conditions appear to be represented by the records from units 4b and 4c, but in unit 5a there is a significant increase in small mammals from woodland (Parfitt, 1999). At Valdoe, however, the first indications of woodland are found in the overlying unit 5b.

Molluscan fauna

Despite the extensive bulk sampling involving the processing of over a tonne of sediment, the number of shells recovered was disappointing. Most of the 52 samples were barren, or virtually so, and only two yielded reasonable assemblages (Table 3), and the yield from these was still only 28 shells/kg and three shells/kg. These samples both came from VTP 6, a test pit excavated with a mechanical digger that had removed blocks of sediment from an area measuring 2 × 3 m. Samples were taken from these blocks, which represent the upper parts of units 4b and 4c, although the distinction between these units was not entirely clear in relation to the most shell-rich sample. The molluscan assemblages from both units were similar, dominated by the same restricted fauna of land snails (Table 3). The lower unit assigned to 4b was the most fossiliferous, yielding 19 species of land snail and two aquatic taxa. Remains of slugs (plates) and earthworms (granules) were also common, and fragments of marine shell (*Mytilus edulis*, *Spisula* sp. and *Cerastoderma* sp.) were also recovered.

Neither of the aquatic taxa require large bodies of water. *Galba truncatula* is amphibious and inhabits wet muddy surfaces and some species of *Pisidium* can exist in films of water in damp places. The succineids and *Carychium minimum* live in similar wetland habitats and most of the catholic species recovered are also typical components of such environments, as is *Vallonia pulchella*, which is common on damp floodplains. Slightly drier conditions are suggested by the occurrence of *Pupilla muscorum* and *Vallonia costata*,

Table 3. Molluscan analyses from Valdoe Quarry

Unit	4b		4c				5a		5b	
	6	4	5	6	9	11	6	7	5	8
Test pit (VTP)	06-1	6	15	06-2	47, 48, 53, 54	57, 58	23	29	17, 18	43
Bulk sample no.	26	20.2	26.1	30	77.3	40.5	15.4	15.2	24.1	12
Sample weight (kg)										
Aquatic species										
<i>Galba truncatula</i> (Müller)	-	-	-	1	-	-	-	-	-	-
cf. <i>Musculium lacustre</i> (Müller)	-	-	-	-	-	2	-	-	-	-
<i>Pisidium</i> sp.	3	-	-	-	-	-	-	-	-	-
Terrestrial species										
<i>Carychium</i> cf. <i>minimum</i> Müller	5	-	-	1	-	-	-	-	-	-
Succineidae	2	-	-	5	-	2	-	-	-	-
<i>Cochlicopa</i> sp.	24	-	-	2	-	-	-	-	-	-
<i>Vertigo</i> sp.	1	-	-	3	-	-	-	-	-	-
<i>Pupilla muscorum</i> (Linnaeus)	5	-	-	-	-	1	-	-	-	-
<i>Vallonia costata</i> (Müller)	39	-	-	1	-	-	-	-	-	-
<i>Vallonia pulchella</i> (Müller)	15	-	-	1	-	-	-	-	-	-
<i>Vallonia pulchella/excentrica</i> (adults are <i>pulchella</i>)	55	-	-	2	-	-	-	-	-	-
cf. <i>Vitrinobrachium breve</i> (Férussac) ¹	15	-	-	6	-	-	-	-	-	-
<i>Vitrea</i> cf. <i>crystallina</i> (Müller)	57	-	-	4	-	-	-	-	-	-
<i>Nesovitrea hammonis</i> (Ström)	10	-	-	1	-	-	-	-	-	-
<i>Aegopinella nitidula</i> (Draparnaud)	6	-	-	1	-	-	-	-	-	-
<i>Oxychilus</i> sp.	15	-	-	-	-	-	-	-	-	-
<i>Retinella</i> (<i>Lyrodiscus</i>) <i>elephantium</i> (Bourguignat)	105	-	-	5	-	-	-	-	-	-
<i>Deroceras/Limax</i>	248	1	1	12	10	2	2	3	20	3
Clausiliidae (mostly <i>Clausilia pumila</i> C. Pfeiffer)	91	-	-	19	-	2	+ fgts.	-	-	-
<i>Trochulus hispidus</i> (Linnaeus)	17	-	-	4	-	1	-	-	-	-
<i>Arianta arbustorum</i> (Linnaeus)	19	-	-	6	-	-	-	-	-	-
Earthworm granules	+	-	-	+	-	-	-	-	+	+
Marine shells										
<i>Mytilus edulis</i> Linnaeus	+	-	-	-	+	-	-	-	-	-
<i>Spisula</i> sp.	+	-	-	-	-	-	-	-	-	-
<i>Cerastoderma</i> sp.	+	-	-	-	-	-	-	-	-	-

¹ May include an additional vitrinid species.

which both prefer better-drained substrates. The environment for both units 4b and 4c at Valdoe therefore seems to have been a predominantly damp, rather open habitat, although some shade-demanding taxa were present. Three taxa (cf. *Vitrinobrachium breve*, *Clausilia pumila* and *Retinella* (*Lyrodiscus*) *elephantium*) no longer live in the British Isles; the last is extinct everywhere (see below). *Vitrinobrachium breve*, which was also recovered from Boxgrove (Preece and Bates, 1999: Fig. 97a), inhabits moist open woods, especially on the floodplain of rivers, and has a central and southern alpine modern range that extends into the Netherlands (Kerney *et al.*, 1983). *Clausilia pumila* lives in damp woods, mainly in the ground litter and under logs, and has a central and eastern European distribution (Kerney *et al.*, 1983).

The extraordinary feature of the molluscan assemblages from Valdoe is the occurrence of *Retinella* (*Lyrodiscus*) *elephantium*. *Lyrodiscus* has sometimes been regarded as a distinct genus but is more usually treated as a subgenus of *Retinella*, a lead followed here. Living members of the subgenus *Lyrodiscus* are confined to the Canary Islands, where they occur in woodland habitats (Rousseau and Puisségur, 1990; Alonso *et al.*, 2013). From the Late Pliocene to Middle Pleistocene, *Lyrodiscus* had a much wider geographical range extending across large areas of north-western Europe, where it has been recorded under a variety of names. Shells of *Lyrodiscus* are identifiable by virtue of their diagnostic sculpture of raised spiral lines interrupted by small gaps (Preece *et al.*, 2007: Fig. 18). *Lyrodiscus* from the Middle Pleistocene has been assigned to several species (e.g. *skertchleyi* Kerney) but they all seem to belong to a single species for which *elephantium* Bourguignat is the oldest available name (Limondin-Lozouet and Antoine, 2006).

Stratigraphical and ecological significance of *Lyrodiscus* at Valdoe

The occurrence of *Lyrodiscus* at Valdoe was completely unexpected because, although known from much older deposits on the continent, this is a characteristic species of MIS 11 and the index fossil of the distinctive *Lyrodiscus* fauna known from this period (Rousseau *et al.*, 1992; Limondin-Lozouet *et al.*, 2006, 2010, 2015, 2020; Limondin-Lozouet and Antoine 2006; Preece *et al.*, 2007; Limondin-Lozouet, 2017). In most of these faunas, *Lyrodiscus* forms only a minor component (~1%) of diverse assemblages dominated by shade-demanding taxa (mostly >55% and occasionally >80%). Its occurrence in unit 4b at Valdoe is fundamentally different in four respects. First, unlike its occurrence in assemblages of the *Lyrodiscus* fauna, it was not recovered from calcareous tufa. Second, it forms part of a land snail assemblage consisting of only about 20 species, far less diverse than those of the *Lyrodiscus* fauna that typically contain 40 taxa or more. Third, shade-demanding species are poorly represented in the associated assemblage, accounting for <30%. Fourth, *Lyrodiscus* accounts for 21.6% of the land snail fauna, a high percentage without precedent elsewhere (Fig. 5).

These findings necessitate a reappraisal of the stratigraphical significance of *Lyrodiscus* and its ecology. The MIS 13 age of Boxgrove, and by extension Valdoe (see above), is well attested by the mammalian biostratigraphy (Parfitt, 1999). The occurrence of *Lyrodiscus* at Valdoe therefore represents its first secure record from MIS 13 in Britain, although the record from Sun Hole Cave in Cheddar, Somerset, may also be of this age (Preece *et al.*, 2007: 1282; Parfitt and Preece, 2022). Despite

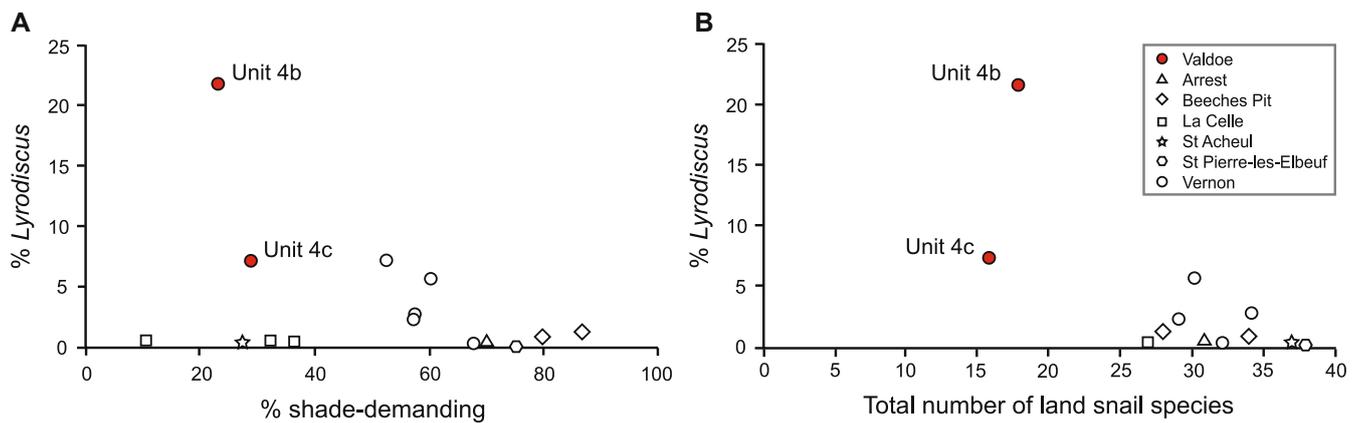


Figure 5. Frequency of *Lyrodiscus*. A. Plotted against the frequency of shade-demanding snails from various Pleistocene localities yielding the *Lyrodiscus* fauna. B. Plotted against the total number of land snail species from the same sites. Note the high frequencies of *Lyrodiscus* at Valdoe and its occurrence in a species-poor assemblage with a relatively low proportion of shade-demanding snails. [Colour figure can be viewed at wileyonlinelibrary.com]

the restriction of modern members of *Lyrodiscus* to woodland and *Erica arborea* scrub on the Canary Islands (Alonso *et al.*, 2013), it seems that the extinct *R. (Lyrodiscus) elephantium* could also live in more open habitats, although it did occur in forest, albeit at much lower frequencies.

Malacological perspectives on the interpretation of the Lower Palaeolithic land surface

Lateral variability of molluscan assemblages: comparisons with Boxgrove

Apart from *Retinella (Lyrodiscus) elephantium*, all other species of land snail found at Valdoe were recovered from the same stratigraphical horizon at Boxgrove (Preece and Bates, 1999; Table 4). However, several snail species found at Boxgrove were not found at Valdoe (Fig. 6).

Looking at the absentees from Valdoe, some can easily be explained by subtle differences in the local environment. For example, the occurrence of the aquatic species *Anisus leucostoma* and *Radix balthica* at Boxgrove (GTP 3 and Q2/B) simply indicates the presence of a small waterbody that might be prone to seasonal desiccation. Paradoxically, the calcareous sediments of the 'pond facies' from Q1/B that had yielded the hominin remains in units 4u (incisors) and 5ac (tibia) yielded no molluscs apart from the occasional slug plate but ostracod carapaces, which are composed of calcite, were abundant (Holmes *et al.*, 2010; Whittaker and Parfitt, 2017). *Succinella oblonga* would have lived on damp surfaces nearby and *Vertigo pygmaea* and *Vallonia excentrica* would have inhabited drier habitats. The occurrence of *Vertigo substriata*, *V. pusilla*, *Aegopinella pura* and *Spermodea lamellata* in some of the samples from the palaeosol (4c) at Boxgrove is perhaps more significant. Together they suggest more heavily shaded conditions than at Valdoe.

The occurrence of *Spermodea lamellata* is especially interesting because it usually lives in leaf litter and under fallen timber in old deciduous woodland (Kerney *et al.*, 1983). Today it has a distinctly north-west European range (Kerney *et al.*, 1983), although there are some isolated records from western Iberia (e.g. Gittenberger, 1989; De Oliveira, 2007). It was a regular member of mid-Holocene land snail assemblages from tufas in southern England, where it accounted for about 5–11% of the faunas dominated (~75%) by woodland taxa (Kerney *et al.*, 1980; Preece, 1998). At Boxgrove it

reached frequencies of 25% (Preece and Bates, 1999: Table 29) but here it occurred in assemblages with a much lower component (30–46%) of shade-demanding species quite different from the diverse woodland assemblages seen in the mid-Holocene or in the *Lyrodiscus* fauna of MIS 11. *Spermodea lamellata*, despite being a woodland species, was not a component of the *Lyrodiscus* fauna. Indeed, *Spermodea* and *Lyrodiscus* have never been found together, and although they both occur, rarely, in the thick tufa sequence at La Celle in the Seine Valley, they come from different stratigraphical levels; *Spermodea* occurring in assemblages both before and after those with *Lyrodiscus* (Limondin-Lozouet *et al.*, 2020). Humidity may be a determining factor, with *Spermodea* inhabiting more humid conditions than *Lyrodiscus*.

There is no evidence that *Spermodea* and *Lyrodiscus* occurred together at Valdoe or Boxgrove but they did live at the same time in the same general area. These faunal differences seem to reflect environmental heterogeneity on this Palaeolithic land surface. Boxgrove appeared to have areas of open water that supported game and attracted human hunters (Pope *et al.*, 2020), and it supported more shaded habitats, at least in some places. However, not all the samples from the same stratigraphical horizon yielded identical assemblages of molluscs. Some species, such as *Spermodea*, only occurred in about half of the samples from Boxgrove, and it is important to explore the reasons for these differences, which might result from decalcification and other post-depositional processes.

Effects of decalcification

Clear evidence of large-scale decalcification can be seen at both Valdoe and Boxgrove in the form of solution hollows and decalcification fronts visible in several sections (Fig. 3). It was therefore no surprise to find that the preservation of non-marine shells at both sites was extremely poor with many samples lacking identifiable material. Moreover, the surviving shells were mostly fragmentary, generally lacking surface sculpture. The preservation of small mammal remains was also generally poor at both sites, although at Boxgrove delicate bones were more abundant and better preserved. Post-depositional decalcification has therefore been a serious problem at both sites and it is instructive to explore how this may have affected species composition and why molluscan and other assemblages have survived better in some samples than in others.

Table 4. Comparison of the non-marine molluscan species from Valdoe and Boxgrove (full data given in Preece and Bates, 1999: Table 29). Shade-demanding species include those from woodland, talus slope, and other dark moist habitats, not all necessarily heavily shaded by trees. Some tall rank grassland in the final stages of succession towards scrub can also support species often classified as 'shade-demanding' (Cameron and Morgan-Huws, 1975)

Unit	Boxgrove						Valdoe		
	4c	4d	5a	5b	5c	LGC	6	4b	4c
Aquatic									
<i>Galba truncatula</i> (Müller)	+	-	+	+	-	-	-	-	+
<i>Radix balthica</i> (Linnaeus) (= <i>Lymnaea peregra</i> (Müller))	+	-	-	-	-	-	-	-	-
<i>Anisus leucostoma</i> (Millet)	+	-	-	-	-	-	-	-	-
cf. <i>Musculium lacustre</i> (Müller)	-	-	-	-	-	-	-	-	+
<i>Pisidium</i> spp.	+	-	-	+	-	-	-	+	-
Total aquatic	4	0	1	2	0	0	0	1	2
Marsh									
<i>Carychium</i> sp. (assumed to be <i>minimum</i>)	+	-	+	+	-	-	-	+	+
<i>Succinella oblonga</i> (Draparnaud)	+	-	-	-	+	+	-	-	-
<i>Succinea/Oxyloma</i>	+	-	+	+	+	+	-	+	+
Total marsh	3	0	2	2	2	2	0	2	2
Catholic									
<i>Cochlicopa</i> sp.	+	-	+	+	+	+	+	+	+
<i>Vertigo substriata</i> (Jeffreys)	+	-	+	+	-	+	-	-	-
<i>Punctum pygmaeum</i> (Draparnaud)	+	-	+	+	+	+	-	+	+
<i>Vitrea</i> cf. <i>crystallina</i> (Müller)	+	-	-	+	-	+	-	+	+
<i>Nesovitrea hammonis</i> (Ström)	+	-	+	+	+	+	-	+	+
<i>Euconulus fulvus</i> (Müller) agg.	+	-	+	+	+	+	-	+	+
<i>Trochulus hispidus</i> (Linnaeus)	+	-	+	+	+	+	+	+	+
<i>Arianta arbustorum</i> (Linnaeus)	+	-	+	+	+	+	-	+	+
<i>Vertigo pygmaea</i> (Draparnaud)	+	-	-	+	-	+	-	-	-
<i>Retinella (Lyrodiscus) elephantium</i> (Bourguignat)	-	-	-	-	-	-	-	+	+
<i>Deroceras/Limax</i>	+	+	+	+	-	+	-	+	+
Total catholic with slugs	10	1	8	10	6	10	2	9	9
Total catholic without slugs	9	0	7	9	6	9	2	8	8
Open-country									
<i>Pupilla muscorum</i> (Linnaeus)	+	-	-	+	+	+	-	+	-
<i>Vallonia costata</i> (Müller)	+	-	+	+	+	+	-	+	+
<i>Vallonia excentrica</i> Sterki	-	-	-	-	-	+	-	-	-
<i>Vallonia pulchella/excentrica</i> (adults are <i>pulchella</i>)	+	-	-	+	+	+	-	+	+
Total open-country	3	0	1	3	3	4	0	3	2
Shade-demanding									
<i>Vertigo pusilla</i> Müller	+	-	-	+	-	+	-	-	-
<i>Acanthinula aculeata</i> (Müller)	-	-	+	+	+	+	-	-	-
<i>Spermodea lamellata</i> (Jeffreys)	+	-	+	+	+	+	-	-	-
<i>Vitrinobrachium breve</i> (Férussac)	+	-	+	+	-	-	-	+ ¹	+ ¹
<i>Aegopinella pura</i> (Alder)	+	-	+	+	+	+	+	-	-
<i>Aegopinella nitidula</i> (Draparnaud)	+	-	+	+	+	+	+	+	+
<i>Oxychilus</i> sp.	+	-	-	-	-	+	-	+	-
Clausiliidae ²	+	+	+	+	+	+	+	+	+
<i>Helicigona lapicida</i> (Linnaeus)	-	-	-	-	-	+	-	-	-
Total shade-demanding	7	1	6	7	5	8	3	4	3
Total number of mollusc species (excluding slugs)	26	1	17	23	38	22	12	19	17
Total number of land snail species (excluding slugs)	22	1	16	21	16	22	5	18	15

¹ May include an additional vitrinid species.

² Mostly *Clausilia pumila* C. Pfeiffer but at Boxgrove (4c) it also includes *Cochlodina laminata* (Montagu).

One factor that might have influenced preservation potential is the depth of burial. It may be significant that apart from the shell-rich samples from TP6, the Valdoe trenches were located furthest from the cliffline where the soil experienced more prolonged exposure and weathering, before burial by calcareous sediments that thin southwards, as at Boxgrove. The most fossiliferous samples were usually those buried by >3 m of calcareous sediment (Fig. 4). In this regard, it is noteworthy that rhizoliths (mineralised root casts) were recovered in nearly every sample analysed from Valdoe, whereas they occurred only rarely at Boxgrove.

Several samples from Valdoe and Boxgrove yielded very few species of mollusc but they did contain relatively large numbers of clausiliid apices and remains of slugs (*Deroceras/Limax*). At Boxgrove fragments of clausiliid shell were relatively frequent, showing that they belonged to at least two species; one with a coarsely ribbed shell, and another with a smooth shell assigned to *Cochlodina laminata* (Preece and Bates, 1999). Interestingly, no clausiliid apertures containing the diagnostic dentition were found at Boxgrove, unlike at Valdoe where a few were recovered allowing attribution of the coarsely ribbed species to *Clausilia pumila*. Clausiliid apices, some obviously juvenile specimens, would be expected to

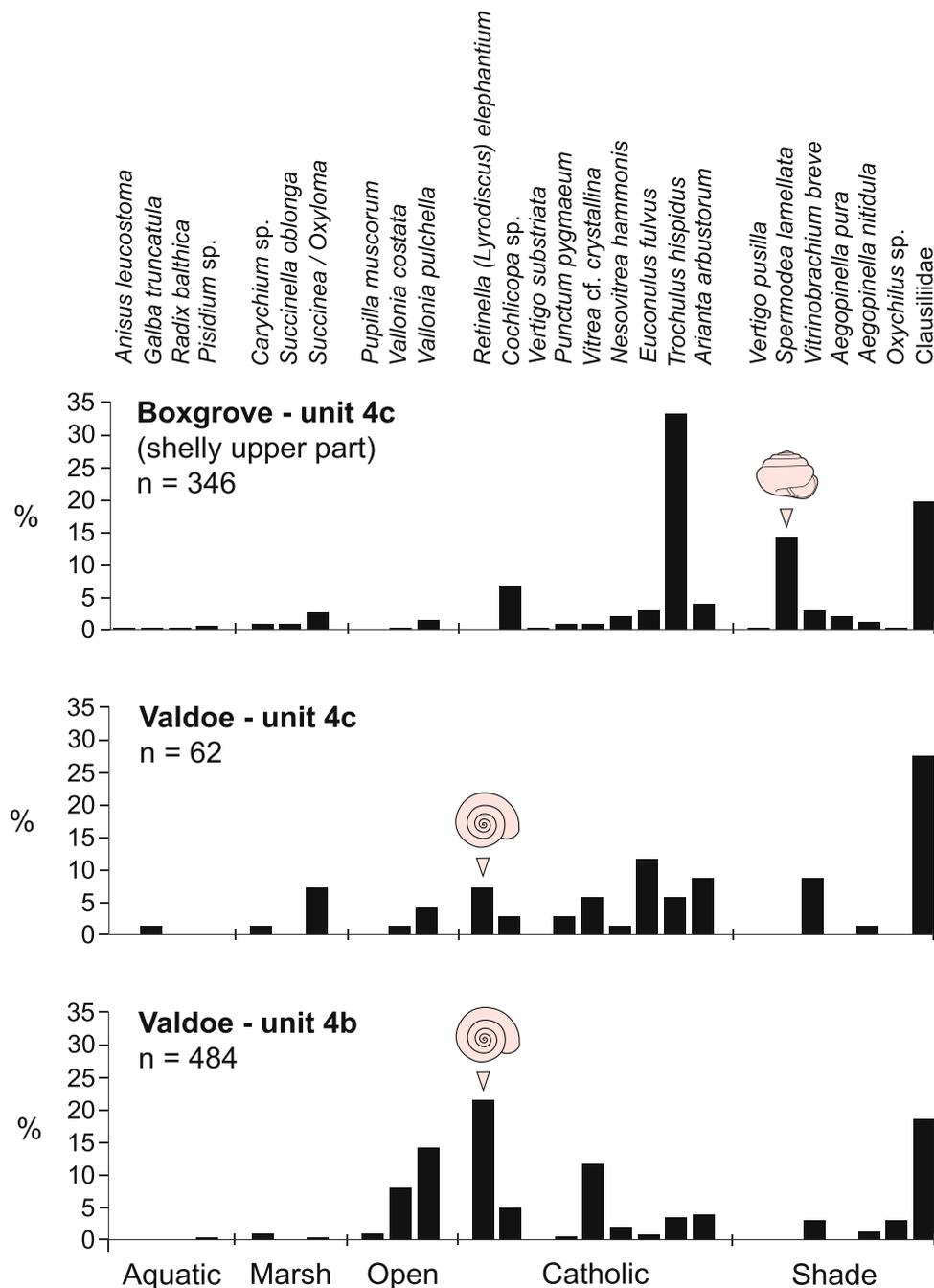


Figure 6. Histograms showing differences in the molluscan assemblages from units 4c and 4b at Valdoe and upper part of unit 4c at Boxgrove (mean of 4 samples: L, C, D and F, see Preece and Bates, 1999: Table 29). Slugs have been excluded from these analyses. Note that *Lyrodiscus* occurs only at Valdoe and *Spermodea* only at Boxgrove. [Colour figure can be viewed at wileyonlinelibrary.com]

outnumber adult shells for demographic reasons but the complete absence of clausiliid apertures in a large sample ($n = 783$) from Boxgrove is somewhat counter-intuitive since it is usually the thickened apertural parts of shells that are the most durable. This issue was investigated by Carter (1990), who showed, for example, that in buried soils the thickened apertures of *Pupilla muscorum* survive far longer than their apices and that the apices of *Cochlicopa*, which are relatively large and thin-shelled, are similarly more vulnerable to destruction than their more heavily calcified apertures. *Azeca* apertures appear to be even more durable, as shown in various comparisons of the representation of different parts of shells of various species through the stratigraphical profile at Beeches Pit, Suffolk (Preece *et al.*, 2007: Fig. 16).

While differential destruction of different parts of snail shells is problematic, it is the differential loss of species that is far more

serious. This has clearly happened at Valdoe and Boxgrove and is particularly obvious in the samples consisting largely of slug remains. Remains of slugs are represented by small plates composed of calcite. In life these are internal structures found beneath the mantle. All of the specimens recovered at Valdoe and Boxgrove had an asymmetrical form, suggesting attribution to *Deroce* in the case of small ones (~2.5 mm) and to *Limax* for those above 4 mm (young *Limax* are not easily separable from *Deroce*). In several of the samples from Valdoe and Boxgrove, slug remains completely dominated the molluscan assemblages at values exceeding 50%, and sometimes reaching values as high as 80% (Preece and Bates, 1999: Fig. 96). In order to put these values into perspective, the representation of slug remains from a range of natural environments from grassland to closed forest is presented (Table 5). In none of the samples from these varied environments does the frequency of slugs reach 50% of the molluscan

Table 5. Representation of slug remains in a range of different natural environments. Note that they seldom account for >30%. Values for *Lyrodiscus* have been combined with the total for Catholic species

Site/Section/Sample	Sediment	Age (¹⁴ C yr BP), Marine Isotope Stage (MIS)	Aquatic	Marsh	Open- country	Catholic	Shade- demanding	Total land (with slug)	Slug remains (% land, incl. slug)	Total number of mollusc species (excl. slugs)	Number of land snail species (excl. slugs)	Reference
Holywell Coombe, Folkestone												
Trench 3, 184-186 cm	Tufa	7650 ± 80	13	16	2	71	261	355	5 (1.4)	31	27	1
Trench 5, 105-110 cm	Tufa	~8600	0	37	48	277	420	804	22 (2.7)	26	26	1
Trench 5, 250-255 cm	Tufa	9460 ± 140	1	254	264	268	405	1214	23 (1.9)	29	28	1
Trench 5, 340-345 cm	Tufa	9760 ± 100	0	39	97	132	17	304	19 (6.2)	14	14	1
Cut-&Cover, 150-155 cm	Allerød soil	11,370 ± 150	0	17	318	130	0	513	48 (9.3)	14	14	1
Trench HV, 322-327 cm	Allerød soil	11,530 ± 160	1	35	66	107	0	252	44 (17.4)	17	16	1
Red Barns, Porchester												
BS6 11	Buried soil	late Middle Pleistocene	0	0	1037	870	3	2094	184 (8.8)	13	13	2
Inchrotry, Banffshire												
150-155 cm	Tufa	<6000	3	3	3	666	195	879	12 (1.4)	21	20	3
345-350 cm	Tufa	7360 ± 60	0	1	0	76	88	174	9 (5.2)	15	15	3
550-555 cm	Tufa	~9000	2	0	2	259	0	270	9 (3.3)	9	8	3
Binnel Point, Isle of Wight												
upper soil, unit e	Buried soil	~4500	0	0	0	78	639	801	92 (11.5)	20	20	4
lower soil, unit c	Buried soil	4480 ± 100	0	0	7	56	769	891	59 (6.6)	22	22	4
St Catherine's Point, Isle of Wight												
75-85 cm, unit b	Buried soil	3960 ± 50	0	0	2	22	269	302	9 (3.0)	17	17	4
Beeches Pit, West Stow, Suffolk												
Cutting 1, 40-50 cm	Tufa	MIS 11	2	0	4	60	424	499	11 (2.2)	30	28	5
Lower tufa	Tufa	MIS 11	157	15	3	166	741	962	37 (3.8)	41	34	5
Boxgrove, West Sussex												
GTP 10, P(5bM), unit 5b	Calcareous marl	MIS 13	1	29	7	245	169	466	16 (3.4)	19	18	6
GTP 13, O(101), unit 5b	Calcareous marl	MIS 13	8	6	1	153	119	300	21 (7.0)	10	9	6
Q2/B, N(68), LGC	Chalky colluvium	MIS 13	0	4	17	73	246	345	5 (1.4)	22	22	6
GTP 17, M(11), unit 5b	Calcareous marl	MIS 13	17	17	10	304	287	639	21 (3.3)	24	22	6
Q1/B, unit 5a	Clayey silt	MIS 13	1	7	2	35	58	105	3 (2.9)	17	16	6
Q2/B, K(39), unit 4c	Buried soil	MIS 13	5	12	4	60	65	158	17 (10.8)	22	18	6
Q2/B, H(22), unit 4c	Buried soil	MIS 13	0	8	4	120	77	225	16 (7.1)	19	19	6
GTP 3, F(14), unit 4c	Buried soil	MIS 13	2	11	6	133	73	261	38 (14.6)	22	20	6
Q2/B, C(38), unit 4c	Buried soil	MIS 13	1	2	0	34	31	75	8 (10.7)	15	14	6
GTP 3, J(260), unit 4c	Buried soil (decalcified)	MIS 13	1	12	0	71	35	623	505 (81.0)	12	11	6
Q2/B, E(26), unit 4c	Buried soil (decalcified)	MIS 13	1	2	0	21	17	90	50 (55.5)	10	9	6
QTP 3, A(263), unit 4c	Buried soil (decalcified)	MIS 13	1	0	0	24	1	99	74 (74.7)	6	5	6
GTP 3, D(13), unit 4c	Buried soil (decalcified)	MIS 13	3	1	0	4	19	38	14 (36.8)	8	5	6
GTP 3, G(19), unit 4c	Buried soil (decalcified)	MIS 13	1	1	1	5	5	25	13 (52)	7	6	6
Q2/B, L(33), unit 4c	Buried soil (decalcified)	MIS 13	1	1	0	10	15	34	8 (23.5)	8	7	6
Valdoe Quarry, West Sussex												
VTP 6, unit 4c	Buried soil	MIS 13	1	6	4	39	20	81	12 (14.8)	17	16	7
VTP 6, unit 4b	silt	MIS 13	2	7	114	252	112	733	248 (33.8)	19	18	7

Ref. 1 = Preece, 1998; Ref. 2 = Wenban-Smith *et al.*, 2000; Ref. 3 = Preece *et al.*, 1984; Ref. 4 = Preece, 1986; Ref. 5 = Preece *et al.*, 2007; Ref. 6 = Preece & Bates, 1999; Ref. 7 = This paper.

assemblage. Samples containing such high frequencies of slug plates have been severely affected by decalcification. This has removed most of the delicate shells composed of aragonite, leaving an over-representation of more durable elements (e.g. clausiliid apices) and slug remains composed of calcite, the more stable form of calcium carbonate.

The frequency of slug remains is therefore a useful index of the extent of decalcification. When these values are plotted from different sampling sites of unit 4c at Boxgrove, interesting patterns emerge (Fig. 7A). Where this unit has only a relatively thin (~1.5 m) cover of overlying calcareous sediment, the frequency of slug remains is higher than where the depth of burial is greater (>1.5 m). Thus, samples taken closer to the buried cliffline generally have lower frequencies of slug plates and it is these samples that mostly contain *Spermodea*, assumed to come from the upper parts of 4c. Fig. 7B plots the number of *Spermodea* against the number of shells from various locations at Boxgrove, showing that samples without *Spermodea* generally have the lowest number of shells and highest frequency of slug plates (>50%).

The effect of decalcification is also apparent when the frequency of species with thin, delicate shells, such as members of the Vitrinidae, is examined from samples containing slug plates at a range of frequencies. The expectation is that delicate shells will be most frequent in samples that are less decalcified, containing a relatively low frequency of slug plates. This expectation is largely borne out by the data (Fig. 8), although the occurrence of vitrinids in the most severely decalcified sample H(22) is anomalous, suggesting that the decalcification might be extremely localised, affecting only part of this bulk sample that was sampled laterally for about a metre.

Decalcification therefore causes marked biases in the preservation of different components and this needs to be taken into consideration when deciding which samples are good enough to include in the environmental reconstructions.

Molluscan and archaeological record within the palaeosol (4c) at Boxgrove

The record from unit 4c is extremely condensed and the interpretation of the faunal succession through it has been hampered by decalcification. Despite their close proximity, samples of 4c from Q2/B differ in faunal composition, particularly with respect to the occurrence of *Spermodea*. There may be several reasons for this patchy occurrence. First, it is possible that it does capture the fine-scale spatial distribution of species on the land surface, reflecting subtle differences in microhabitat (Whittle *et al.*, 1993; Rouse and Evans, 1994). Second, from an ecological standpoint it is likely that the *Spermodea* (and other shade-demanding species) arrived later than the catholic species as moist shaded habitats became available. If so, the analysed assemblages are time-averaged and have simply not been sampled at a sufficiently high temporal resolution. A third possibility is that the absence of *Spermodea* from some samples relates to the loss of the upper parts of the palaeosol by erosion or decalcification. It is interesting to note that shells are not distributed evenly throughout 4c and generally only the upper 2–3 cm are shelly. Samples L, C, F and D were taken specifically from these upper levels and apart from the last, which yielded very few shells, all contained *Spermodea* (Preece and Bates, 1999). None of the other 4c samples from Boxgrove could be subdivided since the palaeosol was so thin (often only 5 cm thick) and so poor in shells. The frequency of slug plates is generally

<25% in these upper shelly samples but in other samples lacking *Spermodea* it is often >50% (Fig. 9). This might indicate that *Spermodea* is particularly susceptible to decalcification, which is another possibility. In GTP3 F and GTP3 J, sampled less than 2 m apart and both yielding >100 shells, *Spermodea* was relatively frequent in the former (slug frequency <25%) but absent in the latter (slug frequency >50%). The frequency of slug remains shows an inverse relationship both to the frequency of shade-demanding snails (Fig. 9B) and to the total number of land snail species (Fig. 9C). Samples with a higher frequency of slugs are sampling earlier parts of the succession, hence the lower percentage of shade-demanding snails in a weathered deposit. Samples from profiles in which the top of 4c has not been truncated are less affected by decalcification, which explains why they combine high proportions of shade-demanding species with low percentages of slug plates. The inverse relationship between the number of species and frequency of slug plates can also be explained by 'truncation' (by erosion and/or weathering) of the profiles in some samples and the survival of an upper shell-rich horizon in others. The latter contain a higher diversity of species because they sample more of the succession from open to closed conditions.

Unlike shells, the occurrence of flint debitage will be unaffected by decalcification, although it might result in loss of temporal resolution. Wilhelmsen (1999) undertook a detailed study of the spatial and vertical distribution of debitage in the palaeosol (4c) at Boxgrove in order to understand the depositional history of artefacts and hence their integrity. He focused on Area A of Quarry 2, where 4c was thicker (~15 cm), enabling more detailed sampling in 1 cm spits. He showed that artefacts were nearly ubiquitous and that surface processes such as wind winnowing and sheet wash had been negligible, as had displacement caused by bioturbation by roots and burrowing organisms. He found that the highest frequency of artefacts (>6 mm) occurred not at the surface of 4c but about 60 mm beneath it (Wilhelmsen, 1999: Fig. 267). Although only one location at Boxgrove was studied in such detail, the vertical occurrence of artefacts appears to be representative of other sections, and so provides a temporal record of the intensity of human activity. There were no associated fossils at this precise location but it is interesting to note that in adjacent sections, it is these upper levels of 4c that have yielded shade-demanding snails, such as *Spermodea*. Perhaps the encroachment of woodland provides an explanation for the decline in the frequency of artefacts, and hence human activity, in the upper levels of 4c.

Shaded conditions persisted and the frequency of shade-demanding species increased further in unit 5, which yielded a range of woodland mammals and land snails, including some (e.g. *Acanthinula aculeata*) not recovered from 4c. Colder conditions ensued (unit 6), as reflected by active colluviation and the occurrence of Norway lemming (*Lemmus*). These events are summarised in Fig. 12.

Duration of subaerial exposure of the Palaeolithic land surface at Boxgrove

There has been much discussion about the length of time that the land surface (unit 4c) was exposed to subaerial weathering. This unit is believed to represent the weathered, partially homogenised and decalcified upper part of the Slindon Silts (unit 4b), a conclusion supported by mineralogy (Catt, 1999). Some indications of sediment ripening were observed in unit 4b but this process must have been far more prolonged in 4c to

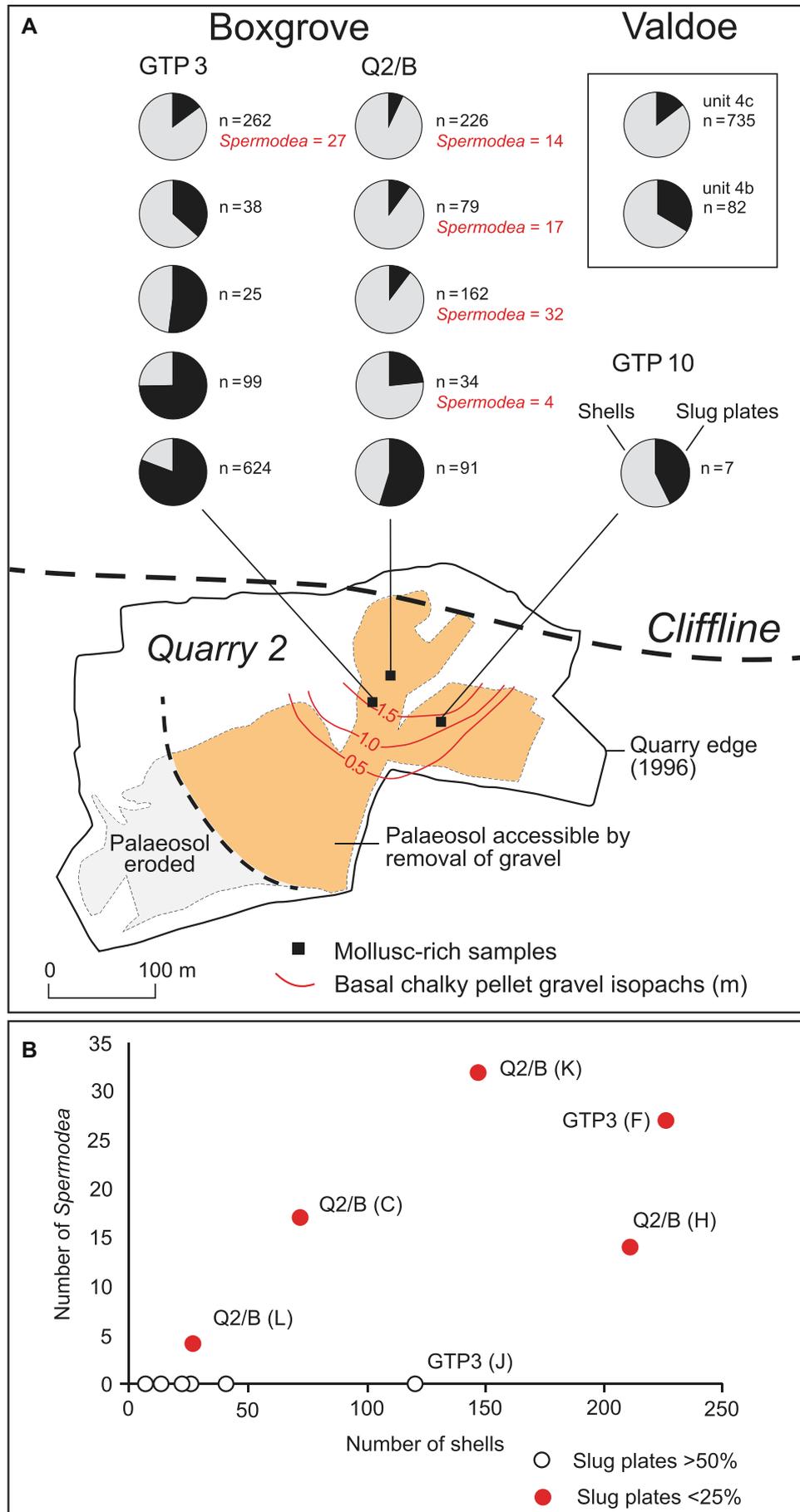


Figure 7. A. Pie diagrams showing the frequency of slug plates from various locations in Q2 at Boxgrove. The frequencies tend to be higher in samples furthest from the buried chalk cliff where the depth of burial by calcareous sediments is less. The counts of *Spermodea*, assumed to come from the upper parts of 4c, show that this species occurred in samples with the lowest frequency of slug plates. B. Number of *Spermodea* plotted against the number of shells from various locations at Boxgrove. The relative frequency of slug plates is also shown. Note that the samples without *Spermodea* generally have the lowest number of shells and the highest frequency of slug plates (>50%). [Colour figure can be viewed at wileyonlinelibrary.com]

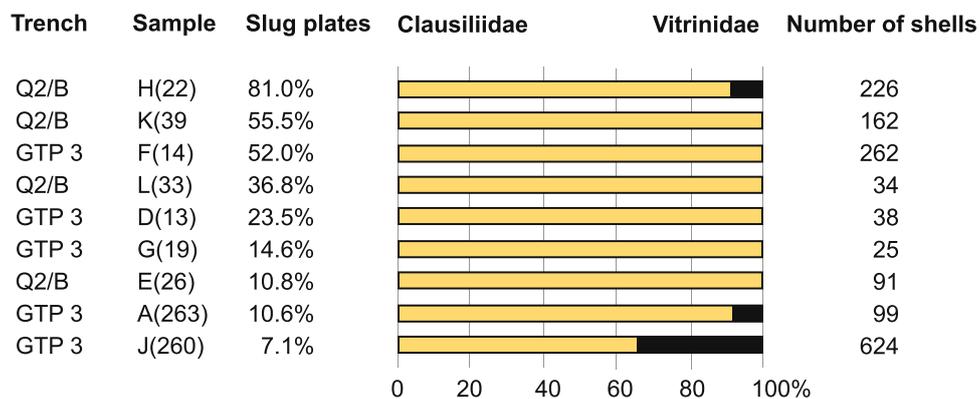


Figure 8. The frequency of slug plates (%) shown against a ratio of the frequency of Clausiliidae (robust) and Vitrinidae (delicate). In general, samples with the highest proportion of Vitrinidae have the lowest frequencies of slug plates. Sample H(22) is an anomaly (see text). [Colour figure can be viewed at wileyonlinelibrary.com]

produce this much more strongly weathered and decalcified unit (Macphail, 1999: 130). Comparisons were made with the pedological features exhibited by soils developed on the recently drained polders on the IJsselmer in The Netherlands. These sediments became rapidly ripened and biologically reworked to a depth of 0.4 m during the 14 years or so that it took to develop a fully terrestrial ecosystem. Macphail (1999: 130) noted that at Boxgrove the depth of soil homogenisation appeared to be shallow, and argued that the period of soil ripening, and the main phase of human occupation, could have been of short duration. Using the Dutch data as an analogue, he suggested that this could have been as little as 10–20 years although, taking other factors into account, he extended the timescale to about 100 years (see also Catt, 1999: 117–118).

This extremely short timescale was based on the assumption that the depth of ripening is a direct measure of time. This assumption is hazardous and there are suggestions from the palaeoecology of the land surface at Boxgrove and Valdoe that much longer timescales were involved. Macphail (1999: 130) noted that at Boxgrove ‘the wooded downland beyond the cliff would have readily supplied seed and animals’. Plant seed and some animals can indeed disperse to new areas relatively rapidly but this hardly applies to land snails, which have extremely limited powers of active dispersal. Empirical data are rather sparse, but it is noteworthy that only a subset of land snails inhabiting Hayley Wood, an ancient wood in Cambridgeshire, managed to spread into an adjoining area of secondary woodland (Paul, 1978). Some of the species of land snail found in the palaeosol (4c) at Boxgrove, such as *Spermodea lamellata*, are often regarded as indicators of ‘ancient woodland’, implying that some time must have elapsed for such ecologically mature habitats to become established. In Holocene tufas in Kent, south-east England, *Spermodea* did not appear until ~7500 yr BP when shade-demanding taxa reached their maximum (Kerney *et al.*, 1980; Preece 1998; Preece and Bridgland, 1999). The occurrence of *Spermodea* at Boxgrove, however, was not accompanied by a full suite of other shade-demanding species, typical of such closed forest environments. *Discus rotundatus*, for example, which is so abundant in such habitats on the South Downs (e.g. Cameron *et al.*, 2006), was completely absent at both Boxgrove and Valdoe. In the interglacial tufa at La Celle, *Spermodea* was also absent in the lowermost parts of the sequence but briefly appeared immediately before and just after the forest maximum (Limondin-Lozouet *et al.*, 2020). This suggests that it also occurs in transitional woodland habitats,

both in those that have not developed into closed canopy forest and those undergoing forest recession. Either way, the occurrence of *Spermodea*, and a few other shade-demanding taxa, at Boxgrove does suggest the presence of some moist shaded habitats, which are likely to have taken far longer than 20, or even 100, years to become established. A confounding factor at Boxgrove/Valdoe is that the ecological succession occurred on a newly exposed land surface that developed during the later part of the interglacial rather than at its beginning, which perhaps accounts for some of the faunal differences.

Comparisons with other fossil and modern assemblages

In order to shed further light on the nature of the environments at Valdoe and Boxgrove and to build a better picture of the contemporary landscape, further comparisons are needed (SI Table 1). The openness of the environment is critical from an archaeological perspective since much of the human activity described from Boxgrove, such as the hunting and butchery, are assumed to have happened in an essentially open landscape. Consequently, the number of land snail species and frequency of shade-demanding taxa from Valdoe and Boxgrove have been plotted alongside comparable data from modern and fossil sites representing different environments ranging from open grassland to closed forest (Fig. 10).

On this ecological spectrum, the Boxgrove/Valdoe assemblages occupy an intermediate position between the open-country faunas from modern grazed and ungrazed rank grassland on the South Downs (Cameron and Morgan-Huws, 1975) and those from woodland in the same region (Cameron *et al.*, 2006). They occupy a similar intermediate position in relation to fossil assemblages ranging from open country, represented by those from the Allerød soil at Holywell Coombe, Folkestone (Preece, 1998), and that from a late Middle Pleistocene palaeosol at Red Barns, Hampshire (Wenban-Smith *et al.*, 2000), to closed forest, exemplified by the mid-Holocene zone d assemblage from Holywell Coombe (Preece, 1998) and the MIS 11 *Lyrodiscus* fauna from Beeches Pit, West Stow (Preece *et al.*, 2007). They are rather more diverse than the grassland assemblages and contain several shade-demanding species absent in those faunas. However, they contain far fewer species, and far fewer shade-demanding taxa than either the mid-Holocene

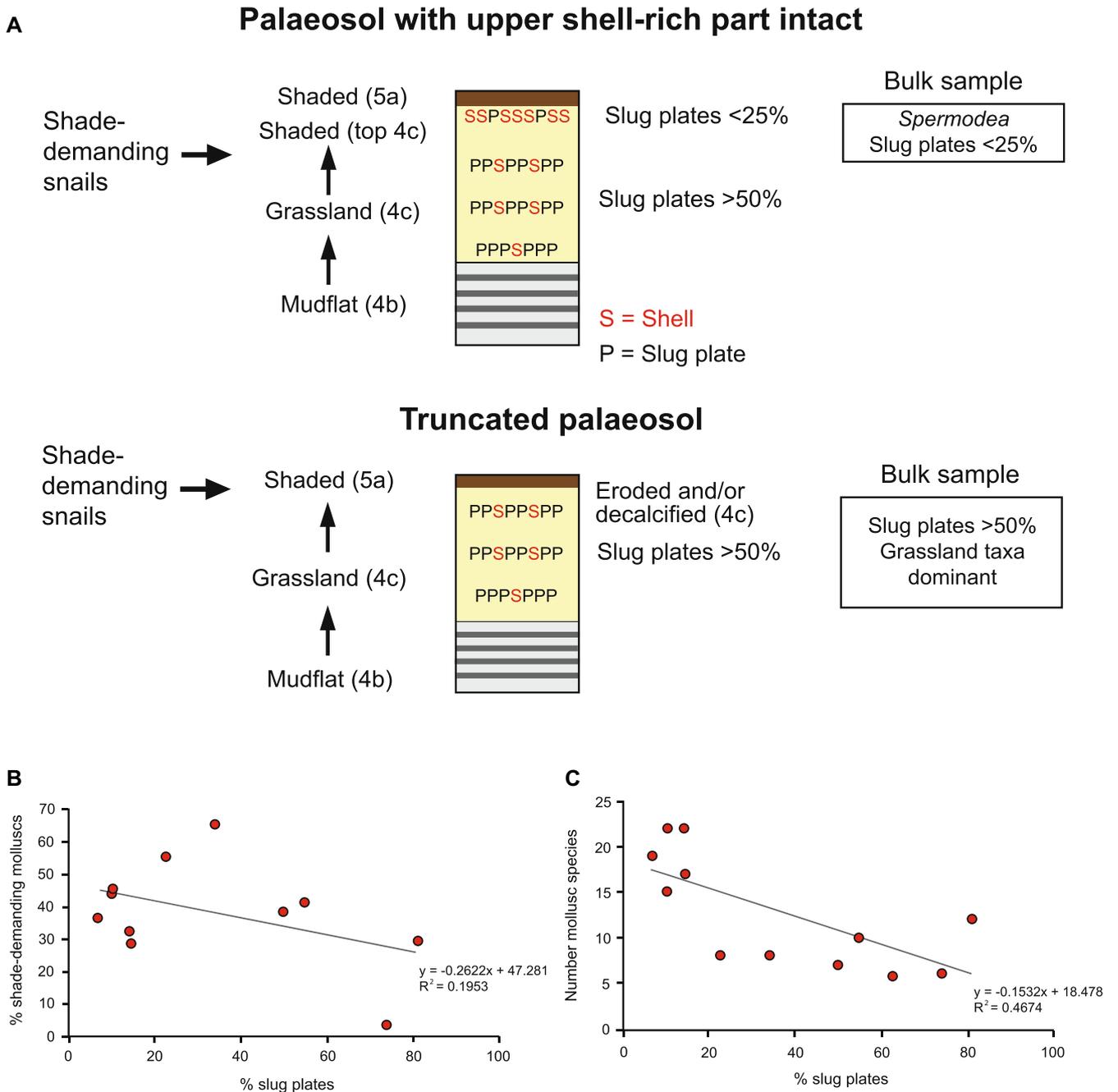


Figure 9. A. Diagrams explaining how faunal differences in samples of 4c taken in close proximity may result from the loss of the upper levels by erosion or decalcification. The composition of the assemblages is also governed by the thickness of sediment sampled. B. Slug plates as a percentage of land snails plotted against the percentage of shade-demanding snails. C. Frequency of slug plates plotted against the number of species of land snail. [Colour figure can be viewed at wileyonlinelibrary.com]

fauna at Holywell Coombe or the MIS 11 assemblages of the *Lyrodiscus* fauna from Beeches Pit.

Another interesting comparison is with the land snail assemblages from Neolithic soils incorporated within landslip debris from sites along the Undercliff on the Isle of Wight (Preece, 1986). The Undercliff occupies a narrow zone (0.3–0.7 km) of landslipped terraces that extends for 11 km around the south coast of the island. The rear scarp and deposits derived from it are Cretaceous Gault Clay, Upper Greensand and Lower Chalk, rather than Upper Chalk, which forms the fossil cliffs at Boxgrove and Valdoe. Nevertheless, the topographic setting is similar, although the terrain of the Undercliff is hummocky rather than a flat coastal plain. The land snail assemblages from two sites (Binnel Point and St

Catherine’s Point) along the Undercliff were dominated by shade-demanding species, quite unlike the assemblages from Boxgrove and Valdoe (Fig. 10). In the lower soil at Binnel Point, remains of both hazel dormouse and red squirrel were also recovered, underlining the wooded nature of the environment.

It is interesting to see how the Boxgrove/Valdoe land snail assemblages compare with various stages of succession from the late-glacial through to the mid-Holocene (Fig. 11). Comparisons were therefore made with representative assemblages from successive mollusc zones from the Allerød (zone z) through the early to mid-Holocene (zones a–d) at Holywell Coombe, Folkestone (Preece, 1998; Preece and Bridgland, 1999). The Boxgrove/Valdoe assemblages are less

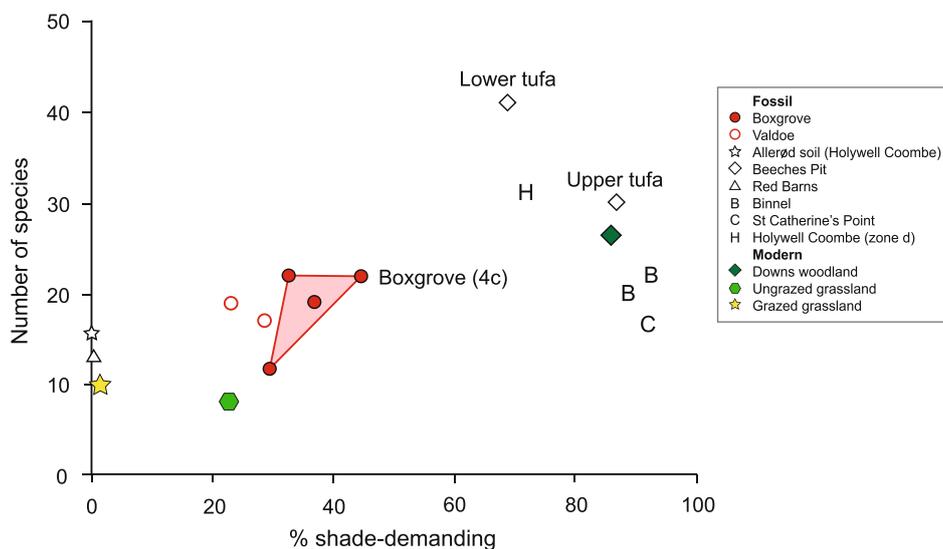


Figure 10. Mean frequencies of shade-demanding land snails plotted against the mean number of land snail species for modern sites on the South Downs ranging from grazed and ungrazed rank grassland (Cameron and Morgan-Huws, 1975) to woodland (Cameron *et al.*, 2006). Comparable data are also shown for fossil assemblages ranging from open country (Allerød soil at Holywell Coombe, Folkestone and a late Middle Pleistocene palaeosol at Red Barns, Hampshire) to closed forest (mid-Holocene zone d of Holywell Coombe and MIS 11 *Lyrodiscus* fauna of Beeches Pit, West Stow). Data from two Neolithic sites (Binnel Point and St Catherine's Point) from the Undercliff on the Isle of Wight are also shown. Valdoo and Boxgrove occupy an intermediate position on this ecological spectrum. [Colour figure can be viewed at wileyonlinelibrary.com]

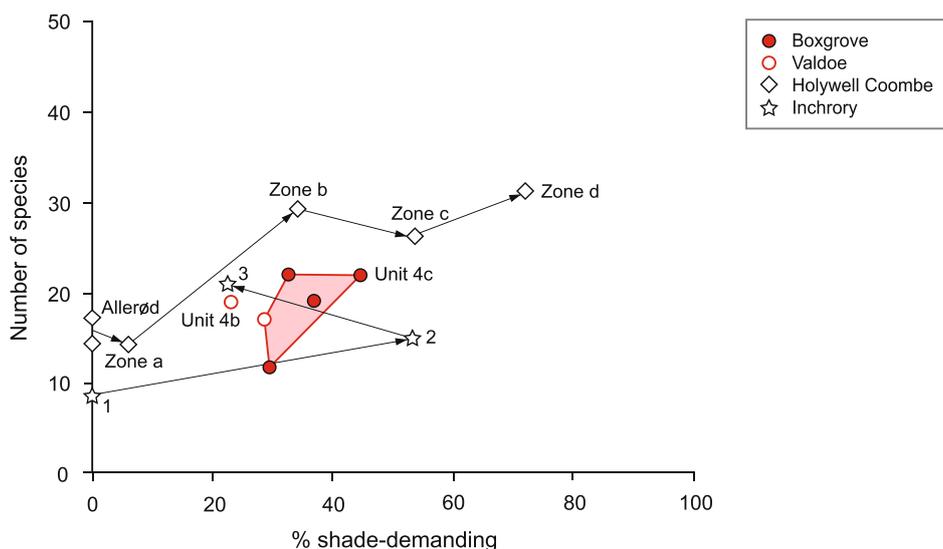


Figure 11. Plots of the percentage shade-demanding snails against the total number of land snails from Valdoo and Boxgrove superimposed on values from late-glacial/Holocene successional sequences from Holywell Coombe, Folkestone (mollusc zones z to d; Preece, 1998) and Inchrory, Scotland (Preece *et al.*, 1984). Approximate uncalibrated radiocarbon ages for the samples are as follows: Holywell Coombe, Folkestone: Allerød soil (11 500 yr BP), Zone a (9800 yr BP), Zone b (9500 yr BP), Zone c (8500 yr BP), Zone d (7650 yr BP); Inchrory tufa, Glen Avon, Banffshire: sample 1 (9500 yr BP), zone 2 (7360 yr BP), sample 3 (6000 yr BP). [Colour figure can be viewed at wileyonlinelibrary.com]

diverse than those of the mid-Holocene forest optimum (zones c and d) and they have lower frequencies of shade-demanding species. However, they are generally richer in species than mid-Holocene assemblages from the Inchrory tufa in Glen Avon in the Scottish Cairngorms (Preece *et al.*, 1984), although the species composition from about 7000 yr BP onwards is remarkably similar (SI Table 2). Of the 23 mollusc species recorded from Inchrory, 12 occurred at Valdoo and 16 in 4c at Boxgrove. Like the Sussex sites, *Discus rotundatus* did not occur but *Vertigo pusilla*, *V. substriata* and *Spermodea lamellata* were all present, as they were at Boxgrove. The main differences relate to the absence of *Vallonia* species and *Trochulus hispidus*, which do not occur inland in this part of Scotland (Kerney, 1999). Their absence at Inchrory therefore results from biogeographical, rather than ecological, reasons.

The tufa at Inchrory was confined to a narrow gully, which is likely to have had its own moist shaded microhabitat suitable to support such snails. They are unlikely to have occurred throughout Glen Avon, except in similar favourable microhabitats and a similar situation is likely to have occurred at Boxgrove/Valdoo.

Environmental summary

The environment of the Palaeolithic land surface that extends from Boxgrove to Valdoo and beyond can be reconstructed at various spatial and temporal scales (Fig. 12). As the relative sea-level fell, nearshore marine sands (unit 3) deposited on an extensive coastal plain beneath a high chalk cliff passed into intertidal mudflats (units 4a–b). These were eventually left high

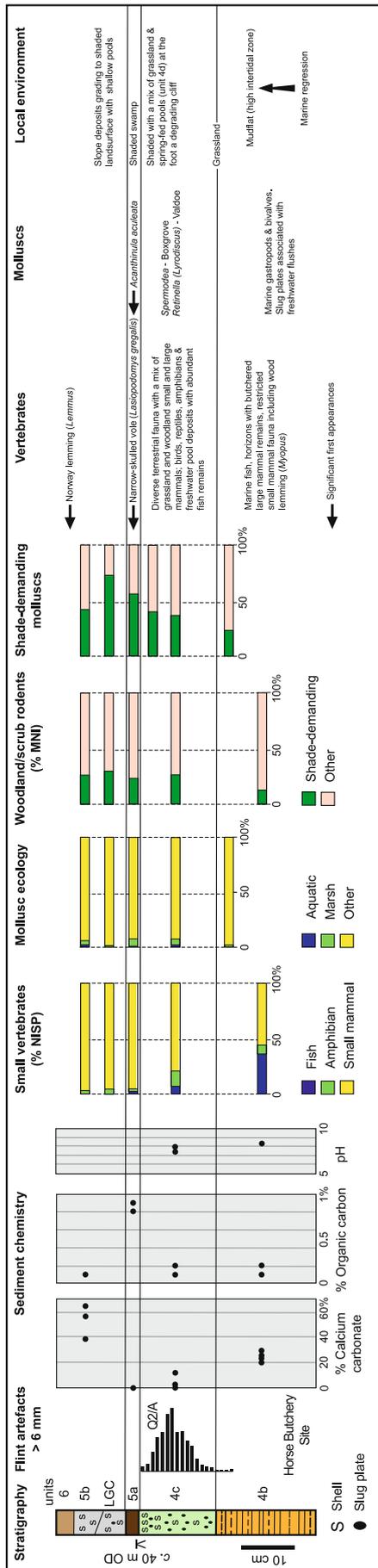


Figure 12. Summary of the environmental history of the sequence at Boxgrove. Note the decline in the frequency of flint debitage in the upper part of 4c, where the frequency of shade-demanding snails increases. [Colour figure can be viewed at wileyonlinelibrary.com]

and dry, allowing the initiation of subaerial weathering in the upper levels of unit 4b. Pedogenesis continued and intensified during the formation of unit 4c, the main fossiliferous horizon of the Palaeolithic land surface from which most of the archaeology was recovered. Grassland developed and was inhabited by a range of grazing herbivores and predators that preyed on them. Several pools and small lakes formed on the coastal plain, which was also crossed by small streams and springs issuing from the chalk. Some of these pools served as watering holes for the larger mammals and were the focus of hunting and butchery activity by early humans. The small vertebrates provide finer spatial resolution but because many seem to have been prey items, their remains are often found a short distance from where they actually lived. The occurrence of hazel dormouse, roe deer and other woodland mammals indicate the presence of scrub/forest. Molluscs provide even finer spatial resolution and can pinpoint more precisely the areas of woodland and other habitats. Woodland habitats developed towards the top of 4c, although evidence for this is frequently lost through truncation of the palaeosol by erosion or decalcification. Archaeological activity reflected by the frequency of flint debitage declined as the frequency of shade-demanding land snails increased, perhaps suggesting that the encroachment of woodland was a causal factor. Shaded conditions persisted and the frequency of shade-demanding species increased further in unit 5, which yielded a range of woodland mammals and land snails, including some (e.g. *Acanthinula aculeata*) not recovered from 4c. Colder conditions ensued (unit 6), as reflected by active colluviation and the occurrence of Norway lemming (*Lemmus*). The combined evidence (Fig. 12) suggests that although the coastal plain was essentially an area of open-country, it supported a variety of wetland and developing woodland habitats before these receded during the ensuing cold stage.

Discussion

The land snail assemblages from the palaeosol at both Boxgrove and Valdoe were dominated by catholic species that are tolerant of a broad range of habitats. Such species often characterise the assemblages that colonise new terrain. For example, they dominated the pioneer assemblages that occurred at the very beginning of the Holocene before the spread of woodland (e.g. Kerney *et al.*, 1980; Preece *et al.*, 1986; Preece, 1998; Preece and Bridgland, 1999). The record from Boxgrove, however, represents a succession that occurred towards the end of an interglacial, which would account for the occurrence of shade-demanding species, albeit represented by rather few species at relatively low frequency. Some of these, especially *Spermodea lamellata*, suggest that the period of subaerial exposure of the land surface may have been longer than the 20–100 years previously suggested on the basis of the pedology. Detailed sampling through the palaeosol was not possible because it was so thin (often only 5 cm thick) and so poor in shells. The temporal resolution was therefore insufficient to establish details of any succession. However, *S. lamellata*, one of the most noteworthy of the shade-demanding species, was not present in all samples, even those taken in relatively close proximity. Several reasons may account for this patchy occurrence but the most probable explanation relates to the fact that if, as seems likely, it were a late arrival it would be restricted to the upper levels of the palaeosol that are most prone to loss through erosion and decalcification.

Other factors act to degrade the integrity of the record. Comparisons of fresh/live specimens and old shells from modern samples often reveal marked differences in

faunal composition (e.g. Cameron and Morgan-Huws, 1975), demonstrating that time-averaging is likely to be a problem in assemblages recovered from buried soils. Bioturbation by earthworms and other burrowing organisms, together with differential rates of shell destruction, will further reduce both temporal and ecological resolution. Shell size, thickness and overall shape will determine patterns of fragmentation and differential rates of loss and not all species are equally recognisable in an advanced state of degradation. Carter (1990), who analysed data from chalk grassland on Martin Down, Hampshire, UK, estimated that shells survive on average from 1–100 years (small and fragile species) to hundreds of years (larger or the most robust species) and up to thousands of years (species with resistant apices). Rates of shell decomposition have also been investigated for a range of species (including several occurring at Boxgrove and Valdoe) from different types of forest habitat in central Europe (Říhová *et al.*, 2018). This study showed increasing susceptibility from dry alkaline habitats to wet acidic ones but shell size, rather than habitat type, was found to be the most important factor that determined the rates of shell destruction. In this 3-year field experiment, small shells, including those of *Vallonia pulchella* and *Carychium minimum*, started to degrade within 6 months of death, with almost total loss after 3 years in humid and acid habitats, such as alder alluvial forest.

The palaeosol horizons at both Boxgrove and Valdoe have been seriously affected by decalcification and most samples are devoid of shell, apart from slug plates (Preece and Bates, 1999: Table 29; Table 3). At these sites it is the chemical composition of the shell material that is of paramount importance in determining preservation potential. Decalcification, which occurred after the burial of the shells, has differentially removed those composed of aragonite, leaving only material composed of calcite, such as slug plates, earthworm granules and ostracods, or species with resistant apices, such as clausiliids. Similar assemblages consisting almost entirely of slug plates (and the calcitic opercula of *Bembridgia*) are known from Eocene deposits, such as the Creechbarrow Limestone, Dorset (Preece, 1980). The percentage of slug remains provides a useful index for the extent of decalcification. Their representation in a range of natural environments (Table 5) indicates that they seldom exceed values of 30%, so values above 50%, seen in several samples from Boxgrove and Valdoe, should immediately raise suspicion.

It is possible that decalcification may have biased the composition of the surviving assemblages by removing the less robust components. Experience from experimental studies (e.g. Říhová *et al.*, 2018) suggests that smaller species are especially vulnerable to loss. Perhaps this might explain the low frequencies of *Carychium* and *Vallonia* at Boxgrove and Valdoe. The percentage of slugs in the richest sample from Valdoe (~34%) does sound a note of caution with regard to the integrity of that assemblage. What is clear is that although the palaeosol horizons (top of unit 4b and unit 4c) at Valdoe and Boxgrove have many species of land snail in common (Table 4), there are some genuine faunal differences that cannot be explained by differential preservation. *Lyrodiscus* occurred only at Valdoe and *Spermodea* was restricted to Boxgrove, where moist shaded habitats existed. The associated species of land snail at Valdoe suggest that *Lyrodiscus* was not living in woodland and its extraordinarily high frequency suggests a possible preference for less shaded habitats. However, it is possible that the high frequencies of *Lyrodiscus* at Valdoe, and *Spermodea* at Boxgrove, might have been inflated by the loss of small species, as discussed above.

Decalcification of the sediments at Boxgrove and Valdoe was not a simple process and certain locations and horizons appear to have escaped its full effect. At Valdoe only a single trial pit (VTP 6) yielded an assemblage of shells, their preservation possibly related to a thicker protective covering of overlying calcareous sediment. Ostracods, however, were recovered from several locations within the quarry (Whittaker and Parfitt, 2017). At Boxgrove the situation was more complex and the intensity of decalcification varied enormously even at locations in close proximity. For a long time, ostracods had never been found in Quarry 1 in the Slindon Silt Member from which foraminiferal assemblages had been recovered. Rich ostracod assemblages from these units were only found in sediments beneath a layer of indurated calcrete, which had prevented dissolution (Whittaker and Parfitt, 2017). Ostracod carapaces composed of low Mg calcite are clearly more susceptible to dissolution than the calcite tests of foraminifera. The later calcareous sediments, which were deposited in ponds and in springs issuing from the chalk, might have been expected to furnish good records of molluscs, as well as ostracods. However, this was not the case and although ostracods were abundant (Whittaker and Parfitt, 2017), only the ubiquitous slug plates and clausiliid apices occurred. A reasonable assemblage of molluscs was, however, recovered from unit 5a higher in the sequence (Preece and Bates, 1999: Table 29). This situation highlights the highly complex nature of decalcification affecting the sediments of the Slindon and Eartham Formations.

The ostracods and herpetiles from the calcareous sediments in Q1/B have been used to derive estimates of palaeotemperature based on mutual climatic range reconstructions (Holmes *et al.*, 2010). These suggest a mean July air temperature of between +15°C and +20°C and a mean January air temperature of between -4°C and +4°C, indicating that although summer temperatures were similar to those of today, winter temperatures may have been rather cooler. Almost identical palaeotemperature estimates (July temperatures ranging between +15°C and +20°C and January temperatures between -3°C and +4°C) have been derived using the same mutual ostracod temperature range (MOTR) method from the limited Holocene ostracod fauna from the Inchroy tufa in Scotland (unpublished data). Despite the different setting and facies, the molluscan assemblages from Inchroy (Preece *et al.*, 1984) provide a reasonable match for those from the palaeosol (4c) at Boxgrove once differences due to biogeography have been taken into account. Comparison with molluscan assemblages from other sites ranging from open grassland to closed forest shows that those from Boxgrove and Valdoe occupy an intermediate position on this ecological spectrum. They are also similar to assemblages that existed during the early stages of an ecological succession and are less diverse than those from the climatic optima of interglacials (Limondin-Lozouet and Preece, 2014).

Further opportunities to explore the lateral variation in faunal assemblages at other sites along this land surface would clearly be worthwhile in the quest for an even more complete understanding of the landscape archaeology.

Conclusions

1. Sections exposed in Valdoe Quarry, 4.8 km west of Boxgrove, revealed a virtually identical stratigraphical sequence to that seen at Boxgrove, including the palaeosol horizon (top of unit 4b and 4c) that had yielded *in situ* Lower Palaeolithic archaeology at that site. A small assemblage of fresh flint artefacts, some showing limited clustering, was also recovered from this horizon at Valdoe. This supports conclusions based on borehole evidence that this palaeosol occurs over a

- distance of about 16 km, making it one of the most extensive Palaeolithic land surfaces known.
2. Small mammal assemblages from the palaeosol at Valdoe contained several biostratigraphically important species, including *Arvicola*, *Pliomys episcopalpis*, *Talpa minor* and *Sorex (Drepanosorex) savini*, which together support correlation with Boxgrove and an MIS 13 age.
 3. The land snail assemblage from the palaeosol at Valdoe was broadly similar to those reported from Boxgrove, except that it also contained the extinct species *Retinella (Lyrodiscus) elephantium*. The occurrence of this species was unexpected because although known from earlier deposits on the continent, it is often regarded as an index fossil of MIS 11 (e.g. Ellis, 1983). However, its occurrence at Valdoe differed in three important respects from MIS 11 assemblages in which it occurred. First, it formed part of a much less diverse land snail fauna consisting of only about 20 species, far fewer than the 40 or more that characterised the MIS 11 assemblages. Second, unlike the assemblages forming the *Lyrodiscus* fauna, shade-demanding species represented only a relatively small component of the associated species. Lastly, *Lyrodiscus* accounted for 21.6% of the land snail assemblage, a frequency far higher than reported elsewhere.
 4. Two important conclusions can be drawn from these observations. First, *Lyrodiscus* occurred during MIS 13 in southern England. Second, it appears that *Retinella (Lyrodiscus) elephantium*, unlike modern members of *Lyrodiscus* on the Canary Islands, could inhabit less shaded environments, although it did occur in closed forest, albeit at much lower frequencies.
 5. The lateral variations in faunal composition between Valdoe and Boxgrove seem to reflect environmental heterogeneity along this Palaeolithic land surface. It appears that Boxgrove had small bodies of open water, as well as areas with more shaded habitats. However, there is considerable variability within each site, as well as between them. For example, only about half the samples from the palaeosol at Boxgrove contained the woodland species *Spermodea lamellata*. This faunal heterogeneity could reflect small-scale spatial differences in the micro-habitat but is most likely to have resulted from erosion and decalcification of the upper part of the palaeosol containing late immigrant woodland species.
 6. The occurrence at Boxgrove of *Spermodea lamellata*, often regarded as indicative of 'ancient woodland', suggests that the period of subaerial exposure of land surface (4c) was considerably longer than the 20–100 years previously suggested by the pedology.
 7. Woodland conditions persisted, as revealed by the occurrence of hazel dormouse, *Spermodea lamellata* and a new arrival, *Acanthinula aculeata*, in units 5a and 5b.
 8. Some of the faunal differences in samples from Valdoe and Boxgrove are the result of differential post-depositional decalcification. In samples where this effect is minimal, remains of small and delicate shells (e.g. vitrinids) survive but these are generally absent in samples showing even moderate decalcification. In the most severely decalcified samples only the most durable shells (clausiliid apices) survive, together with slug plates, earthworm granules and ostracods, which are all composed of calcite. The representation of slug plates in a range of natural environments seldom exceeds 30% but in several samples from Valdoe and Boxgrove the frequency of slug remains exceeds 50% of the molluscan assemblage and occasionally may even account for as much as 80%. Decalcification may therefore cause serious biases in the faunal

- composition resulting from loss of certain delicate taxa and over-representation of more durable components.
9. The molluscan assemblages from Valdoe and Boxgrove are compared with others from habitats ranging from open grassland to closed interglacial forest. They occupy an intermediate position on this ecological spectrum, indicating that the landscape was neither completely open nor closed forest but reflect a mosaic of different habitats. The molluscan assemblages are similar to those that existed during the early stages of an ecological succession and are less diverse than those from the climatic optima of interglacials.
 10. The decline in flint debitage previously reported from the upper levels of the palaeosol (4c) appears to coincide with an increase in shade-demanding snails. If the decline in flint debitage reflects a general reduction in local human activity, then the encroachment of woodland reflected by the land snails may provide an explanation.

Supporting information

Additional supporting information can be found in the online version of this article.

SI Figure 1. Stratigraphical logs of the sequences at Valdoe, Boxgrove and the Steyne Wood Clay at Bembridge, Isle of Wight, showing their similarity in height and the context of the palaeosol/organic horizons on the surface of the marine deposits.

SI Table 1. Details of sites used in the comparisons with Valdoe and Boxgrove.

SI Table 2. Comparison of the molluscan fauna from Boxgrove (4c) with that from a mid-Holocene tufa at Inchrory, Banffshire (Preece *et al.*, 1984).

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Data Availability Statement

The data that support the findings of this study are available in the online supporting information.

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