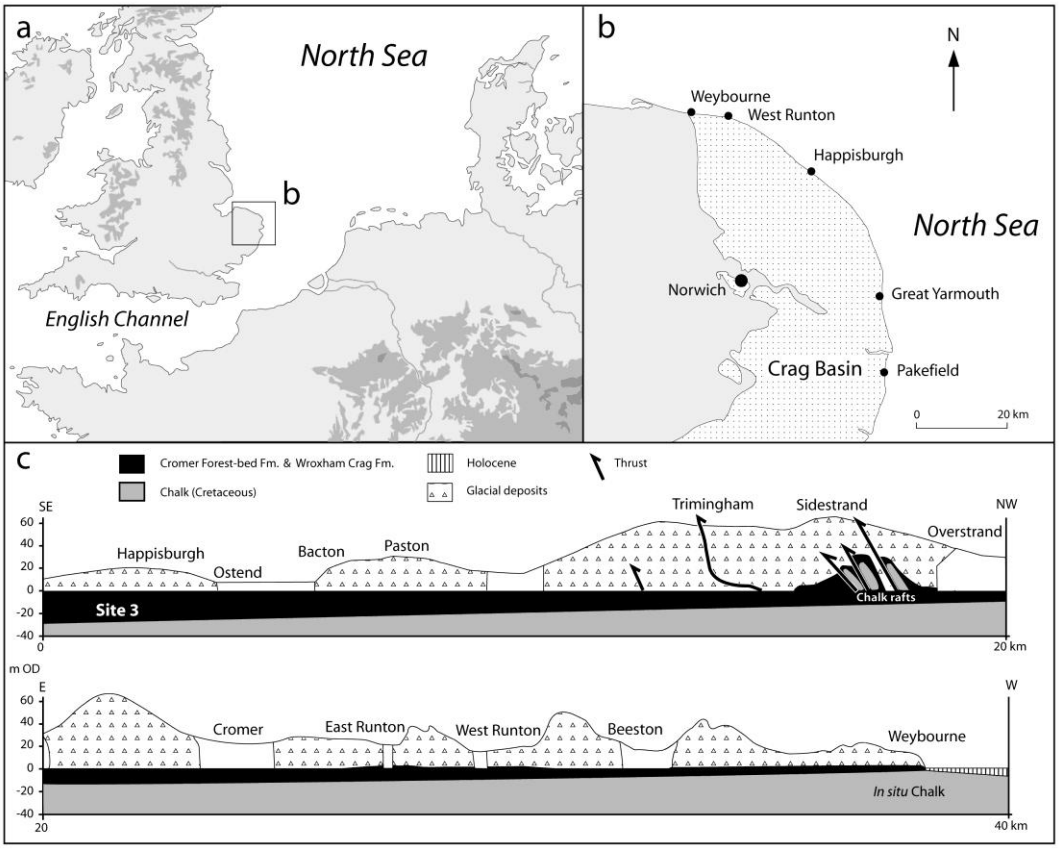
Stratigraphical, palaeoenvironmental and palaeogeographical context of the Early Pleistocene archaeology from Happisburgh Site 3 (Norfolk, UK)

Introduction

In June 2005, geological investigations on the foreshore at Happisburgh (Norfolk, UK, 52°49′36″ N, 1°31′58″ E; NGR TG 380313; SI Fig. 1) recovered flint tools from gravels, sands and silts sealed beneath a thick sequence of glacial sediments. This site, referred to here as Happisburgh Site 3 (HSB3), is the focus of continuing excavations by members of the *Ancient Human Occupation of Britain* (AHOB) project, in collaboration with a range of specialists. The artefact-bearing gravels are stratified within a sequence of fine-grained estuarine sediments and are rich in fossils that indicate accumulation during a period of deteriorating climate at the end of an Early Pleistocene interglacial. Associated with the artefacts is a remarkable range of biological remains, including large mammals, small vertebrates, insects, barnacles, molluscs, foraminifera, seeds, pollen and wood (Supplementary Information 2). This evidence provides an unusually detailed picture of the environment occupied by humans during the Early Pleistocene.



SI Fig. 1a–c. a, Location map of Happisburgh, showing its position in relation to the East Anglian Crag Basin (**b**). **c,** Schematic drawing of the coastal sections between Happisburgh and Weybourne, showing the location of Happisburgh site 3 (HSB3) in relation to the glacial succession and other sites along the Norfolk coastline (adapted from Lee *et al*.[S62]).

Previous work

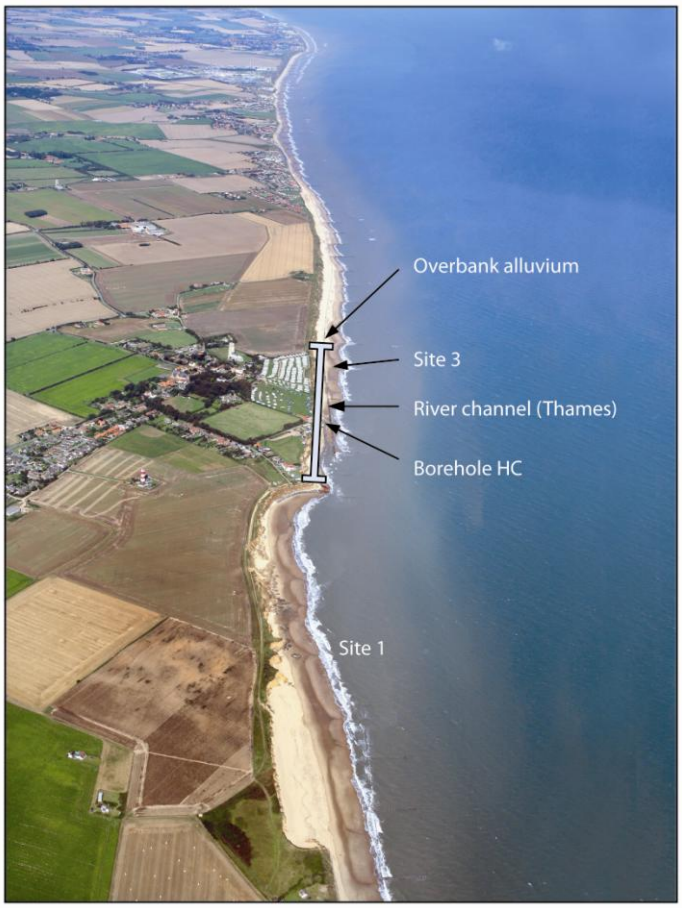
The original geological mapping of the north Norfolk coast by Reid[S1,S2], including the area in the vicinity of Happisburgh, recorded 'lignite with many fir-cones and seeds, resting on hard weathered green stony loam penetrated by roots'. To the south of this exposure, Reid observed that 'the Forest-bed is traceable at the base of the cliff, and consists of laminated clay, sand, and clay pebbles, with drifted wood and tree stumps'(ref. S2, p172).

During the nineteenth century, Happisburgh was famous for the large numbers of bones and teeth of southern mammoth *Mammuthus meridionalis* dredged from the 'Oyster Beds' about 1 km offshore[S2]. Although the foreshore and cliff deposits were not noted as being fossiliferous, a significant find was the type antler of the extinct elk *Cervalces latifrons*, which according to Newton[S3] was found in 'part of the Forest Bed Series exposed at low water on the beach at Happisburgh' (ref. S3, p77; also see refs S4, S5). Although this specimen appears to have been found *in situ*, other mammalian fossils found at this time probably derive from submerged deposits of early Middle Pleistocene age. This material may also be the source of at least some of the Lower Palaeolithic handaxes from this stretch of the Norfolk coast[S6,S7]. In addition to these artefacts, butchered early Middle Pleistocene large mammal bones have been discovered in museum collections[S8].

West[S9] resurveyed this part of the coast and mapped exposures of ferruginous gravels and estuarine silts on the foreshore. Borehole HC (NGR TG 38343113) sunk in 1966 on the old slipway beside the (former) Lifeboat Station at Happisburgh demonstrated the depth of Pleistocene sediments, reaching Chalk bedrock at –27.7 m OD. West divided the Pleistocene deposits into a succession of near-shore marine sands (Beds a–h) succeeded by at least 2 m of fluvial gravels and estuarine laminated silts (Beds i–j), which he mapped for a distance of approximately 630 m. The latter deposits yielded pollen spectra characteristic of an Early Pleistocene interglacial cycle[S9,S10], which West correlated with the Pastonian Stage. Immediately overlying these interglacial deposits is a thick and complex sequence of glacial deposits, which includes the Happisburgh Till[S11]. Recent geological work at Happisburgh has focused mainly on the glacial succession[S11,S12], with opposing views on the glacial history of the region and the age of the glacial succession[S13-S15]. Independent geochronological evidence[S15] has clarified these arguments, supporting the traditional view that the entire glacial succession was emplaced by a fluctuating ice sheet during the Anglian Stage (Marine Isotope Stage (MIS) 12, 478–424 ka).

Regional setting

Happisburgh is located within the East Anglian Crag Basin (SI Fig. 1). This feature, which occupies an area of approximately 42 000 km^2, is a structural depression resulting from downwarping of the crust due to the weight of Neogene sediment in the North Sea Basin[S16,S17]. The interaction of tectonic movements, sea level fluctuations and climatic oscillations has resulted in a sedimentary record that contains a detailed archive of the palaeoenvironmental and palaeoclimatic information from the mid-Pliocene to the early Middle Pleistocene, when the area was over-ridden by glaciers[S18]. The pre-glacial sediments comprise upwards of 70 m of shallow marine, estuarine and fluvial deposits[S9,S16,S17]. The earliest marine sediments (the so-called crags) record the transition from the relatively gentle climatic oscillations of the Pliocene (Coralline Crag Formation) to the more severe fluctuations during the Early and early Middle Pleistocene (Red Crag, Norwich Crag and Wroxham Crag formations), which included periods of arctic severity. During periods of high sea level, the area was part of a wide embayment at the edge of the North Sea. Later sedimentation (Cromer Forest-bed Formation) was predominantly fluvial, with deposition in a complex of floodplains, tidal channels and rivers draining land to the west[S19]. These largely interglacial deposits are famous for their rich fossil flora and fauna[S2], and more recently for the steadily growing number of Lower Palaeolithic sites[S7,S8,S20].



SI Fig. 2. Aerial view of Happisburgh from the southeast. The channel of the ancestral River Thames and its overbank alluvium have been mapped from foreshore exposures, boreholes, test pits and archaeological excavations. Located close to the northern bank of the channel, excavations at Site 3 yielded Early Pleistocene flint tools and biological remains. Artefacts from Site 1[S7] include a handaxe recovered from sediments dating to the end of the early Middle Pleistocene. (Photograph courtesy of Mike Page).

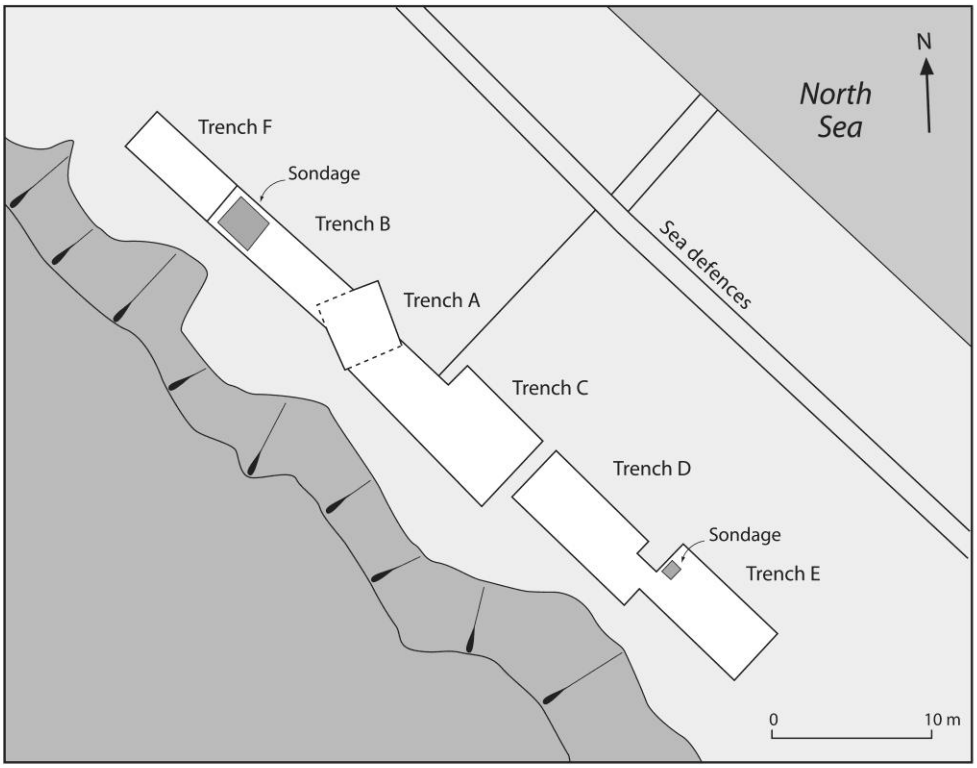
SI Fig. 3. HSB3 from the southeast. The archaeological excavations (middle distance) are located above mean high-water mark, between the sea defences and the cliff. (Photograph courtesy of Mike Pitts).

Today, the coastline of north Norfolk is dominated by undulating cliffs of unconsolidated Pleistocene sediments that extend from Happisburgh to Weybourne. These deposits are largely of glacial origin and were deposited during the Anglian Stage (MIS 12), when ice sheets covered much of the British Isles. Coastal erosion now poses a significant threat, but also provides a rare opportunity to examine sites that have hitherto been inaccessible because they are either buried beneath a thick sequence of glacial sediments or otherwise obscured by the modern beach and sea defences.

SI Fig. 4. Archaeological excavations in progress at HSB3 (Trenches A and B), 2006. The deposits under excavation include Bed E2 (brown gravel), which has yielded artefacts; the overlying laminated sands and silts (Bed F) are devoid of artefacts. (Photographs by Phil Crabb, Natural History Museum, London).

Field investigations and sampling

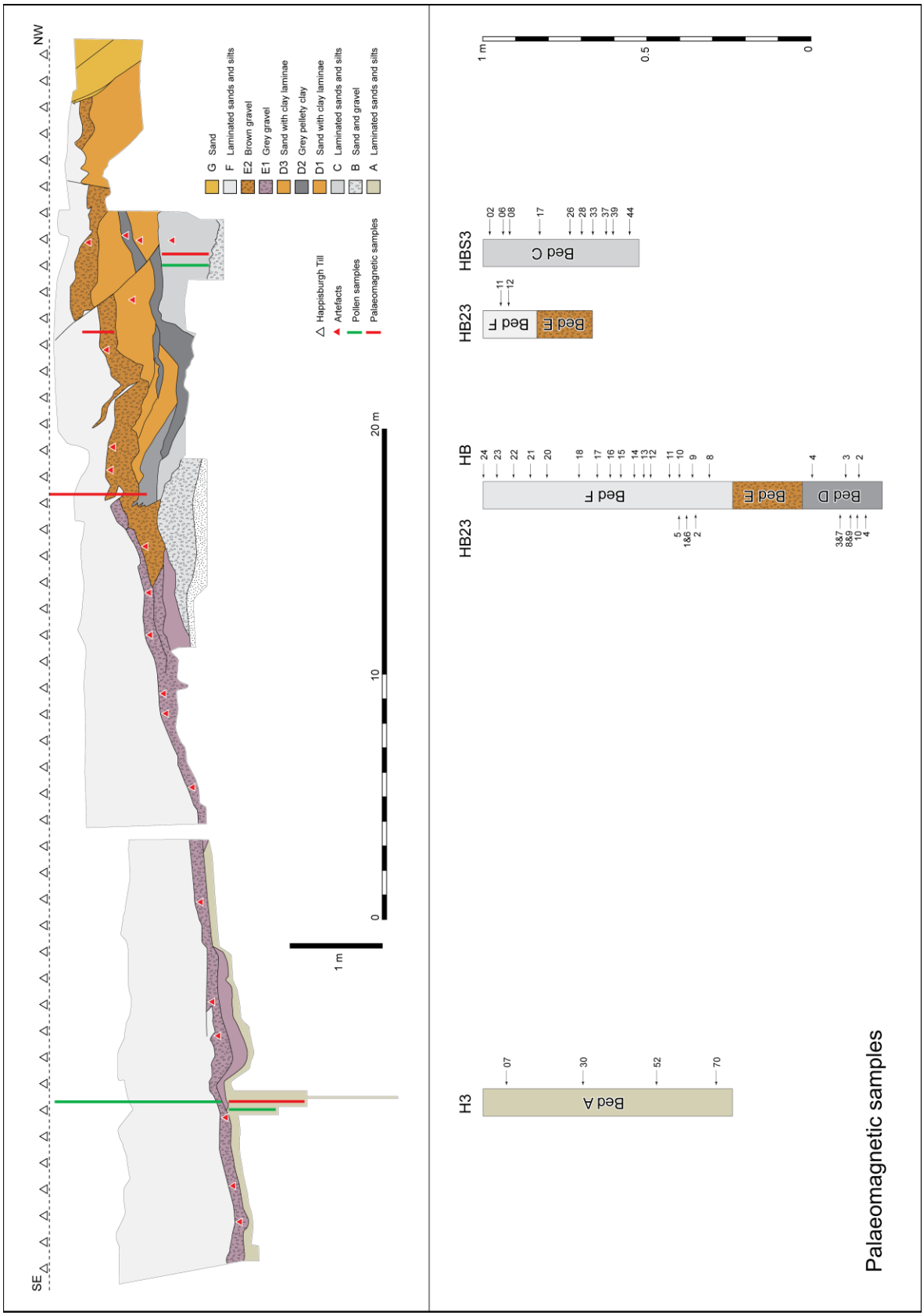
Field work at HSB3 between 2005 and 2008 has investigated a sequence of channel sediments and their associated overbank alluvium, which was mapped along a *c*.1 km coastal section (SI Fig. 2). Exposures on the foreshore and the cliff were logged and the subsurface stratigraphy was investigated using a series of shallow test pits and borings. Large-scale archaeological excavations (*c*. 200 m^2) were undertaken close to the northern edge of the channel and an assemblage of artefacts was recovered (SI Figs 3–5). The artefacts were associated with gravel layers that sloped gently to the SE from just below beach level in the northern part of the excavated area. This bed was excavated by hand and was all hand-sieved at 10 mm mesh. In addition to the bulk sampling for artefacts, column samples were taken for palynology and palaeomagnetism both above and below the archaeological horizon. Spot samples were also taken for analysis of plant macrofossils, molluscs, insects, small vertebrates and clast lithology.



SI Fig. 5. Plan of HSB3 trenches excavated between 2005 and 2008.

Stratigraphy and Sedimentology (Simon G. Lewis and Peter G. Hoare)

The Pleistocene succession at HSB3 comprises sediments exposed in the cliffs backing the modern beach together with those which lie beneath the beach and are known only from boreholes, test pits and the current archaeological excavations (SI Figs 6 and 7). West's description of the sequence was based on the cliff section and on borehole HC[S9]. In the light of the present investigations it is necessary to re-evaluate the stratigraphy, in particular the assignment of West's beds i–j and their correlatives in the HSB3 excavations to the Cromer Forest-bed Formation (CF-bF). The revised succession is summarised in SI Table 1.



SI Fig. 6. Drawing of the geological succession exposed in the north-facing wall of Trenches A–E, showing the location of columns sampled for pollen and palaeomagnetism in relation to the artefact horizons.

Chalk

Cretaceous Chalk lies below the Pleistocene sequence and was reached at a depth of –27.7 m OD in borehole HC[S9]. Chalk bedrock is deeply buried by Pleistocene sediments throughout the district, the nearest on-shore outcrop being 25 km away at Sheringham (TG 1643).

Marine deposits (beds a–h of West[S9])

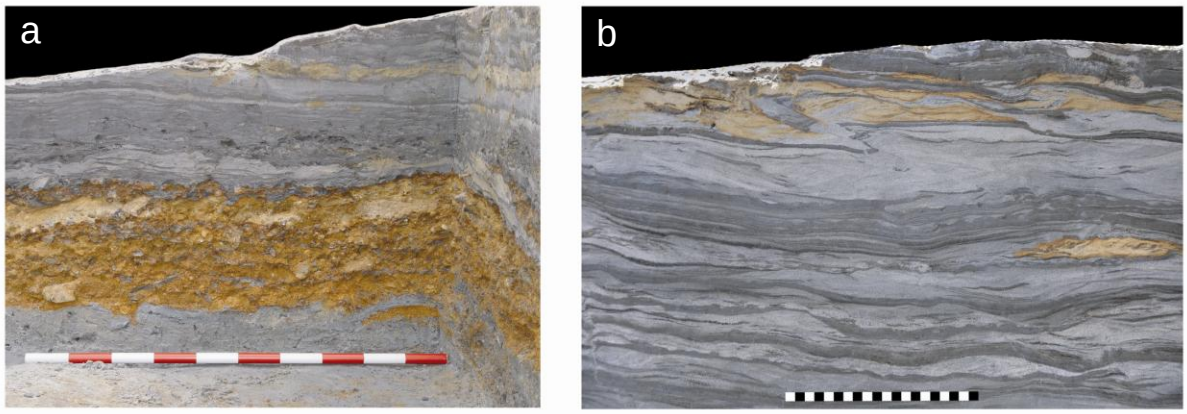
In borehole HC the Chalk is overlain by 23.4 m of sands with layers of silty clay and sandy gravel. The sedimentology and marine Mollusca indicate a near-shore marine environment[S21]. Beds a–h form part of the Norwich Crag Formation and are of Pre-Pastonian or earlier age[S9].

Channel deposits (beds i–j of West[S9])

Gravel (bed i) and the overlying laminated silty clay and sand (bed j) in borehole HC record fluvial and estuarine environments. The excavations at HSB3 have exposed deposits equivalent to these, which are described in detail below. Beds i and j were assigned to the CF-bF by West[S9] on the basis of their stratigraphical position, depositional environment and pollen assemblage characteristics. The beds were correlated with the Pastonian Stage on palynological grounds. These deposits display a clearly defined geometry and sedimentology and may be traced for a considerable distance along the coast. It is proposed, therefore, that this mappable unit is referred to as the Hill House Formation (HHF) (SI Table 2).

Glacial and related deposits

The glacial succession at Happisburgh has been described by Lunkka[S11] and Hart[S12] and most recently by Lee *et al.*[S22] (SI Table 1). A substantial diamicton, silts, clays and glaciolacustrine sands of the Happisburgh Formation occupy the greater part of the exposed sequence. The Happisburgh Till (equivalent to bed k of West[S9]) represents the basal member of the formation; it was deposited by an ice sheet that advanced from the NW or NNW. The Walcott Till Member of the Lowestoft Formation may be seen towards the top of the succession throughout the exposure[S22] (ref. S23, figure 4).



SI Fig. 7a–b. a, Photograph of the Trench A section showing the artefact-bearing Bed E2 (brown gravel) beneath Bed F (laminated sands and silts). Scale divisions = 100 mm. **b,** Bed F (laminated sands and silts). Scale divisions = 10 mm.

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SI Table 1. Stratigraphy at Happisburgh Site 3.

West [S9] lithology	Bed	Formation	UK Stage	Lee[S22] lithology	Lithofacies	Member	Formation	This paper lithology	Bed	Formation	MIS
				Diamicton	F	Walcott Till	Lowestoft				
				Sand	E	Corton Sand					
				Diamicton	D	Corton Till					
				Sand	C	Happisburgh Sand	Happisburgh				12
				Stratified diamicton, silts and clays	B	Ostend Clay					
Till	k		Anglian	Diamicton	A	Happisburgh Till					
Laminated silty clay and sand	j	Cromer Forest-bed	Pastonian					Rootlet bed	H		
Gravel	i							Sand	G		
Sand with detritus mud	h							Laminated sands & silts	F		
Sand with silty clay laminae	g							Sand & gravel	E	Hill House	21 or 25
Laminated silty clay	f		Pre-Pastonian					Sand with clay laminae	D		
Sand with silty clay laminae	e							Laminated sands & silts	C		
Gravelly sand	d							Sand & gravel	B		
Silty clay, sand and gravel	c							Laminated sands & silts	A		
Sandy gravel	b										
Sand with silty clay laminae	a										
Chalk											

The Hill House Formation (HHF)

The HHF represents a complex series of eight beds (A–H) (SI Table 3), which can be readily mapped on the basis of their sedimentology. The sequence A–G suggests the evolution of a number of channel forms and their subsequent infilling with gravels, sands and interbedded sands and silts. These deposits occur throughout the *c.* 50 m archaeological section and have been proved in test pits to the SE of the excavated area. They are equivalent to West's beds i and j in borehole HC[S9]. Gravels of bed i were also recorded by West at locations HD and HG, a further 325–350 m SE of the slipway. If, as proposed here, bed i is a correlative of the sand and gravel at HSB3, and bed j is equivalent to the laminated sands and silts, the channel complex has a lateral extent of at least 700 m.

The HHF accumulated in the lower reaches of a large river system, most probably in the central or upper part of its estuary (cf. ref. S24). The latter is more likely as there are few saline indicators in the biota from the laminated sands and silts. A fluvially dominated regime with limited tidal influence is therefore thought to be the most probable setting. The sediment geometry indicates the development of a series of stacked, overlapping channels and their infilling sediments. There is no indication of the river's planform, though a single, possibly sinuous channel is thought most likely. Lag gravels usually mark the lower bounding surface of each channel fill; subsequently, laminated sands and silts accumulated by vertical accretion, with erosion and reactivation taking place to form stacked architectural elements that can be traced laterally over several metres to tens of metres. The laminated sands and silts suggest the formation of mud-flats within the estuarine environment. A number of channels have been identified, each recording the position of the main channel as it migrated across the floodplain. Sandy channel-fills are also present; these may indicate shifting of the principal channel within the estuary or possibly a change in the river's regime. At Happisburgh Site 2 (HSB2), 200 m to the NW of HSB3, sands of Bed G interdigitate with the rootlet bed (Bed H). Since the latter represents overbank sediments, the channel infill deposits of the HHF may be related to the adjacent floodplain.

SI Table 2. The Hill House Formation.

Formation:	Hill House Formation
Type locality:	Happisburgh, Norfolk, HSB3 excavations; sections beneath the modern beach (NGR TG380313; 52°49′36″N, 1°31′58″E). Borehole HC[S9] (NGR TG383311; 52°49′29″N, 1°32′10″E)
Constituent members:	None formally defined
Upper boundary:	Top of bed j in borehole HC and Bed F in HSB3 excavations; forming the contact with overlying till of the Happisburgh Formation
Lower boundary:	Base of bed i in borehole HC
Total thickness:	Proved to a thickness of *c.* 4 m in borehole HC[SI9]; *c.* 4 m in HSB3 excavations
Lithological characteristics:	Laminated sands and silts, with thin gravel beds and sand units deposited in a series of channels. See SI Table 3 for detailed description.
Distribution:	Extends from GR TG379314 to GR TG386309, a distance of at least 700 m
Age:	Early Pleistocene

Clast lithology

Six samples from Bed E and one from Bed B were selected for clast lithological analysis. In addition, non-flint cobbles were retained during field sieving of large quantities of Bed E. These were washed, dried and searched for far-travelled crystalline rock-types. A sample of these was examined, first in hand specimen and subsequently in thin-section.

There are no major differences in the clast lithological results from the seven samples (SI Table 4); individual data sets may therefore be regarded as representative of a single assemblage. Without exception, flint (37–57%), derived from the Cretaceous Chalk, is the largest component. Vein quartz (13–28%), quartzite (8–20%) and sandstone (up to 7%), mainly derived from the Triassic pebble beds of the Midlands, form the other main constituents. Among the less abundant lithologies are three distinctive varieties of chert: Carboniferous, *Rhaxella* and Lower Greensand. The ultimate

provenance of the Lower Greensand chert is the Hythe Formation (Lower Cretaceous) of the Weald of southern England[S25]; *Rhaxella* chert occurs in the Corallian beds (Oxfordian, Upper Jurassic) in the Howardian Hills of North Yorkshire[S26]. The third variety is derived from Carboniferous Limestone successions and thus may have been carried from the Peak District, Pennines or, possibly, from Welsh bedrock sources. Igneous and metamorphic rocks occur in very small quantities in all the samples analysed. A single pebble of 'Hertfordshire Puddingstone', a siliceous conglomerate which crops out within the Palaeogene (Tertiary) strata of Hertfordshire[S27], was recorded. Three large pieces of Hertfordshire Puddingstone were also recovered from Bed E.

Clast lithological characteristics may be used to place the HHF within the regional stratigraphical and palaeogeographical framework. Prior to the Anglian glaciation (MIS 12) two major rivers flowed across East Anglia: the ancestral Thames entered the region via the Vale of St Albans; the Bytham River flowed from the English Midlands (ref. S28, figure 2). Both river systems provided flint, vein quartz, quartzite and sandstone in significant but varying quantities. The gravels of the proto-River Thames generally have a greater abundance of vein quartz[S29,S30], while those of the Bytham River typically have more quartzite than vein quartz[S31]. In addition, while a red/brown coloration is characteristic of the Triassic pebble beds in the English Midlands, the colour is lost through bleaching of river terrace gravels by acid groundwater[S32]. Thames sediments tend to have a higher proportion of white/colourless quartzose clasts compared with those of the Bytham River[S28]. Therefore the vein quartz:quartzite and white/colourless:coloured quartzose ratios may be used to differentiate deposits of these ancient river systems. In all HHF samples the number of white/colourless quartzose clasts greatly exceeds those that are red/brown (SI Table 5), suggesting an association with the proto-River Thames, particularly the Sudbury Formation[S28]. The ratio of vein quartz to quartzite clasts points to the same conclusion. The presence of Hertfordshire Puddingstone also suggests a Thames origin for these gravels as its geographically restricted outcrop falls entirely within the catchment of the ancestral River Thames.

The presence of three varieties of chert in beds B and E at Happisburgh may suggest both Thames and Bytham influences. Lower Greensand chert was brought to East Anglia by the ancestral River Thames and its right bank Wealden tributaries (ref. S28, figure 2). Reworking of this chert type from older Pleistocene gravels, such as the Wroxham Crag in which it is present in quantities of *c*. 1% (ref. S28, figure 3), would have led inevitably to its dilution and cannot therefore account for the proportions in which it occurs at Happisburgh (up to 1.8%). Carboniferous chert, which is found in small quantities in the gravels of the Colchester and Sudbury formations of the proto-River Thames[S28], is a more significant component of the Bytham River sediments (ref. S28, figure 2). This suggests that the Bytham River was a tributary of the ancestral Thames at the time of deposition of the HHF. *Rhaxella* chert is not found in either the Thames or Bytham river gravels, though it is present in the Norwich and Wroxham Crag Formations, having been brought into the district either by rivers or by littoral transport or indirectly by glacier ice prior to the accumulation of the HHF.

The identification of selected larger clasts from Bed E, in hand specimen initially (35 clasts) and subsequently in thin-section (12 specimens), indicates that there are two distinct suites of exotic rock-types (Richard Herrington and Chris Halls, pers. comm. 2009). The first, represented by seventeen specimens, comprises acid volcanic rocks, most probably derived from Wales. This suite is comparable to that reported from the Kesgrave Sands and Gravels[S33,S34] and provides further evidence for a contribution from the River Thames to the deposits at Happisburgh. The second is a suite of high grade metamorphic rocks, probably from Caledonian outcrops in Scotland. These may have been carried towards East Anglia by ice sheets flowing from northern Britain. Their subsequent transport history and incorporation into the HHF is uncertain. Exotic rock types have been found in the East Anglian Crag deposits which may be the immediate source (Nigel Larkin and Jonathan Lee, pers. comm. 2008). An ice-sheet and/or ice floes may have approached the northern extremity of the southern North Sea Basin bringing Caledonian-type rocks; there is no evidence that Scottish rocks were transported via the ancestral River Thames or former Bytham River.

SI Table 3. Lithostratigraphy of the Hill House Formation, HSB3.

Bed	Lithology	Description	Interpretation
H	Rootlet bed	This bed of grey, massive silt and clay is not present at HSB3 but occurs some 200 m to the NW at HSB2.	Overbank alluvium
G	Sand	Light yellowish brown, cross-stratified sands with minor fine-grained laminations resting on a concave-up, erosional surface. Displays both normal and reversed (thrust) faults. It interdigitates with, and is overlain by, laminated silts of bed F.	Estuarine; in-channel deposition
F	Laminated sands and silts	Laterally extensive laminated sands and silts with some clay laminae (SI Fig. 7), locally >*c.* 4 m thick; grey save for yellowish brown oxidised upper part. The bed is composed of a number of laminated sand and silt 'packages' separated by erosional reactivation surfaces. The lower bounding surface with bed E dips towards the SE extremity of the exposure, and the unit thickens in that direction. The contact with the base of the overlying Happisburgh Till is sharp, planar to slightly undulating and erosional. Deformation structures penetrate Bed F from above.	Estuarine; mud-flats
E	Sand and gravel	This is exposed across most of the section, but from a maximum of *c.* 0.3 m the bed thins towards the NW. Its lower bounding surface dips SE. Shear structures penetrate from above; it is also affected by normal faulting. Two laterally continuous sub-units may be identified: E2: brown gravel: orange-brown oxidised, weakly iron-indurated, largely massive, medium–coarse flint-rich gravels occur at the NW end of the section (SI Fig. 7a). E1: grey gravel: Bed E2 dips towards the SE, thins and passes laterally into grey gravels lacking oxidation and iron-staining. E1 is 0.1–0.2 m thick and composed of coarse gravels and cobbles in a sandy matrix. Large pieces of fresh, unworn nodular flint are present. Thin discontinuous sand-filled scours, up to 0.2 m thick and 5 m wide, lie below the gravels but are considered part of E1. Significant organic remains include wood, twigs, cones and roots, the latter displaying growth around large cobbles, and clasts of peaty material reworked from bank sediment elsewhere on the floodplain.	Estuarine; gravel bedform and lag-gravel
D	Sand with clay laminae	This consists predominantly of orange, coarse–medium sands with clay laminae, displaying flaser or lenticular bedding. The bed is present at the NW end of the section and attains a maximum thickness of *c.* 0.8 m. The lower erosional bounding surface is concave-upwards. Three interstratified sub-units are recognised: D3: sand with clay laminae preserved within a channel with a maximum depth of *c.* 0.8 m and which cuts out both D2 and D1 at the NW end of the section. The bedding dips gently in sympathy with the channel base. A thin pebbly stringer indicates minor reactivation. D2: grey pellety clay up to *c.* 0.2 m thick consisting of clay-rich clasts and some gravel in a grey clay matrix. Poorly developed stratification is disrupted in places giving rise to a massive, poorly sorted mixture of gravel and clay. D1: sub-horizontal to gently dipping, medium–coarse sand with clay laminae occupying a number of small shallow channels; the lower part of each channel fill is marked by a thin (> 0.05 m) pebbly clay. Bed D is disrupted by both thrust and normal faults.	Estuarine; in-channel deposition
C	Laminated sands and silts	Grey, sub-horizontally laminated sands and silts seen at the NW end of the section. The bed forms a wedge-shaped unit and conformably overlies Bed B with a shallow concave-up bounding surface. A number of shear structures penetrate from the overlying glacial deposits.	Estuarine; mud-flats
B	Sand and gravel	A poorly exposed bed *c.* 0.2 m thick, seen only at the NW end of the excavated area, composed of coarse gravel and cobbles of flint, rounded vein quartz, quartzite and sandstone. The tabular body overlies a shallow concave-up bounding surface.	Estuarine; lag- gravel
A	Laminated sands and silts	Sub-horizontally laminated grey sands and silts lying at the base of the exposure at the SE end of the section. Excavation and coring proved a thickness of 2.75 m. They are overlain by bed E.	Estuarine; mud-flats

SI Table 4. Clast lithological analysis, 11.2–16.0 mm fraction, beds B and E, HSB3. Carb. = Carboniferous; L Gnsand = Lower Greensand (Cretaceous); meta = metamorphic; * mainly ironstone, some authigenic, the remainder Jurassic/Lower Cretaceous in ultimate provenance; *n* = number of clasts counted.

Sample	Bed	Flint	Vein quartz	Quartzite	Sandstone	Carb. chert	*Rhaxella* chert	L Gnsand chert	Silicified limestone	Igneous/ meta	Others*	*n*
15	E	41.4	27.7	16.1	2.0	5.0	0.1	0.9	0.4	0.7	5.6	954
44	E	37.4	21.5	18.1	4.5	8.5	0.3	0.2	1.0	0.8	7.7	601
45	E	42.4	21.5	20.1	1.2	5.1	0.0	1.0	0.8	0.0	7.9	493
56	E	40.3	27.1	11.4	3.4	2.9	0.3	0.0	1.6	0.4	12.5	678
76	E	50.7	22.3	17.1	0.2	2.0	0.5	1.1	1.8	0.9	3.4	444
85	E	47.5	13.2	14.3	6.8	6.4	0.7	1.5	3.5	0.2	5.9	545
55	B	57.3	16.9	8.3	3.4	6.3	0.0	1.8	1.0	0.2	4.8	504

SI Table 5. Proportions of white and coloured vein quartz and quartzite clasts, beds B and E, HSB3.

Sample	Bed	Quartzite					Vein quartz				
		Coloured		White			Coloured		White		
		n	%	*n*	%	Σ	*n*	%	*n*	%	Σ
06.05.15	E	61	39.6	93	60.4	154	92	34.7	173	65.3	265
44	E	55	50.5	54	49.5	109	51	39.5	78	60.5	129
45	E	44	44.4	55	55.6	99	23	21.7	83	78.3	106
56	E	32	41.6	45	58.4	77	45	24.5	139	75.5	184
76	E	24	31.6	52	68.4	76	29	29.3	70	70.7	99
85	E	26	33.8	51	66.2	77	10	14.1	61	85.9	71
55	B	11	26.2	31	73.8	42	9	10.6	76	89.4	85

Discussion

The succession at HSB3 indicates deposition in the central or upper part of the estuary of a large river, within the zone of tidal influence. The sedimentary succession records channel scouring followed by the accumulation of gravels, then vertical accretion of laminated sands and silts. A number of channel-fill sequences can be identified, indicating at least three phases of channel formation and infilling. Channels infilled with sand with clay laminae (Bed D) and cross-stratified sands (Bed G) are also present within the sequence. These may represent the main active channel, which would have migrated across the estuary. The clast lithological data suggest that the sediments were laid down by a confluent Thames/Bytham River.

The identification of gravels of proto-Thames origin in northeast Norfolk is of significance for two reasons. First, the most recent reconstructions of the pre-diversion River Thames in East Anglia have suggested that it did not flow into Norfolk, but had a northern limit to the south of Great Yarmouth[S35,S36]. The data from HSB3 indicate that the Thames must have followed a more northerly route into Norfolk as suggested by Hey[S29,S32,S37]. There is no evidence to suggest that Happisburgh Site 3 lay in the path of the Ancaster River (*contra* ref. S36, figure 21). Second, the presence of Thames gravels in Norfolk provides some age constraint for the HHF. The Thames followed successively more southerly courses into the North Sea Basin during the early Middle Pleistocene, culminating in the route through Essex immediately prior to its diversion during MIS 12[S38,S39]. The more northerly routes into Norfolk, including that responsible for the deposition of the HHF, probably represent the earliest phases of the development of the Thames. The evolution of the Bytham River as a separate drainage system across central East Anglia must therefore have taken place after the HHF had formed. Thus the HHF pre-dates the artefact-bearing Wroxham Crag Formation and CF-bF at Pakefield[S20].

Lithic assemblages (Nick M. Ashton). See Supplementary Movies 1–10

The lithic assemblages consist of 74 artefacts from the gravel (Bed E), two each from beds D and C (SI Table 6). Most artefacts were recovered *in situ* during excavation with additional pieces retrieved through sieving (1cm mesh) of all the excavated sediment (*c*. 50 m^3). All the artefacts are made from flint, which occurs occasionally as medium size nodules (maximum dimension 25 cm) within the various gravels at the site. The assemblage from the gravel is generally in fresh condition, with some pieces showing a small amount of edge abrasion (SI Table 7). Their condition suggests that they are contemporary with the gravel and that they have undergone very limited fluvial transport.

The artefacts consist of flakes, cores and flake tools, without any evidence of handaxe technology. The three cores suggest a simple flake and core technology, with no indication of platform preparation. This is reflected in the flakes, which are from hard hammer percussion with pronounced bulbs, and generally have wide plain or cortical butts. The flake scar patterns are usually from the proximal or lateral margins. The ten flake tools consist of notches, multiple notches and flakes with limited areas of retouch. There is little patterning as to where this occurs on the artefacts, suggesting an *ad hoc* approach to flake tool manufacture.

There are several indications that the assemblage is not part of a knapping scatter. The size distribution of the artefacts shows that the smallest elements from knapping are absent. Although this could be an indication of winnowing, the comparatively low proportion of fully cortical flakes and of cortical butts suggests that the primary flakes from the knapping process are also missing. In addition, there is a relatively high proportion of flake tools and quite a low proportion of cores compared to most Lower Palaeolithic assemblages. In combination, these observations suggest that much of the assemblage at HSB3 does not reflect the waste from a primary knapping zone, but has been selectively carried to the location by hominins. This interpretation is perhaps supported by several of the flakes having a good cutting edge on one side, opposed by a cortical edge on the other.

The occurrence of the artefacts in Bed C and several different gravel bodies (Bed E) indicates that hominins revisited the location several times, probably reflecting a sustained presence in the area.

SI Table 6. Summary of flint artefacts from HSB3.

Type	Bed C	Bed D2	Bed D3	Bed E
Core	0	0	0	3
Flake	2	0	1	59
Scraper	0	0	0	1
Notch	0	0	0	7
Retouched flake	0	1	0	4

SI Table 7. Technological attributes and condition of flakes from Beds C and E, HSB3.

Cortex		Butts		Condition	
Cortical	2	Cortical	17	Fresh	53
>50%	27	Natural	3	Slightly abraded	23
<50%	31	Plain	46	Abraded	2
Non-cortical	14	Dihedral	3	rolled	0

Micro-CT scanning of flint artefacts (Richard L. Abel)

Micro-CT data were collected at the Natural History Museum (London, UK) with a Metris X-Tek HMX ST 225 cone beam system (X-Tek, Tring, UK). In order to minimise beam hardening and noise, the scans were collected perpendicular to the long axis of the tools. External surfaces were made to stand out clearly by applying low energy X-rays: 180 kV, 100 µA and a molybdenum target with a 0.1 mm copper pre-filter. The scans were reconstructed in 3142 projections from a four mega pixel panel giving an isotropic voxel size of 40–50 µm, depending on the size of the specimen. Reconstructions were calculated with CT Pro 2.0 (Metris, Leuven, Belgium). Contrast between the tools and background was very high so the outer surfaces were visualised by applying a global threshold. The tools were animated and rendered with lights and false colour (Supplementary Movies 1–10) using VG Studio MAX 2.0 (Volume Graphics, Heidelberg, Germany).

Biological remains

The waterlogged anaerobic channel sediments at HSB3 provided an environment ideally suited to the preservation of fragile organic material including plant remains (e.g. pollen, spores, seeds and wood), insects and bone. Mineralisation has affected some of the bone material and also preserved calcareous fossils, such as barnacles and molluscs, which would otherwise have been destroyed in the acidic burial environment at the site. A systematic strategy was undertaken to obtain samples for biological analysis, which focused on the artefact-bearing sediments. Surprisingly, these coarse-grained gravels yielded rich assemblages of fragile insect and plant remains, and intercalated finer-grained horizons contained exceptionally well-preserved palynomorphs. As a result of the unusually good conditions of preservation, the biological remains provide a rare opportunity to examine changing climates and environmental conditions that can be related directly to the period of Early Pleistocene hominin occupation. The entire dataset of biological remains from Happisburgh, including that from West[S9] as well as the current investigation at Happisburgh Site 3 is given in Supplementary Information 2. A summary of the palaeoecology is shown in SI Table 8.

SI Table 8. Summary of the biota and environmental history of the Early Pleistocene channel-fill at HSB3.

Bed	Lithology	Pollen assemblage zone	Archaeology	Biological remains	Depositional environment	Climate	Pollen subzone (after West[S9])
H	Rootlet bed			Barren	Alluvium	?	?
G	Sand			Barren	Tidally-influenced river (estuarine)		?
F	Laminated sands and silts	p.a.z. 3		Coniferous wood dominant. *Azolla filiculoides*	Tidally-influenced river (estuarine)	Late interglacial	IVa
E	Sand and gravel	p.a.z. 3	Artefacts	Mammals, fish (*Acipenser* and *Esox*), anurans, beetles, barnacles, marine molluscs, Foraminifera. Wood: Coniferous > deciduous. *Azolla filiculoides*	Lag-gravel and bar form (estuarine)	T_{max} 16 to 18°C T_{min} –3 to 0°C (Beetle MCR) Cool temperate	IVa
D	Sand with clay laminae	p.a.z. 3	Artefacts	Vertebrates, beetles, barnacles, marine molluscs. Wood: coniferous = deciduous	Tidally-influenced river (estuarine)	Cool temperate	IVa
C	Laminated sands and silts	p.a.z. 2	Artefacts	Beetles, barnacles, marine molluscs. Wood: coniferous = deciduous	Tidally-influenced river (estuarine)	Cool temperate	
B	Sand and gravel			Large mammals, barnacles	Lag-gravel (estuarine)		
A	Laminated sands and silts	p.a.z. 1		*Azolla filiculoides*	Tidally-influenced river (estuarine)	Fully temperate	III

Pollen analysis (Sylvia M. Peglar and Mark D. Lewis)

Samples from beds A-F were prepared for pollen analysis. In addition, a sample was extracted from the interior of a hyaena coprolite recovered from Bed E1 and analysed for pollen (SI Fig. 8).

Methods

The coprolite and sediment samples were prepared for pollen analysis by standard chemical procedures. The samples were stained with safranin, and the coprolite preparation was mounted in glycerine jelly. The sediment samples were dehydrated in tertiary butyl-alcohol, and the residues mounted in 2000 cs silicone oil. Slides were examined at a magnification of 400x (1000x for critical examination) by equally-spaced traverses across slides to reduce the possible effects of differential dispersal on the slides[S40]. With the sediment samples the aim was to achieve a count of 500 grains of pollen and spores from terrestrial plants. With the coprolite sample, six slides were prepared and a total of 1306 palynomorphs counted from the richest slide. Pollen identification, where necessary, was aided using the key of Moore *et al.*[S41] and a modern pollen reference collection. Indeterminable and unknown grains were recorded as an indication of the state of pollen preservation. Other identifiable palynomorphs (i.e. vegetative remains, *Sphagnum* spores, dinoflagellate cysts, pre-Quaternary spores and algal remains) encountered on the slides were also recorded, the inclusion of which can add to the interpretation of the pollen analytical results. Plant nomenclature follows Stace[S42].

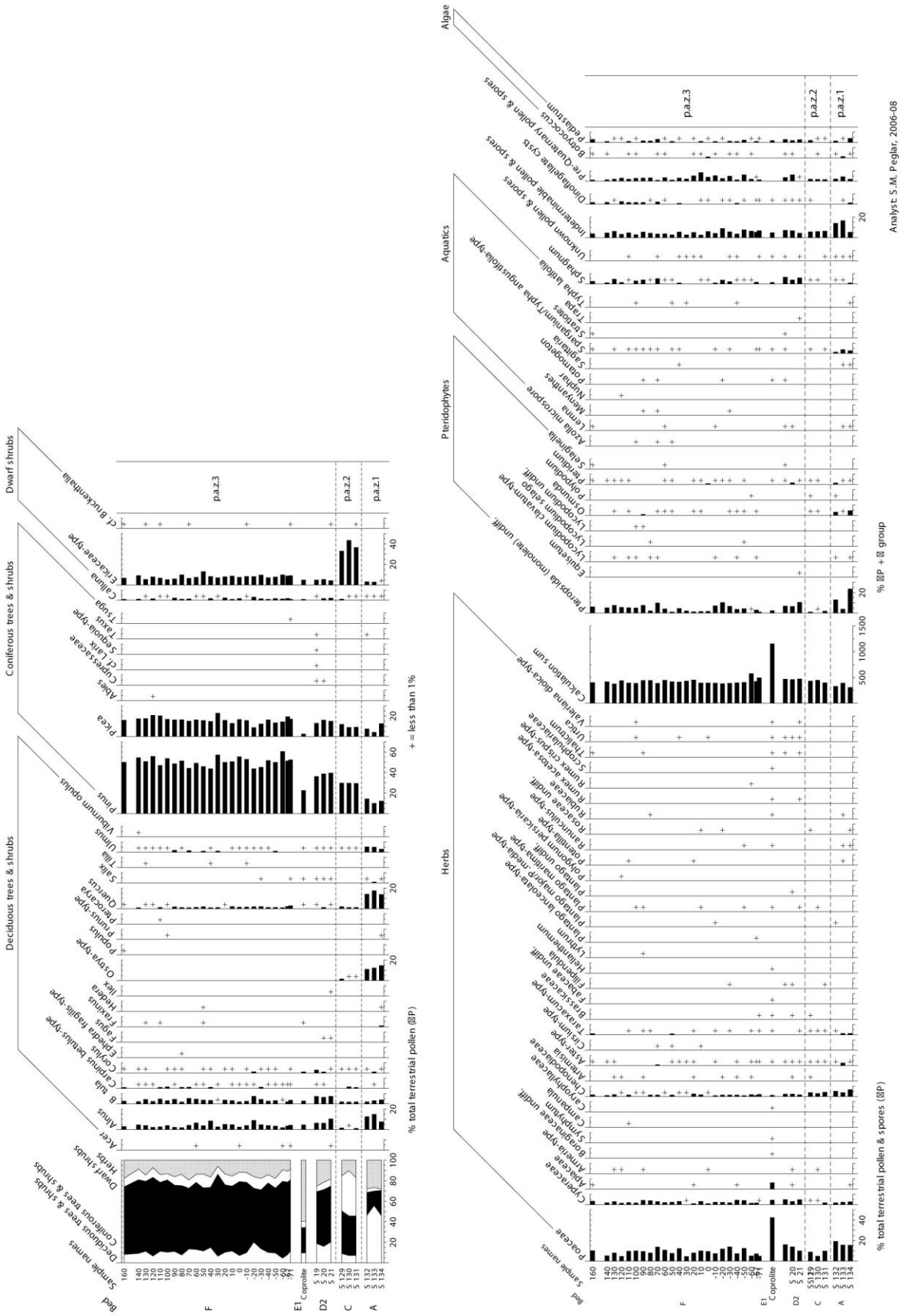
The results are presented as pollen diagrams with taxa expressed as percentages of the total terrestrial pollen sum (sumP/calculation sum) in order to be directly comparable with the pollen diagrams of West[S9]. Pteridophytes, obligate aquatic taxa and other palynomorphs are presented as percentages of sumP + the sum of the category to which they belong. Calculations and diagrams were made using the programs TILIA and TILIA.GRAPH in TGView[S43].

Results

Pollen from all samples was well preserved (mostly <10% indeterminable) suggesting rapid incorporation into sediments following dispersal. The tidally-influenced nature of the depositional environment is likely to have resulted in the usual biases[S44], especially the over-representation of bisaccate pollen grains (pine and spruce) in marine/estuarine sediments. Nevertheless the following vegetational history can be suggested (SI Fig. 8).

***Quercus* – *Ostrya*-type – *Ulmus* – *Alnus* pollen assemblage zone (p.a.z.) 1**
The oldest samples analysed (Bed A) are all dominated by deciduous tree pollen (*c*.50% of the terrestrial pollen -TP), particularly *Quercus* (oak), *Ostrya*-type (hop-hornbeam type), *Ulmus* (elm) and *Alnus* (alder) together with *Betula* (birch), *Corylus* (hazel) and *Salix* (willow). This indicates the proximity of mixed deciduous woodland, with alder and willow growing in damper areas. The relatively high values of coniferous pollen (*Pinus* and *Picea*) probably result from the greater productivity of conifers but their over-representation may also result from taphonomic causes (see above). Either pine and spruce occurred as scattered trees within the mixed woodland, or were present some distance from the site.

Herb pollen, particularly that of grasses (Poaceae) and sedges (Cyperaceae), suggests damp grassland/fens, whereas the occurrence of Chenopodiaceae, together with Asteraceae pollen types (*Aster*-type, *Taraxacum*-type), could indicate either proximity of saltmarsh or open disturbed ground. Pteridophyte (fern) spores, including those of *Osmunda*, are characteristic of woodland and fens. Pollen of telmatic taxa, including *Sparganium/Typha angustifolia*-type, *Typha latifolia* (bulrush) and *Sagittaria* (arrowhead), provide evidence of local wet areas, whereas *Lemna* (duck weed) and remains of the green algae *Pediastrum* and *Botryococcus* indicate open water.



SI Fig. 8. Pollen percentage diagram from HSB3.

The occurrence of *Ostrya*-type pollen (SI Fig. 9) at values of *c*. 12% is significant. Subsumed within this pollen taxon are *Ostrya* (hop-hornbeam) and some *Carpinus* (hornbeam) species, including *Ostrya carpinifolia* (European hop-hornbeam) and *Carpinus orientalis* (oriental hornbeam) both of which are native in southern Europe but are absent from Britain today[S45]. The pollen of the European hornbeam (*Carpinus betulus*), which is native in Britain, can be distinguished and is not included in the *Ostrya*-type. However, the *Ostrya*-type pollen taxon could potentially include other species of *Ostrya* and *Carpinus* found today in North America. Godwin[S46] recorded scattered grains of *Ostrya*-type pollen at a few Early Pleistocene sites (Ludhamian–Pastonian) in East Anglia, but not at the frequencies found here.

Ericaceae-type – *Pinus* – *Picea* p.a.z. 2
This p.a.z., from Bed C, differs significantly from the previous zone in being dominated by heathland taxa (*Calluna* and Ericaceae-type) at values of *c*.40%; the deciduous tree taxa characteristic of the previous zone have now virtually disappeared but *Pinus* and *Picea* expand in relative frequency. This p.a.z. suggests the local development of heathland with some coniferous woodland within the catchment.

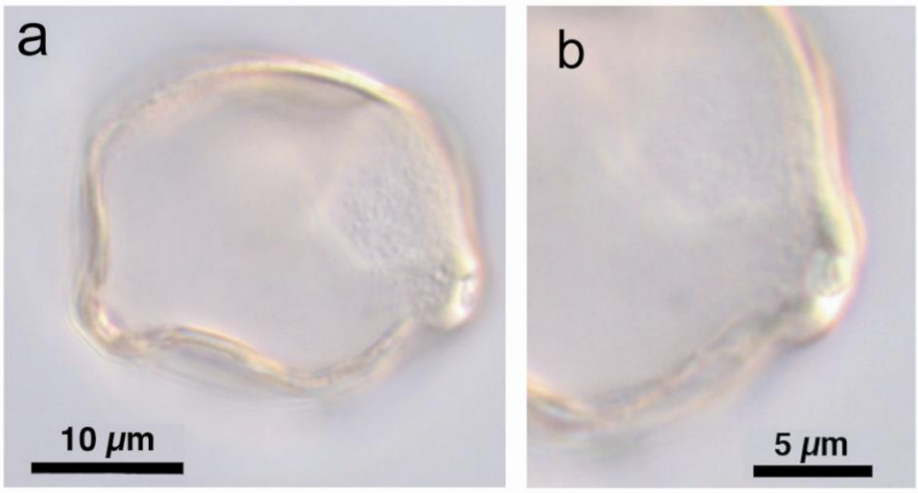
***Pinus – Picea – Betula – Alnus* p.a.z. 3**
In this p.a.z., (beds D2, E1 and F) pine and spruce dominate but heathland taxa decline to ~10%. Alder and birch occur as important subordinate elements and there is a consistent record for other deciduous trees. A range of aquatic plants occur including *Azolla* (water-fern), *Lemna* (duck weed), *Nuphar* (yellow water-lily), *Sagittaria* (arrowhead), *Stratiotes* (water soldier) and *Trapa* (water chestnut). This assemblage indicates mixed deciduous/coniferous woodland. Sporadic grains of *Abies* (silver fir), *Fagus* (beech), and cf. *Larix* (larch) occur together with some Tertiary relicts such as *Pterocarya* (wingnut) and *Tsuga* (hemlock).

The preservation of pollen from the hyaena coprolite was good and the spectrum obtained was broadly similar to those analysed from p.a.z. 3, in being dominated by pine and spruce, although the frequency of Poaceae (grasses) was considerably higher (~65%). Since the pollen was well preserved, this difference must relate to contrasting taphonomic pathways. The most likely source of the pollen in the coprolite is from hide and/or gut contents that were ingested by the hyaena. The high Poaceae values suggest the presence of extensive grassland nearby, possibly on the floodplain of the river.

Conclusions

The earliest spectra reported here can be correlated with the upper part (above 2.6 m) of the pollen diagram reported by West (ref. S9, figure42) from borehole HC. Pollen assemblages with a significant deciduous component that included *Quercus*, *Betula* and *Alnus* were also reported. A peak in *Carpinus* is shown at this level, although *Ostrya*-type is not listed. However, it is possible that these pollen taxa represent the same palynomorph. If this is the case, then the *Quercus–Ostrya*-type–*Ulmus–Alnus* pollen assemblage zone from HSB3 correlates with the p.a.z. l from borehole HC, which was assigned by West to the late temperate zone of the Pastonian (Pa III). West ascribed biozone m to the post temperate zone (Pa IV), which is broadly similar to the two upper zones from HSB3, although here there are slightly higher percentages of deciduous trees and Ericaceae-type vegetation. Duigan[S10] and West[S9] also recorded the consistent occurrence of *Tsuga*, which is unknown in northern Europe after the Early Pleistocene[S47-S49].

The pollen record from HSB3 indicates a change from deciduous woodland in the basal samples to mixed deciduous/coniferous woodland in the higher levels. Heathland was an important component at certain periods and aquatic and riparian plants indicate the existence of open freshwater and surrounding marshland. The pollen record therefore suggests that the climate deteriorated through the sequence, from a fully temperate climate, perhaps slightly warmer than present (cf. occurrence of *Ostrya/Carpinus orientalis*), to conditions similar to those at the ecotonal boundary between deciduous and coniferous woodland, such as occurs in southern Sweden and Norway today.



SI Fig. 9a–b. a, Photograph of *Ostrya*-type pollen grain showing surface sculpture and two of the three pores. **b,** Close-up showing non-vestibulate structure of pore. (Photo courtesy of Susanne Feist-Burkhardt, Natural History Museum, London)

Plant macrofossils (Mike H. Field)

The state of preservation of the plant macrofossils was generally poor with at least 27 taxa recovered but only eight identifiable to species (SI Table 9). Aquatic plants are well represented and suggest that deposition took place in still or slow-moving freshwater. Floating aquatic plant taxa include *Azolla filiculoides*, *Hydrocharis morsus-ranae*, *Ranunculus* subgenus *Batrachium* and *Stratiotes aloides*. Where light could penetrate the water column, submergent plants such as species of Characeae existed. At the margins of the water-body there is evidence of a reedswamp that included taxa such as Alismataceae, *Carex*, *Juncus*, *Ranunculus sceleratus*, *Typha* and *Urtica dioica*. *Alnus*, a tree tolerant of damp ground, is likely to have inhabited areas at the edge of the channel. Woodland was predominantly coniferous with *Pinus* cf. *sylvestris* and cf. *Picea* present (SI Fig. 10, SI Table 10). *Betula* was also growing in the vicinity along with other taxa associated with woodland such as cf. *Prunus* and *Rubus idaeus*. The occurrence of *Selaginella selaginoides* together with *Sphagnum* indicate that acidic conditions occurred near the site of deposition. These edaphic conditions may have formed because of the influence of the coniferous trees. It is interesting to note that the surfaces of some of the *Pinus* cones are abraded (SI Fig. 10b), whereas others are well preserved and allow determination to *Pinus* cf. *sylvestris* (SI Fig. 10a). The abraded pine cones may have been subjected to higher-energy conditions than most of the aquatic taxa. This suggests that material derived from a number of sources and was altered by different taphonomic processes in this fluvial environment.

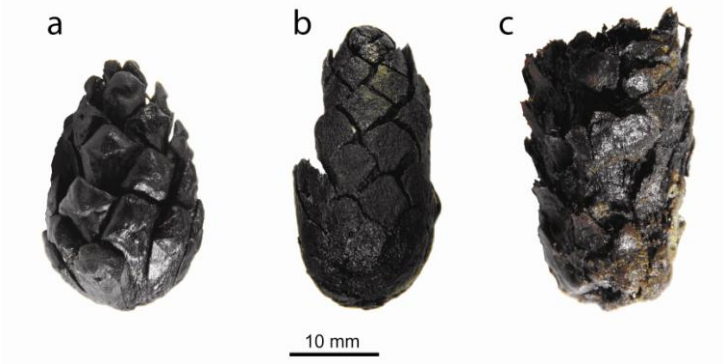
Today *Azolla filiculoides* and *Picea* are non-native to the British flora. Godwin[S46] comments that it is difficult to make inferences about past climate from the occurrence of *Picea*. However, the occurrence of sexual structures of *A. filiculoides*, which do not survive prolonged exposure below –4°C (ref. S50), does provide palaeoclimatic information. Janes[S50] noted that *A. filiculoides* sporophytes died after a short exposure to –4°C. If winter temperatures at the time of deposition were lower than –4°C, the survival of *A. filiculoides* would have depended upon sporulation occurring regularly in the population. Survival under these conditions depends on sporocarps being viable and thus forming a spore bank in the sediment, with germination in the following growing season[S51]. Ashton[S52] found that in South African populations, sporulation took place above 17.5°C, but Janes[S51] notes that in Britain it can occur below this value. Other factors, such as light intensity, sporophyte density, and phosphate supply, must also be considered when understanding the amount of sporulation. Germination of sporocarps takes place above 5°C with the rate and extent of germination increasing up to 20°C (ref. S51). Sporeling survival and growth were optimal at 15°C. Therefore, if sexual reproduction of *A. filiculoides* was taking place when the HSB3 sediments were deposited, summer temperatures would have been around 15°C.

SI Table 9. Macroscopic plant and fungal remains from HSB3. Taxonomy follows Stace[S42].

Bed		**A**	**D2**	**E1**	**F**
Sample		**87**	**43**	**133**	**28**
Volume processed (cm^3)		**200**	**200**	**200**	**200**
	Part				
Alismataceae	embryo	-	-	10	6
Alnus sp.	cone scale	-	-	-	1
Azolla filiculoides Lam.	megaspore	2	-	5	1
Betula sp(p).	fruit without wing	-	-	5	4
Bidens sp.	barbed spine	-	-	1	-
Callitriche sp.	fruit	-	-	1	-
Carex sp(p).	nutlet fragment	1	-	1	1
Cenococcum geophilum Fr.	sclerotium	1	-	4	1
Characeae	oospore	-	-	-	1
cf. *Dryopteris* sp(p).	sporangium	-	-	19	1
Elatine hydropiper L.	seed	-	-	7	2
Poaceae	caryopsis	-	-	2	2
Hydrocharis morsus-ranae L.	fruit	-	-	-	1
Juncus sp(p).	seed	-	-	4	4
Lamiaceae	nutlet	-	-	-	1
Musci	stem fragment	-	-	2	-
Pinus sp.	leaf tip	-	-	1	-
Potamogeton sp.	fruit fragment	-	-	1	-
cf. *Prunus* sp.	fruitstone fragment	-	-	-	1
Ranunculus subgenus *Batrachium* sp(p).	achene	-	-	-	3
Ranunculus subgenus *Ranunculus* sp(p).	achene	-	-	1	1
Ranunculus sceleratus L.	achene	-	-	9	1
Rubus idaeus L.	fruitstone	-	-	1	-
Selaginella selaginoides (L.)	megaspore	-	-	11	2
Sphagnum sp(p).	leaf	-	-	15	6
Stratiotes aloides L.	leaf spine	-	-	5	-
Typha sp(p).	fruit	2	-	6	2
Apiaceae	fruit	-	-	2	-
Urtica dioica L.	achene	-	-	4	7
Undetermined bud		-	-	-	2
Undetermined budscale		-	-	2	-
Wood fragments		-	-	-	present

SI Table 10. Pine-cones from Bed E, HSB3.

	Number of cones
cf. *Picea* sp(p).	4
Pinus cf. *sylvestris*	9
Pinus sp(p).	12



SI Fig. 10a –c. Pine-cones from Bed E1. **a,** Cone of *Pinus* cf. *sylvestris*. **b,** Cone of *Pinus* sp. **c,** Cone of cf. *Picea* sp.

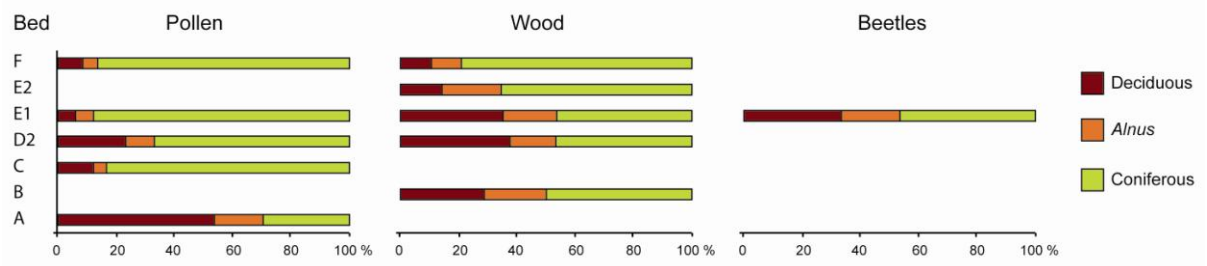
Wood and charcoal (Rowena Gale)

Substantial quantities of waterlogged wood were recovered during routine sieving of all excavated contexts. Although sometimes fairly abundant, a high proportion of fragments were structurally degraded and impossible to identify. The largest specimen included the root bole and trunk of an unidentified conifer, approximately 1 m in length, but the samples mostly comprised small pieces of degraded wood. These consisted of both narrow roundwood (<20 mm in diameter) and slivers from wider roundwood or largewood, many of which were partially or totally mineralised. Several of the wood fragments are also abraded by fluvial transport, and loose pieces of bark were also frequent. Rare charcoal fragments (<10 mm) were recovered from sieved residues, but these were mostly too small to identify. In all, more than 180 fragments were identified (SI Table 11). This assemblage is the only large collection of wood yet to have been studied at a British Lower Palaeolithic site; the only comparable assemblage is that from Gesher Benot Ya'aqov, Israel[S53].

The samples were prepared using standard methods[S54]. Anatomical structures were examined using incident and transmitted light on a Nikon Labophot-2 compound microscope at magnifications up to 400x and compared to prepared reference slides of modern wood. When possible, the maturity of the wood was assessed and stem diameters recorded.

The structure of some of the coniferous wood was difficult to interpret, since, in many respects, it was similar to pine (*Pinus* sp.) and in particular the *sylvestris* group, which includes Scots pine. This observation is based on the presence of ray tracheids and large tracheid/ray pits typically of the *sylvestris* type[S55]. There was no evidence, however, of either axial or horizontal resin canals but since these are sometimes sparse in modern wood their absence in the sample could be due either to an insufficient area of wood available for examination or to the collapse of structures. Some of these features are common also to *Tsuga*, which was identified from pollen in the same laminated sediments. For example, whereas *Tsuga* also has ray tracheids, resin canals are absent, which could suggest this taxon as the more likely; however the tracheid/ray pitting in *Tsuga* is predominantly cupressoid (i.e. small oval-shaped pits – thus differing from those in the Happisburgh sample). On balance, the structure suggests slightly atypical pine rather than *Tsuga*.

The taxa present in each bed are shown in SI Table 11. The mix of conifers and broad-leaved trees was common to each of the horizons, with alder (*Alnus glutinosa* (L.)) the most frequently represented of the broad-leaved species. Other taxa included the hawthorn/*Sorbus* group (Pomoideae), willow (*Salix* sp.) or poplar (*Populus* sp.), ash (*Fraxinus excelsior* L.) and elm (*Ulmus* sp.). Conifers included at least two species of pine, one of which was provisionally named as Scots pine (*Pinus sylvestris*), and possibly either spruce (*Picea* sp.) or larch (*Larix* sp.). Resin canals appeared to be absent in a number of the coniferous wood fragments and, although this observation may be spurious owing to degradation of the wood structure, if correct, suggests additional taxa to those named above. The frequency of alder suggests that at least part of the site remained damp or wet and the presence of heather macrofossils in Bed E1 could be indicative of heathland. The evidence suggests that mixed broad-leaved and coniferous woodland existed at the site throughout the period. Moreover, vegetational change in the woodland composition is indicated by the increasing dominance of coniferous wood through the sequence (SI Fig. 11).



SI Fig. 11. Indicators of woodland composition by horizon. Alder (*Alnus* sp.) is probably over-represented due to its preference for river-marginal habitats.

SI Table 11. Wood and charcoal from HSB3. Taxonomy follows Tutin *et al.*[S45].

Bed	B	D2	E1	E2	F
Coniferous trees and shrubs					
Juniperus		1			
Pinus type A		1			
Pinus type B					1
Pinus		1	3		
Picea/*Larix*			6	2	
Picea/*Larix*/*Pinus*			8	2	3
Conifer (?canals absent)	6	12	4	31	9
Conifer	1	1	4	7	
Total	**7**	**16**	**25**	**42**	**13**
Broad-leaved trees and shrubs					
Alnus	3	5	10	13	2
Corylus			5		
Fraxinus		3	3		
Pomoideae	1	8	9	6	
Prunus		1			
Quercus	1				
Rosa/*Rubus*	1				
Salicaceae				2	
Salix/*Populus*	1		1	1	
Ulmus	1		1		
Ericaceae			2		
Total	**8**	**17**	**31**	**22**	**2**
Charcoal		+	+	+	

Notes on identification:

Pinaceae

Pinus Type A. This group included axial and radial resin canals, dentate ray tracheids and large tracheid/ray pitting and therefore more typical of the *sylvestris* group of pines, which includes Scots pine.

Pinus Type B. This group included axial and radial resin canals, smooth-walled ray tracheids and smaller tracheid/ray pitting often with four pits per window. Charcoal from this group appears to represent a different (although unidentified) species of pine.

Picea sp./*Larix* sp./*Pinus* sp. Several poorly preserved wood samples presented features common to these three taxa. *Picea* and *Larix* are anatomically similar but can be distinguished from pine by thick-walled epithelial cells in the resin canals (as opposed to thin-walled epithelial cells in pine) and piceoid tracheid/ray pitting. However, in degraded wood it is often impossible to separate these genera. Epithelial cells were only visible in a specimen from the base of Bed F, and these appeared to be thick-walled and thus characteristic of *Picea*/*Larix*.

Conifer. A large number of wood samples were clearly coniferous and did not, apparently, include resin canals, although preservation was poor and canals, if present, may have been too sparse to be evident. The short rays were similar to those of pine but ray tracheids were not observed and the wood was too degraded to examine the ray/tracheid pitting. It was not possible to provide a more conclusive identification for these samples.

Salicaceae. *Salix* sp., willow, or *Populus* sp., poplar. In most respects these taxa are anatomically similar.

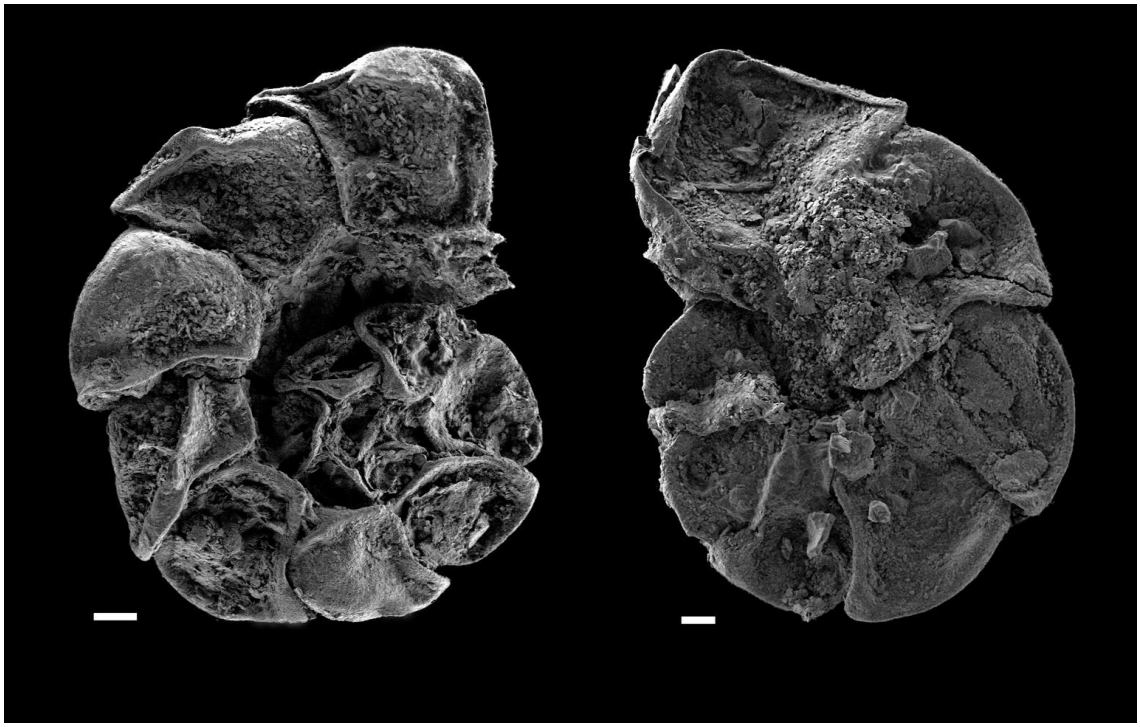
Ericaceae. *Erica* sp. and *Calluna* sp., heathers and ling. Many members of the heather family are anatomically similar.

Rosaceae. Subfamily Pomoideae, which includes *Crataegus* sp., hawthorn; *Malus* sp., apple; *Pyrus* sp., pear; *Sorbus* spp., rowan, service tree and whitebeam. These taxa are anatomically similar; one or more taxa may be represented.

Foraminifera (John E. Whittaker)

Foraminifera were recovered from a thin silt layer within Bed E1. A close examination under the scanning electron microscope shows a low trochospiral species and some of the specimens can be seen to have prominent projecting siphonate (secondary) apertures on the face of the final chamber, as well as the primary interiomarginal aperture at the base of the final chamber. These features are characteristic of *Jadammina macrescens* (Brady). Its test ('shell'), in life, has a thick inner organic layer (which is all that is here preserved) with a thin outer layer of agglutinating mineral grains. Moreover, it is highly flexible and often shows collapse features, as is indeed the case here (SI Fig. 12). It occurs epifaunally, sometimes on decaying leaves or is infaunal down to *c*.0.6 m. It is thus a herbivore/detrivore and today is widespread on high to mid saltmarshes throughout mid to high latitudes[S56]. If *in situ* it would indicate the presence of saltmarsh in that part of the estuary, although some degree of transport on floating plants cannot be ruled out. *Jadammina macrescens* is strongly euryhaline, as saltmarshes can be low brackish right through to hypersaline, dependent on the range and state of the tide and local conditions (rainfall and river flow).

Saltmarsh, as a preserved palaeoenvironment, appears to be exceptionally rare in the Pleistocene. Of course such marginal environments will be readily susceptible to subsequent reworking/erosion. Moreover, the small and fragile nature of these foraminiferal tests, coupled with the difficulty of recognising them in organic-rich sediments, must contribute to their apparent rarity.



SI Fig. 12. Scanning electron micrographs of two specimens of *Jadammina macrescens* from Bed E. Left: spiral side (scale bar 30 µm). Right: umbilical side (scale bar 20 µm).

Molluscs and barnacles (Richard C. Preece)

Some poorly preserved fragments of marine bivalves and barnacle plates were recovered in several samples (SI Table 12). In most specimens the carbonate shells showed mineral replacement and were consequently black or dark-coloured. Most of the bivalves were cockles, represented by fragments of the outer margin bearing ribs, allowing identification of some as edible cockle *Cerastoderma edule* (L.); most fragments were not identifiable to species. Many of the cockle shell fragments from Bed E2 had been bored by the polychaete worm *Polydora* sp. (family Spionidae), a common inhabitant of coastal, estuarine and marine benthic environments. One umbonal fragment belonged to *Macoma balthica* (L.), a marine bivalve that first entered the North Sea Basin during the late Middle Tiglian[S57]. This occurrence therefore provides a maximum age constraint on the age of HSB3. The barnacle plates were also poorly preserved but were far more numerous (one sample yielding at least 82 fragments) than the bivalves. Identification to species is problematic, although some appear to be *Balanus crenatus* Bruguiére. All these species characterize shallow, near-shore coastal environments.

SI Table 12. Molluscs and barnacles from HSB3. [1]cf. *C. edule* bored by the polychaete worm *Polydora*, [2]*Cerastoderma edule*.

Bed	Sample	Fragments of barnacle plate	Fragments of *Cerastoderma*	*Macoma balthica*
E1	40	5	1	-
D2	7	26	3[1]	-
D2	16	7	2	-
D2	51	82	+	-
C	42	5	1[2]	1

Insect remains (G. Russell Coope)

Fifteen samples from sediments below, within and above Bed E1 (grey gravel) yielded insect fossils. The samples were wet sieved at 300 μm and the insect remains recovered from the residue retained by the sieves were concentrated by paraffin (kerosene) flotation[S58]. Altogether 167 coleopteran taxa were recognised of which 119 could be recognised to species or species group; nine taxa are no longer live in the British Isles (SI Table 13). The richest samples were those from the grey gravel (Bed E1) that were directly associated with most of the archaeological remains. The beetle assemblage provides a detailed picture of the environment at the time.

Bed E1 (grey gravel)

The assemblage of beetle species from this bed reflects a wide range of habitats from fully aquatic through marshy to dry land environments, probably brought together by flood-water from a nearby river (SI Fig. 13). Running water species were extremely rare and were represented by *Hydraena riparia, Oulimnius tuberculatus* and *Riolus.* The presence of larval sclerites of the caddisfly *Hydropsyche bulgaromanorum* Mallicki indicates that the samples came from the lower reaches of a mature river upstream from tidal influences (M. Greenwood pers. comm. 2008). However, the isolated occurrences of saltmarsh species such as *Bembidion fumigatum, Bembidion minimum* and *Paracymus aeneus,* suggests the proximity of saline habitats.

In contrast, species that inhabit stationary or slow-flowing water were well represented. These included the most of the dytiscids, such as *Agabus bipustulatus, Nartus grapei, Colymbetes fuscus* and *Cybister lateralimarginalis.* Amongst the hydrophilids, significant species included *Limnoxenus niger* and *Hydrophilus* (*Hydrochara*) *caraboides*. Various aquatic plants are indicated by phytophagous species. Thus *Donacia semicuprea* feeds largely on the aquatic grass *Glyceria. Litodactylus leucogaster* feeds on *Myriophyllum,* whereas *Tanysphyrus lemnae* feeds on the duckweed *Lemna.* A large number of species in this assemblage indicate marshy freshwater habitats, dominated by reed

swamps. These include *Plateumaris affinis* and the weevil *Notaris scirpi* that feed principally on *Carex*. Muddy areas are indicated by the burrowing species *Heterocerus*. Bare, unvegetated, sandy banks are the preferred habitat of the predator *Bembidion velox*.

Drier grassy habitats are indicated by *Agriotes obscurus*, whereas the chafer *Homaloplia* is characteristic of dry, sun-exposed sandy places. The weevils *Barynotus obscurus, Tanymecus palliatus* and species of *Otiorhynchus* are all polyphagous feeding on a variety of herbaceous plants; their larvae feed underground on roots.

Many species in this assemblage indicate the local presence of both coniferous and deciduous trees (SI Fig. 11). Conifer-dependent species include *Hylurgops palliatus, Blastophagus piniperda, Polygraphus poligraphus* and *Rhyncolus elongates*, which attack sickly branches of *Picea, Abies, Larix* and *Pinus*. Beetles that are restricted to deciduous trees were also numerous and include *Hylesinus crenatus*, while other species such as *Rhyncolus punctulatus*, *Xestobium rufofillosum* (Death-watch Beetle*), Gastrellus immarginatus* and *Dorcus parallelopipedus* (Lesser Stag Beetle) also burrow into dead timber of deciduous trees. Other species also attack dead wood of both coniferous or deciduous trees; these include *Melanotus rufipes* and *Anobium punctatum* (Woodworm Beetle).

The extensive beetle fauna from the grey gravel of Bed E1 is entirely made up of temperate species, most of which still live in southern England at the present day. The few non-British species live in central Europe and there are no strictly boreal species present. Precipitation levels were adequate to maintain continuous flow in the adjacent river throughout the year and to maintain the marginal swamp during the summer months.

Using the Mutual Climatic Range (MCR) method to quantify the palaeotemperatures[S59] the following figures were obtained from thirty-four species of predatory or general scavenging species in the assemblage recovered from Bed E1 which are also on the MCR database (SI Table 14). In these MCR estimates T_{max} is the mean temperature of the warmest month (July) and T_{min} is the mean temperature of the coldest months (January/February):

T_{max} lay somewhere between 16°C and 18°C
T_{min} lay somewhere between -3°C and 0°C

These figures suggest that summer temperatures were as warm, or slightly warmer than East Anglia at the present day. The estimates of winter temperatures suggest slightly cooler temperatures than Britain today, although they may be less reliable. A few species (e.g. *Cybister lateralimarginalis*) would seem to find present British summers inadequately warm to enable them to establish permanent colonies there. The geographical ranges of several other species in this assemblage do not reach as far north as the British Isles.

SI Table 13. List of Coleoptera from HSB3. Nomenclature and taxonomic order follow Lucht[S63]. The numbers indicate the minimum numbers of individuals. Non-British species are indicated by *. The species used to generate the MCR temperature estimates are denoted by ✓.

	Clasts	Bed C	Bed D2	Bed E1	MCR
Carabidae					
Carabus sp.	1			1	
Notiophilus palustris (Duft.)	1				
Blethisa multipunctata (L.)				1	✓
Elaphrus cupreus Duft.			1	1	✓
Loricera pilicornis (F.)	2				
Dyschirius aeneus (Dej.)				2	✓
Trechus secalis (Payk.)	5			2	✓
Trechus rivularis (Gyll.)	2			3	✓
Trechus obtusus Er.	1				
**Bembidion* cf. *velox* (L.)				1	✓
Bembidion obliquum Sturm.				1	
Bembidion schueppeli Dej.	1				
Bembidion fumigatum (Duft.)				2	✓
Bembidion assimile Gyll.	1			9	✓
Bembidion clarki (Daws.)				1	✓
Bembidion minimum (F.)				1	✓
Bembidion doris (Panz.)				3	✓
Bembidion guttula (F.)	2			1	
Bembidion spp.	1			2	
Patrobus atrorufus (Ström)	4			1	✓
Acupalpus sp.				1	
Pterostichus strenuus (Panz.)	2			2	✓
Pterostichus diligens (Sturm.)	2			3	✓
Pterostichus nigrita (Payk.)	2			2	✓
Pterostichus minor (Gyll.)	1			2	✓
Pterostichus niger (Schall.)	1				
Agonum livens (Gyll.)	1				
Agonum gracile (Gyll.)				1	✓
Agonum fuliginosum (Panz.)				1	✓
Agonum thoreyi Dej.	1			1	✓
Amara convexiuscula (Marsh.)			1	1	
Odacantha melanura (L.)				2	✓
Dytiscidae					
Hydroporus palustris (L.)	1				
Hydroporus sp.	1			3	
Potamonectes assimilis (Payk.)				1	✓
Agabus bipustulatus (L.)				2	✓
Agabus sp.	2				
Ilybius sp.	3		1	2	
Nartus grapei (Gyll.)	1			1	
Rhantus sp.				1	
Colymbetes fuscus (L.)	1		1	4	✓
Acilius sp.				2	
Dytiscus sp.				3	
**Cybister lateralimarginalis* (Geer)				1	
Hydraenidae					
Hydraena gracilis Germ.				1	✓
Hydraena riparia Kug.	46			5	✓
Ochthebius bicolon Germ.				5	✓
Ochthebius minimus (F.)	2			1	✓
Limnebius aluta Bedel	1			1	
Helophorus small spp.	1			2	
Hydrophilidae					
Coelostoma orbiculare (F.)	1			1	✓
Cercyon marinus Thoms.				1	
Cercyon convexiusculus Steph.				1	
Cercyon sternalis Shp.	2			6	
Cercyon sp.	2			1	
Paracymus aeneus (Germ.)				2	
Hydrobius fuscipes (L.)				2	✓
Limnoxenus niger (Zsch.)				1	
Laccobius sp.	7			2	
Enochrus sp	8			2	

SI Table 13 cont.

	Clasts	Bed C	Bed D2	Bed E1	MCR
Cymbiodyta marginella (F.)	6				
Chaetarthria seminulum (Hbst.)				1	✓
Hydrophilus (Hydrochara) caraboides (L.)				1	
Silphidae					
Thanatophilus sp.				1	
Phosphuga atrata (L.)	1				
Orthoperidae					
Orthoperus sp.	1				
Corylophus cassidoides (Marsh.)	4			1	
Ptiliidae					
Ptenidium spp.	3		1	2	
Acrotrichis sp.	1	1		1	
Scaphidiidae					
Scaphisoma boleti (Panz.)			1		
Staphylinidae					
Micropeplus porcatus (Payk.)				1	
Megarthrus depressus (Payk.)	1				
Eusphalerum sp.	1			1	
Olophrum fuscum (Grav.)	1	2			
**Arpedium quadrum* (Grav.)				1	✓
Eucnecosum brachypterum (Grav.)			3		
Acidota crenata (F.)				1	
Lesteva sicula v. *heeri* Fauv.	19				
Trogophloeus sp.	9	1		6	
Oxytelus rugosus (F.)	2			2	✓
Platystethus nitens (Sahlb.)				1	✓
Bledius sp.				1	
Stenus juno (Payk.)	8			2	✓
Stenus spp.	24	1	1	8	
Euaesthetus bipunctatus (Ljungh)	1				
Paederus riparius (L.)				1	
Lathrobium sp.	2			1	
Gabrius sp.		1			
Tachyporus sp.		1			
Lomechusa strumosa (F.)	3			1	
Aleocharinae gen. et sp. indet.	5	1	2	8	
Pselaphidae					
Bryaxis sp.	1			1	
Brachygluta fossulata (Reichb.)	1			1	
Pselaphidae gen. et sp. indet.				2	
Throscidae					
Throscus sp.		1		1	
Elateridae					
Agriotes cf. *obscurus* (L.)	2			2	
Melanotus cf. *rufipes* (Hbst.)	1			1	
*Actenicerus sjaelandicus (*Müll.)				2	
Helodidae					
Helodidae gen. et sp. indet.	6			6	
Dryopidae					
Dryops sp.	4			2	
Oulimnius tuberculatus (Müll.)		1		1	
Riolus sp.				1	
Heteroceridae					
Heterocerus sp.				3	
Dermestidae					
Dermestes murinus L.	1				
Byrrhidae					
Simplocaria semistriata (F.)			1	1	
Cytilus sericeus (Forst.)				1	
Nitidulidae					
Cateretes sp.	1				
Epuraea sp	1				
Cucujidae					
Laemophloeus ater (Ol.)	1				
Cryptophagidae					
Telmatophilus caricis (Ol.)	1			1	
Phalacridae					
Phalacrus caricis Sturm.	3				
Stilbus testaceus (Panz.)				1	

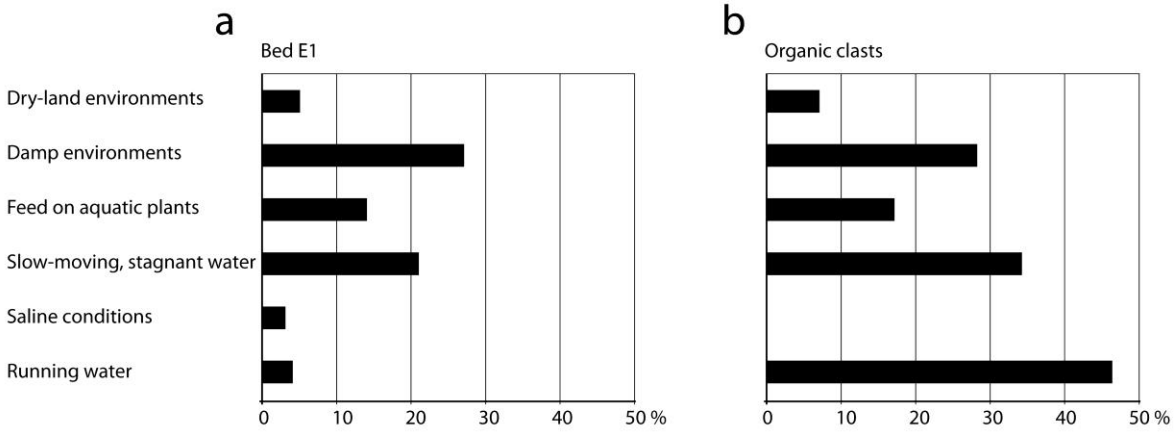
SI Table 13 cont.

	Clasts	Bed C	Bed D2	Bed E1	MCR
Colydidae					
Colydium elongatum (F.)	1				
Lathridiidae					
Corticarina sp.	1	1		3	
Colydiidae					
Cerylon histeroides (F.)	3				
Anobiidae					
Grynobius planus (F.)	1				
Xestobium rufovillosum (Geer)	3			1	
Gastrallus immarginatus (Müll.)	6			1	
Anobium punctatum (Geer)	4			2	
Scarabaeidae					
**Aphodius* sp. (exculpted head)				2	
Aphodius sp.	1			2	
Serica brunnea (L.)	2				
Homaloplia ruricola (F.)				1	
Lucanidae					
Dorcus parallelopipedus (L.)	1			1	
Cerambicidae					
Cerambicidae gen. et sp. indet.	1				
Chrysomelidae					
Donacia semicuprea Panz.	3		1	4	
Donacia cf. *thalassina* Germ.	2			2	
Donacia cinerea Hbst.				1	
**Donacia polita* Kunze				1	
Plateumaris sericea (L.)	2		1	1	
Plateumaris affinis (Kunze)	5	1		6	
Pachnephorus tesselatus (Duft.)				1	
Chrysomela sp.	1		1		
Phaedon sp.	2				
Prasocuris phelandrii (L.)	4			1	
Phyllodecta sp.				1	
Phyllotreta nemorum (L.)				1	
Haltica sp.				1	
Scolytidae					
Scolytus rugulosus (Müll.)	1				
Hylurgops palliatus (Gyll.)				1	
Blastophagus piniperda (L.)	1			2	
Polygraphus poligraphus (L.)	2		1	3	
Hylesinus crenatus (F.)	1			1	
Hylesinus oleiperda (F.)	3				
Leperisinus varius (F.)	1				
Pteleobius vittatus (F.)		1			
Xyleborus dispar (F.)	1				
Curculionidae					
Rhynchites sp.				1	
Apion sp.	3				
Otiorhynchus clavipes (Bonsd.) group	1	1		1	
Otiorhynchus cf. *arcticus*				1	
Otiorhynchus rugosostriatus (Goeze.)				1	
Otiorhynchus ligneus (Ol.)				1	
Otiorhynchus ovatus (L.)				1	
Otiorhynchus sp.		1			
Barynotus obscurus (F.)				1	
Tanymecus palliatus (F.)				1	
**Cossonuslinearis* (F.)				1	
**Rhyncolus elongatus* (Gyll.)				2	
Rhyncolus chloropus (L.)				2	
**Rhyncolus punctulatus* (Boh.)	2			1	
Bagous sp.				1	
Tanysphyrus lemnae (Payk.)	4			2	
Notaris scirpi (F.)	1			3	
Limnobaris pilistriata (Steph.)				2	
Litodactylus leucogaster (Marsh.)				2	
Phytobius sp.				2	
Rhynchaenus testaceus (Müll.)	94		1	4	

Other insect assemblages

The small fauna from the grey pellety clay (Bed D2) also suggests slightly cooler conditions indicated by the presence of three individuals of the boreo-montane species *Eucnecosum brachypterum.* This species is currently restricted to northern and western parts of Britain, but it is widely distributed throughout Fennoscandia and at high altitudes across Europe. In contrast, *Amara convexiuscula* is widespread in Britain, but does not occur in Fennoscandia north of 59°N, suggesting that any cooling at this time was moderate.

Clasts of peaty material that were found in the grey gravel (Bed E1) and in the laminated sands and silts (Bed F) also contained insect remains (SI Fig. 13). These include large numbers of individuals of *Rhynchaenus testaceus*, which is a weevil that mines the leaves of *Alnus*. Palynological evidence from these clasts also suggests that alder trees were abundant and that they derive from older pollen substage III (*sensu* West[S9]) sediments.



SI Fig. 13a–b. Ecology of beetles from Bed E (**a**) and reworked organic clasts (**b**). Pollen spectra from the clasts (n = 7) are similar to those of West's[S9] pollen assemblage biozone i.

Summary

The insect fossils from Bed E1 help to reconstruct the environment at the time when humans occupied the area. The diversity of species represented suggests that the fossils were swept together from a wide range of local habitats and deposited as flood debris from some nearby river. The insect fauna is entirely made up of terrestrial and freshwater species, indicating a sluggish river meandering through a reedy swamp across its flood plain. Trees in the damp marginal ground included both *Alnus* and *Salix.* Grassland interspersed with various species of herbaceous plants occupied the drier, sandy ground. Mixed woodland with both coniferous trees, including *Pinus*, as well as deciduous trees, including *Quercus*, *Fraxinus* and *Ulmus*, grew in the drier parts of the immediate neighbourhood with many of the trees dead or dying. There is extremely little evidence of any marine component in the environment but the rare and isolated occurrences of halophytic beetle species suggests that tidal influences may not have been far away. Climatically the beetles of Bed E1 indicate temperatures at least as warm as those of southern England at the present day or possibly slightly warmer, although winter temperatures may have been slightly cooler. Precipitation levels were adequate to support a river that flowed continuously throughout the year and also to maintain the marshy habitats at least throughout the summer months, required by so many of the coleopteran species.

Vertebrates (Simon A. Parfitt)

The vertebrate fauna includes mammals (both large and small), fishes and anurans (SI Table 14)). Relatively large assemblages were recovered from Bed D2, Bed D3, Bed E1 and Bed E2. These all originate from the same pollen biozone (p.a.z. 3); they therefore are considered to be broadly contemporary and will be considered together. Smaller assemblages were recovered from Bed B and Bed C in association with the earlier Ericaceae-type–*Pinus*–*Picea* pollen assemblage zone (p.a.z. 2).

Due to the degree of fragmentation, only about 16 of the large mammal bones and teeth can be reliably identified to anatomical element and taxon. Of the identifiable vertebrate remains, those of mammals comprise more than 95% of all specimens recovered, followed by the remains of fishes and anurans. Small mammals are most abundant in the sands and silts, and almost absent from the gravels. Large mammal remains, on the other hand, are rare in the fine-grained sediments and are concentrated in the poorly sorted gravels of beds E1 and E2, which accumulated near the edge of the channel. The bones show a marked difference in the degree of rounding. Some bones are in perfect condition suggesting minimal transport (SI Fig. 14), whereas others are rounded indicating longer-distance transport. This suggests that the bones were an integral part of the sediment load, transported to the site with the rest of the sedimentary particles. This strong taphonomic overprinting has destroyed any evidence for earlier taphonomic alterations on most of the bones and, consequently, it is not possible to identify the relative role of carnivores or hominins, if any, in the accumulation of the assemblage. Indirect evidence of carnivore activity is provided by hyaena coprolites (one complete specimen from Bed E1 and a small fragment from Bed D2). Some of the small mammal teeth also exhibit abrasion from water transport. A few of the microtine molars exhibit digestive corrosion, indicative of accumulation by raptors, owls or small carnivores.

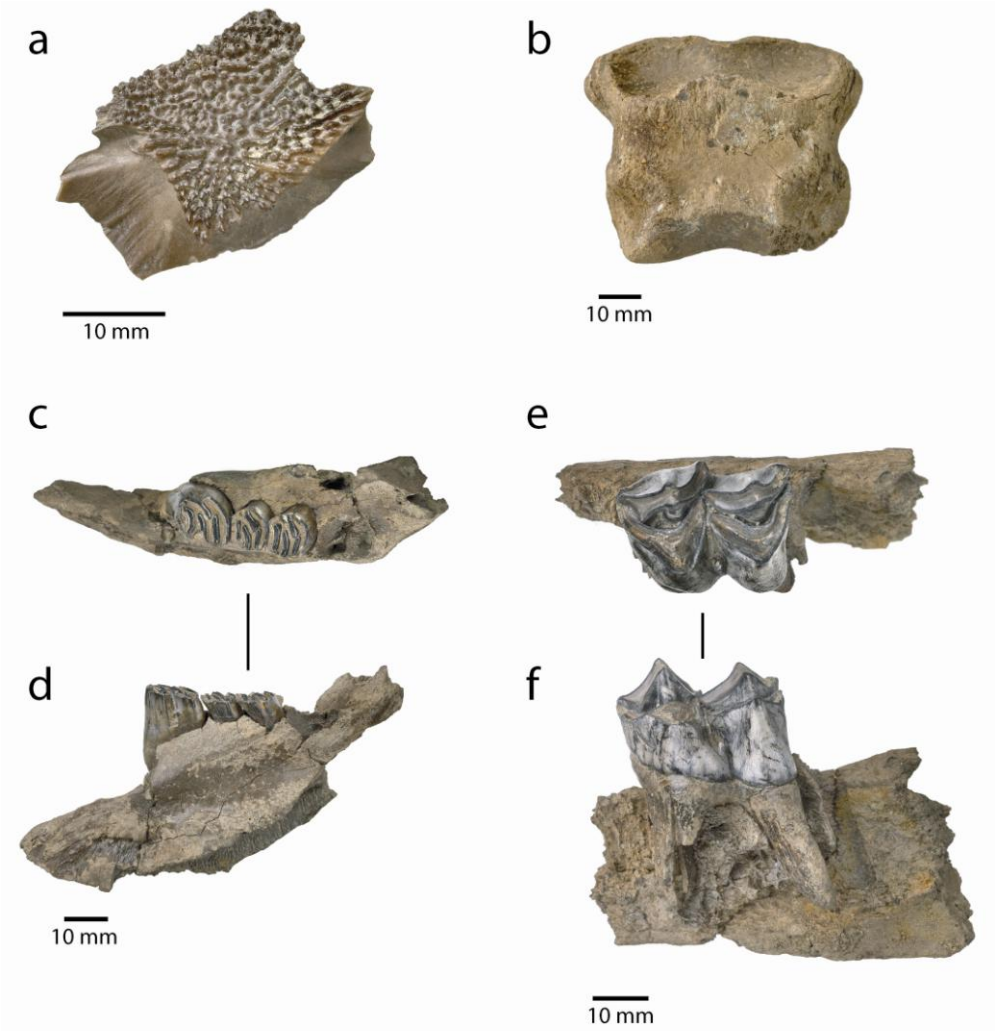
The vertebrates, like the other groups studied, reflect the nature of the local environment, but at a much coarser scale. The ecology of the extinct taxa can be inferred from aspects of their functional morphology and fossil history, but ecological interpretation of the HSB3 assemblage is hampered by the difficulties of identification due to the fragmentary nature of the remains. Larger herbivores include the southern mammoth *Mammuthus* cf. *meridionalis*, which is generally regarded as a woodland browser. Species likely to have inhabited grassland areas include the extinct equid *Equus suessenbornensis*. *Cervus elaphus* feeds by grazing and browsing and it occupies diverse habitats ranging from deciduous and Mediterranean woodland in western Europe to steppic habitats in central Asia. In northern Europe its range is limited by deep winter snow cover, which prevents access to food in the tundra and taiga.

The habitat of *Cervalces latifrons* was probably similar to that of its living descendant *Alces alces*, which spends the greater part of its life in swampy areas and rivers, where it feeds on aquatic and waterside plants and deciduous trees and bushes. The fossil range of *C. latifrons* suggests that it too was mainly a taiga-adapted species that occupied the northern coniferous forest and northern part of the deciduous forest zone[S5,S60].

Aquatic environments are indicated by the presence of the beavers *Castor fiber* and *Trogontherium cuvieri*. *Castor fiber* is a large aquatic rodent that requires year-round access to water and woody vegetation. It is found in a wide range of waterbodies, including lakes, swamps, streams and rivers, where it feeds on aquatic and waterside vegetation in summer and the bark of deciduous trees for the rest of the year. The extinct beaver *Trogontherium cuvieri* (SI Fig. 14c-d) is also closely associated with aquatic environments, but is more prevalent in fine-grained deposits, suggesting that it favoured slower-flowing water than *Castor fiber*.

The degree of fragmentation of the small mammal bones makes identifications difficult but nevertheless seven species have been identified. The most common small mammal is the water vole *Mimomys savini*, which is generally regarded as an aquatic animal. A second smaller species of *Mimomys* (*M. pusillus*) is also present in low numbers. Most other species of small mammal are uncommon being represented by a few isolated teeth only. Of these, the most abundant species of microtine rodent was identified as *Microtus oeconomus*. Today, this vole thrives in marshy grassland and saltmarsh in the northern Palaearctic. It is found in the tundra zone, but it is more commonly encountered in taiga, particularly amongst herbaceous vegetation in marshes and along the banks of

rivers and lakes. Relict populations also occur in such favourable habitats in the northern part of the deciduous woodland zone. Red-backed voles (*Myodes* sp.) prefer a wide range of densely vegetated conditions, including scrub, woodland edge and forest glades, which would have provided suitable habitats for *Apodemus* sp.



SI Fig. 14a–f. Selected vertebrate remains from the Hill House Formation. **a,** Skull bone of *Acipenser* cf. *sturio* (Bed E). **b,** Phalanx II of *Equus* sp. (Bed D). **c–d,** Mandible with P_4–M_2 of *Trogontherium cuvieri* in (**c**) occlusal view and (**d**) lingual view (Bed D). **e–f,** Mandible fragment with M_2 of *Cervalces latifrons* in (**e**) occlusal and (**f**) labial views (Bed E).

The most noteworthy small mammal is lemming, either *Lemmus* sp. or *Myopus*. This record is based on a lower second molar from Bed D2. Dental remains of *Myopus* and *Lemmus* are notoriously difficult to distinguish, a problem compounded by the presence of extinct forms in the Early Pleistocene. Ecologically, *Myopus* would seem to be the most likely candidate as it is closely associated with taiga forest, in particular marshy woodland such as pine-bogs and old spruce-dominated forests with a thick moss layer. Today *Lemmus* is more closely associated with alpine and subarctic areas, favouring bogs and mires, but fossil finds suggest that it had wider ecological tolerances in the Early Pleistocene.

The fish fossils belong to *Esox lucius*, *Acipenser* cf. *sturio* (Bed E1) and indeterminate cyprinids (Bed D2). The *Esox lucius* specimens are all large, with some specimens comparable to a modern individual measuring between 0.5 and 1.0 m. In general, *Esox lucius* lives in fresh waters, which are not too fast flowing. It is generally found in lakes, slow flowing rivers and in the slack areas of faster-flowing rivers, but it also occurs in brackish waters at the mouths of large rivers and coastal lagoons in the Baltic.

A large river is also indicated by sturgeon, which is represented by a well-preserved cranial bone from an adult individual (SI Fig. 14a). Today *Acipenser sturio* is the only sturgeon species in western European waters, but as many as six additional species are native to the Black, Caspian and Adriatic Seas. *Acipenser sturio* spends most of its life at sea, returning to spawn in deep water in the lower reaches of large rivers. Here, spawning takes place in fast turbulent waters at least 2 m deep over clean gravel, where the sticky eggs sink to the river bed and adhere to stones. The young stay in freshwater for about three years before migrating to the sea where they live for at least five years before their first spawning run.

The fish taxa present at HSB3 also provide information on water temperatures. For example, Cyprinidae indicate that from May to August water temperatures must have reached a minimum of 15°C, with a maximum of 22°C (ref. S61). Sturgeon eggs also hatch in the spring and early summer, when temperatures rise to between 14°C and 20°C.

The vertebrate fauna associated with the artefacts includes *Mammuthus*, *Equus suessenbornensis*, *Cervalces latifrons*, the red deer *Cervus elaphus*. This mix of grazers and browsers and mixed-feeders indicates a rich and diverse habitat. Hyaena is the only carnivore present, but species indicative of riparian and aquatic environments are particularly well represented. The presence of sturgeon indicates that the site was located close to the river estuary. Overall, the terrestrial vertebrates are consistent with regional conifer-dominated forest with extensive areas of grassland in the river floodplain.

SI Table 14. Vertebrates from HSB3. Most of the large mammal remains were recovered *in situ* during excavation with additional specimens retrieved through sieving (1cm mesh) of all the excavated sediment (*c*. 50 m^3). Small vertebrate remains were recovered through wet-sieving of bulk samples (*c*. 10 tonnes).

Taxon	Bed
Pisces	
Acipenser cf. *sturio*, sturgeon	E1
Esox lucius L., pike	E1
Cyprinidae gen. et sp. indet, carp family	D2
Pisces indet., fish	B, C, D2, E1, E2
Amphibia	
Anuran gen. et sp. indet, frog or toad	C, D2
Mammalia	
Primates	
Homo sp. (artefacts), hominid	C, D2, D3, E1, E2
Rodentia	
Castor fiber L., beaver	C, E1
Trogontherium cuvieri Fischer, extinct beaver-like rodent	D2
Lemmus or *Myopus*, lemming	D2
Myodes sp., red-backed vole	C, D2, D3, E2
Mimomys pusillus (Méhely), extinct vole	D2, D3
Mimomys savini Savin, extinct water vole	B, C, D2, D3, E1, E2
Microtus arvalis morph, vole	D2
Microtus oeconomus (Pallas), northern vole	D2
Microtus sp., vole	B, D2, E2
Apodemus sp., mouse	C, D2
Carnivora	
Hyaenidae gen. et sp. indet. (coprolites), hyaena	D2, E1
Proboscidea	
Mammuthus cf. *meridionalis*, southern mammoth	E1
Mammuthus sp., mammoth	D2, E1
Perissodactyla	
Equus cf. *suessenbornensis*, extinct equid	D2
Equus sp., equid	D2
Artiodactyla	
Cervus elaphus L., red deer	E1
Cervalces latifrons (Johnson), extinct elk	E1
Cervidae indet., deer	E1
Bovidae indet., bovid	E2

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