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# Middle to Late Pleistocene palaeoecological reconstructions and palaeotemperature estimates for cold/cool stage deposits at Whittlesey, eastern England<sup>1</sup>

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<sup>1</sup>This article is dedicated to the memory of the late Professor Russell Coope, whose untimely death meant that he did not see its publication.

## Abstract

Fossiliferous beds in a complex sequence of late Middle to Late Pleistocene deposits at Whittlesey, eastern England, provided a rare opportunity for a multidisciplinary study of the palaeoecology of cool/cold stage deposits from different glacial stages. The fossiliferous sediments investigated form part of the River Nene 1st Terrace. Three of the four fossil assemblages investigated pre-date the last interglacial stage (Ipswichian/Eemian/marine oxygen isotope stage (MIS) 5e), whereas the other dates to part of the MIS 3 interstadial complex (Middle Devensian/Weichselian). Pollen, plant macrofossil, molluscan, coleopteran, ostracod, foraminifera and vertebrate data are available to a greater or lesser extent for each cool/cold stage assemblage, and they broadly present the same ecological picture for each one: a continuum from low-energy permanent to non-permanent aquatic habitats through marshland with associated waterside taxa, together with flood influxes of fluvial, riparian and ruderal taxa. Although each fossil assemblage records cool/cold climatic conditions, to a greater or lesser extent, these conditions are more apparent in the insect and ostracod faunas. In comparison with results published for the Last Glacial Maximum (LGM) stadial in The Netherlands, palaeotemperature estimates based on ranges of mutual agreement between independent coleopteran and ostracod methods for the three pre-Ipswichian/Eemian assemblages indicate minimum mean July air temperatures that

are from +1° to +3°C warmer, but January values that embrace the –8°C estimate for the LGM. There is, however, a disparity between the coleopteran and ostracod palaeotemperature estimates for the Middle Devensian/Weichselian fossil assemblage, which are based on two different sample stratigraphic levels; the lower, coleopteran assemblage is indicative of very cool, continental climates, whereas the stratigraphically slightly higher ostracod assemblage suggests a climatic amelioration. Lack of numerical age-estimates prevents a robust stratigraphical interpretation, but the youngest pre-Ipswichian/Eemian fossil assemblage could date to the marine oxygen isotope stage 7–6 transition, at a time when cooling possibly preceded glacially driven sea-level fall. It is apparent from the rich coleopteran data that some continental cold-indicator taxa also appeared in pre-Ipswichian/Eemian cold stages and therefore assignment of continental cold-indicator taxa to particular Devensian/Weichselian intervals should be undertaken with care.

**Keywords:** palaeoecology; palaeotemperature; Middle and Late Pleistocene; cool/cold stages; fossil assemblages; River Nene.

## 1. Introduction

A complex sequence of late Middle to Late Pleistocene deposits at Whittlesey, eastern England (Fig. 1a) contains a number of fossiliferous beds of both cool/cold or temperate character. The palaeoecology of these have yet to be reported in detail (although see Langford (1999) and Langford et al. (2004a,b,c) for preliminary accounts and Langford et al. (2007) for initial stratigraphic details and age estimates). The investigated sedimentary succession at Whittlesey forms part of the River Nene 1st Terrace (BGS, 1984; Horton, 1989; the Ecton Member of Maddy, 1999) and the deposits concerned are located in West Face (previously known informally as Funtham's Lane East; see Langford et al., this issue) and Bradley Fen quarries (Fig. 2a): more details of the geographical and geological contexts of the Bradley Fen and West Face quarries have been presented by Langford et al. (2007, this issue).

This article presents a multidisciplinary investigation into the palaeoecology of four fossiliferous beds (units 1a, 1c[WF], 3a and 5d; Fig. 3) within the sedimentary succession at Whittlesey that contain cool/cold stage fossil assemblages, and also reports palaeotemperature estimates for these. Relevant stratigraphical parameters for units 1a, 1c[WF], 3a and 5d are outlined in section 1.1, followed in section 1.2 by details of their sedimentary context (Fig. 4). Sample collection and processing methods are described in section 2, and the results of palaeobotany, palaeozoology and palaeotemperature analyses are presented in section 3. Section 4 provides palaeoecological and stratigraphical syntheses and a discussion of the palaeotemperature estimates, and concluding remarks are presented in section 5.

Schematic stratigraphical sections and idealized stratigraphical logs in Fig. 3 show the relationship of units 1a, 1c[WF], 3a and 5d with other units within the sedimentary succession at Whittlesey. In this site-stratigraphy scheme, in order to avoid ambiguity because possible temporal equivalents may occur in different quarries, the qualifiers [BF] and [WF] (e.g. 1c[BF] and 1c[WF] in Fig. 3) are used: in this instance it is unit 1c[WF] that is investigated, but qualifiers for the other units are not used because there is no ambiguity in the context of this article. In order to avoid confusion Table 1 shows the relationship of the nomenclature used here with that previously used.

### 1.1. Stratigraphical parameters

Amino acid racemization (AAR) measurements obtained for shells and *Bithynia* opercula from the temperate deposits of channel B (Fig. 2b) indicate an age in marine oxygen isotope stage (MIS) 7 (unit 2 in Table 1; Penkman, 2005; Langford et al., 2007, this issue). Unit 1a is demonstrably older than this because it underlies channel B deposits in West Face Quarry (Fig. 2b, location 1). Biostratigraphy and sedimentary stratigraphical relationships indicate a possible age of MIS 3 for unit 5d (channel D, Fig. 2b; Langford et al., 2004b; unpublished data). Units 1c[WF] and 3a are demonstrably older than MIS 5b because they underlie units 5a and b of the early Devensian channel A in West Face Quarry (Fig. 2b, locations 2 and 3), which are dated by optically stimulated luminescence (OSL; Langford et al., 2007). Amino acid racemization data place a maximum age constraint on unit 1c[WF] of MIS 8 (Langford et al., 2007). A sand ribbon near the top of unit 3b (Table 1), which also underlies units 5a and b, in the south face of West Face Quarry (Fig. 2b, location 2) has yielded a temperate marine and estuarine ostracod and foraminifera fauna (unpublished data). This fauna is not reworked from the underlying channel B. A minimum age for this temperate fauna and the high sea level implied is therefore MIS 5e. The cool/cold stage fossil fauna of unit 1c[WF] is therefore demonstrably older than MIS 5e because it too underlies unit 3b. In the north face of West Face Quarry (Fig. 2b, location 3), unit 3a underlies deposits with a clast-lithology assemblage and sedimentary facies architecture that resemble unit 3b. Although this correlation cannot be demonstrated unequivocally, it is likely that unit 3a also pre-dates MIS 5e, but it is not a correlate of unit 1c[WF]. A more detailed consideration of the age of these cool/cold stage fossiliferous beds is given in section 4.3.

Two, possibly three, of these cool/cold stage fossil assemblages therefore pre-date the last interglacial stage (Ipswichian/Eemian/MIS 5e), which at Whittlesey is represented by the deposits of channel C (Fig. 2b). This makes them unusual because few cold stage fossil assemblages have sufficiently good numerical age control to definitively place them within this period. For example: although there are strong site-stratigraphy arguments supporting a pre-Ipswichian age for the molluscan and ostracod assemblages, as well as some of the insect samples recovered, the *ex situ* mammalian fossil assemblage of the Balderton Sand and Gravel (forming a River Trent (Fig. 1b) terrace) is dated by electron spin resonance (ESR) to MIS 6 although the possibility of a more recent age could not be ruled out (Grün, in Brandon and Sumbler, 1991), as noted by Howard et al. (1999) – a similar conclusion is drawn from the AAR data; the Lapwing Bed (Chelford, Cheshire; Fig. 1b) is attributed to MIS 6 based on its relationship with glacial till deposits (Maddy, 1999), but an Early Devensian age may be a possibility (Worsley et al., 1983). As little is known of the palaeontology of pre-Ipswichian fluvial cold-stage deposits within a British late Middle Pleistocene context, the pollen, molluscan, beetle and ostracod assemblages from the sedimentary succession at Whittlesey therefore provide novel insights into the environmental and temperature conditions of late Middle Pleistocene cool/cold stages.

Unit 5d falls within the Late Pleistocene (see section 4.3), possibly MIS 3 – a period of dramatic temperature variations lasting about 35,000 years from about 60 ka to about 25 ka (Johnsen et al., 2001). In contrast to pre-Ipswichian cold stages, there are many cold-stage floras and faunas reported from this part of the last glacial stage, although their relative ages and correlation are poorly established due to problems of contamination at the limits of the radiocarbon technique (see discussion in Briant and Bateman, 2009). The palaeoecological data of unit 5d will therefore be compared with the more recent palaeoecological studies that have been dated to MIS 3 by other

means, including Lynford in Norfolk (Fig. 1b; Boismier et al., 2012), Whitemoor Haye in Staffordshire (Fig. 1b; Schreve et al., 2013), Baston (Fig. 1a; Briant et al., 2004a) and Stanwick in Northamptonshire (Fig. 1b; Briant et al., 2008), with the latter two having radiocarbon- and OSL-dated tie points, as well as Latton in Wiltshire (Fig. 1b; Facies Association B, Lewis et al., 2006), for which the dating is less secure.

## *1.2. Sedimentary contexts*

### *1.2.1. Unit 1a*

The deposits of unit 1a (Figs 2b, 3 (log 1) and 4a) range from pebbly matrix-supported diamictons to pebbly stratified (low angle; apparent dip to the east) clast-supported gravels (reworked Jurassic Oxford Clay clasts form part of the gravel component), with an isolated horizontally stratified sand lens and occasional silt drapes (Langford et al., 2004a). These sediments infilled a channel trending SW–NE that deepened toward the northeast, and they were deposited by cohesive flows (matrix-supported diamictons) moving downslope from the west into a low-energy body of water. Horizontally stratified organic muds that developed on a fluvial gravel/Oxford Clay substrate on the land surface to the west are preserved as rip-up clasts in the cohesive flows of unit 1a, as well as in the cold-stage braided stream deposits (Langford et al., 2004a) of the overlying unit 1b (log 1, Fig. 3). (Pollen data (see below) suggest that the rip-up clasts were contemporaneous with the host sediments, rather than reworked from an earlier cold-stage deposit.) As the cohesive flows of unit 1a moved downslope from the land surface to the west they became increasingly saturated and subject to sorting processes (clast-supported stratified gravels) by low-energy currents that transported most of the clay to silt fractions downstream, but temporarily suspended silt and organics occasionally settled to form drapes on matrix- to clast-supported gravel beds. The isolated sand lens indicates an increase in energy level, which led to shallow channel incision and deposition of sand by traction in a channel trending N–NE to S–SW. Deepening of the main channel (comprising the sediments forming unit 1a) towards the northeast suggests flow in that direction.

### *1.2.2. Unit 1c[WF]*

Unit 1c[WF] (Figs 2b, 3 (log 2) and 4b) is dominated by a pebbly, clast-supported gravel at its base. Discontinuity surfaces within the gravel, marked by continuous to discontinuous pockets of clayey silt (fossiliferous in places) and trails of Oxford Clay rip-up clasts at the base of individual beds, suggest aggradation from west to east. At the top of unit 1c[WF] there are two laterally continuous beds of organic mud separated by a thin bed of gravel. At both the western and eastern ends of the organic mud beds, small-scale ( $\leq 1$  m wide) gravel-filled channels occur containing rip-up clasts of organic mud and Oxford Clay. The thin bed of gravel separating the organic mud beds can be traced laterally to the earlier of these small-scale gravel-filled channels. This interrelationship of organic mud beds and adjoining gravel-filled channels suggests the following sequence of events: initial abandonment by the main channel, periodic stream activity at the margin of the lower mud bed, reactivation of the channel during a major flooding event (when the bed of intervening gravel was deposited) and recommencement of periodic stream activity at the margin of the upper mud bed.

### *1.2.3. Unit 3a*

Deposits of unit 3a (Figs 2b, 3 (log 3) and 4c) comprise: (i) organic, cobbly matrix- to clast-supported gravel with reworked clasts of Oxford Clay; (ii) organic clay to fine sand with interbedded organic clast-supported gravel; (iii) pebbly clast-supported gravel and structureless to horizontally stratified sand; and (iv) pebbly clast-supported gravel. Facies (i) to (iii) form horizontally and vertically nested cut-and-fill channels incised into Oxford Clay at the base of the sedimentary succession at log 3. Upwards, vertically stacked cut-and-fill channels comprising facies (ii) interdigitate with gravel sheets of facies (iv). At the top of unit 3a a bed of stratified silt to fine sand coarsening upwards to horizontally stratified sand overlies horizontally stacked cut-and-fill channels comprising facies (ii). The sequence overall records repeated channel incision with episodic infilling, followed by deposition of gravel sheets with organic channel-fill development in the east, giving way upwards to laterally extensive, individual organic channel cut-and-fill generally prograding eastwards. Two-dimensional channel architecture indicates N–NE to S–SW trending channels.

#### *1.2.4. Unit 5d*

Unit 5d deposits (Figs 2b, 3 (log 4) and 4d) are mainly organic, shelly, grey structureless silts overlying a basal, pebbly clast-supported gravel, contained within a well-defined channel form (channel D, Fig. 2b). The deposits appear to represent the silting-up of a river channel during an interval of low-energy discharge following high-energy incision or possibly following channel abandonment in a high water table setting. In addition to the basal lag gravel, there appear to be signs in the marginal sequence of minor slumping events causing the deposition of coarser sediments from the channel sides.

## **2. Methods**

In general, field sampling methods involved collecting in September 2003 separate bulk samples of 10–12 kg field weight from fossiliferous beds in each of the units investigated (Figures 3–5) for analyses of molluscs and subfossil beetles; separate smaller bulk samples and samples in plastic tubes 75 mm long by 15 mm diameter were collected at the same time for ostracod and pollen analyses, respectively. More specific details are provided below.

A single bulk sample for beetle analysis, a smaller bulk sample (> 300 g) for ostracod analysis and a pollen sample were collected from an organic mud clast in unit 1a. Pollen samples were also collected from a fossiliferous silt bed above the organic mud clast and from a pocket of structureless mud at the base of the sequence.

For the mud beds of unit 1c[WF] two bulk samples were collected for beetle analysis, a small bulk sample of about 1 kg field weight for mollusc analysis, a smaller bulk sample of about 500 g field weight for ostracod analysis and a single sample for pollen analysis were collected.

Four bulk samples were collected from the top of unit 3a: two of these were analysed for subfossil beetles and a subsample of about 500 g of one of the others was used for ostracod analysis, with the remainder plus the other bulk sample being used for mollusc analysis. Specimens picked from the mollusc samples supplemented the ostracod sample, as well as a small subsample (ca. 100 g) of the  $\geq 250 \mu\text{g}$  fraction.

A bulk sample for beetle analysis and a stratified sequence of three small bulk samples each weighing about 2 kg field weight for mollusc analysis were collected from the basal gravel and overlying 10 cm of organic mud of unit 5d. A vertical sequence above the basal gravel of seven samples was collected for pollen analysis. A

subsample ( $\leq 200$  g) of a small bulk sample ( $\sim 600$  g) collected in 2012 was used for ostracod analysis. Small bulk samples of about 1 kg were collected in 2012 from each of the units 5c and 5d for analysis of plant macrofossils. The ostracod and plant macrofossil samples from unit 5d were collected a few metres to the west of the pollen, mollusc and insect samples, about 50 cm above the top of the basal gravel.

Volumetric  $1\text{ cm}^3$  pollen samples were prepared using the standard hydrofluoric acid technique, and counted for pollen using a high-power stereo microscope at  $\times 400$  magnification, with  $\times 1000$  used for critical determinations.

Mollusc samples from units 1c[WF] and 5d were washed through 2 mm, 1 mm and 500  $\mu\text{m}$  sieves and shells were picked by eye or under a binocular microscope at  $10\times$  magnification. The total counts of species follow the conventions of Sparks (1964), where each gastropod apex counts as one individual and each intact bivalve hinge counts as half an individual. The taxonomy follows Kerney (1999), Killeen et al. (2004) and Cameron (2008) for current British species and Gittenberger et al. (1998) for species no longer found in Britain. For these samples the nomenclature used by J. Merry and the late Professor D. H. Keen in Langford et al. (2004b, 2007, respectively) has been changed, where appropriate, in accordance with the revision of Mollusca by Anderson (2010). The mollusc samples from unit 3a were processed by HEL in the same way as above, but the counts reported are not finalized for reasons explained in the table footnotes. Environmental preferences and geographical distributions of the molluscs are based on Kerney (1999) and Killeen et al. (2004).

Beetle fossils were extracted using the standard technique described by Coope (1986): beetle remains were recovered by wet sieving over a mesh size of 0.3 mm, concentrated using the standard kerosene flotation method and sorted under a binocular microscope. The taxonomy is based on Lucht (1987), as revised by Böhme (2005) and Gustafsson (2005). Counts listed against each taxon indicate the minimum number of individuals (MNI) in each sample(s). Species habitat information was obtained from the BugsCEP database (Buckland and Buckland, 2012).

The ostracod samples (one of which yielded foraminifera) were processed as follows. First they were dried in an oven and then soaked in hot water for several hours, with a little sodium carbonate added to aid breakdown. Washing took place through a 75  $\mu\text{m}$  sieve with hand-hot water, before the remaining residues were decanted back to their bowls for drying in the oven. Their identification and environmental preferences are based on Meisch (2000) and other sources listed in the text.

Temperature estimates were calculated with the coleopteran Mutual Climatic Range (MCR) method (Atkinson et al., 1987) using the BugsMCR function of the BugsCEP database (Buckland and Buckland, 2012), to calculate TMAX (July temperature) and TMIN (January temperature) for each sample investigated: TRANGE determines the level of continentality. The MCR method enables reconstructions of the thermal palaeoclimates to be quantified using carnivorous and scavenging beetle species with food requirements that are independent of particular macrophytes or terrestrial plants. The Mutual Ostracod Temperature Range (MOTR) method (Horne, 2007; Horne and Mezquita, 2008) measures mean January (coldest month), mean July (warmest month) and mean annual air temperatures. For the MOTR the most up-to-date (unpublished) calibrations were used, based, where possible, on combined datasets from the Ostracod Metadatabase of Environmental and Geographical Attributes (OMEGA: Horne et al., 2011) and differ in some cases from those published by Horne (2007) and Horne and Mezquita (2008).

### 3. Results

#### 3.1. Palaeobotany

##### 3.1.1. Pollen and spores

Pollen has been analysed from three samples of unit 1a, taken from a large silty clay rip-up clast, an organic silt bed and a pocket of structureless mud (Fig. 3, log 1). The sample from the rip-up clast had a pollen assemblage dominated by grass and spores, but including 8% pine. The organic silt-bed sample had a similar assemblage, but with pine (17%) and birch (7%). Pollen preservation in these two samples was not particularly good, although pollen concentrations were 43 000 and 107 000 grains  $\text{g}^{-1}$ , respectively. The sample from the pocket of structureless mud produced an impoverished pollen signal dominated by grass (55.6%), with spruce (22.2%), herbs and lower plant spores: aquatic plants were represented by the pollen of the emergent aquatic bur-reed (*Sparganium erectum*). Given the low main sum (18) and the low concentration (4801 grains  $\text{g}^{-1}$ ), extreme caution should be exercised in interpreting the assemblage from this sample.

Combined, the sequence of samples from unit 1a appears to represent pre-temperate conditions (*sensu* Turner and West, 1968), and could be interpreted as an open grassland environment with scattered boreal woodland, but the presence of tree pollen can be misleading in such assemblages (see section 4.1). Although there is some evidence for tall-herb communities, overall the pollen suggests a moderately harsh glacial environment during the deposition of unit 1a.

A sample from the organic-rich bed at the top of unit 1c[WF] (Fig. 3, log 2) yielded a total count of 110, which was reported by Langford et al. (2007, unit F1). The count was dominated by grass pollen (40.2%) and pine (31.8%), with a range of herbs (Cyperaceae, 4.5%; Apiaceae, 0.9%; Brassicaceae 1.8%; *Helianthemum*, 1.8%; *Plantago lanceolata*, 3.6%), aquatics (*Sparganium erectum*, 4.2%; *Typha latifolia* type, 2.5%) and lower plants (undifferentiated Pteropsid (trilete) spores, 1.8%; undifferentiated Pteropsida (monolete) spores, 13.6%). This assemblage represents pine stands within grassland with tall-herb communities, riparian and disturbed habitats and emergent vegetation at the water's edge. The pollen concentration in the sample was relatively high (78 000 grains  $\text{g}^{-1}$ ) and the palynomorphs were moderately well preserved.

As with unit 1a the pollen spectrum from unit 1c[WF] appears to represent pre-temperate conditions (*sensu* Turner and West, 1968), and although the presence of tree pollen again should be treated with caution, > 30% pine represents quite an emphatic signal and therefore its local presence should not be discounted. Taken together the pollen assemblage suggests a cool, but perhaps not harsh, glacial environment.

Pollen and charcoal were analysed from seven levels (16, 45, 75, 105, 135, 165 and 195 cm) within unit 5d (Figs 3 (log 4) and 5). The sequence was dominated by grass pollen ( $\geq 55$ –75%) with pine (10–20%) and spruce (2–5%). Other sparse arboreal taxa present include birch, oak, hazel, willow and juniper. A variety of herbs, spores and aquatic plants were also present. Pollen concentrations were moderate to high (70 000–250 000 grains per  $\text{g}^{-1}$ ), and charcoal concentrations were elevated (4–8  $\text{cm}^2 \text{cm}^{-3}$ ) suggesting extensive regional burning.

The sequence from unit 5d represents an open grassland environment with scattered boreal woodland (but see above comments) and juniper scrub. Tall-herb, riparian and marginal vegetation are also indicated locally. The inferred vegetation is post-temperate or interstadial in character, and the presence of tiny quantities of oak

and hazel pollen is not significant enough to suggest temperate conditions. The presence of spruce (*Picea*) is sometimes taken as a characteristic feature of interstadials within the Early to Middle Devensian in southern Britain (cf. Chelford Interstadial; Rendell et al., 1991).

### 3.1.2. Plant macrofossils

Seeds extracted during picking of molluscs from the samples of unit 3a (Fig. 3, log 3) by HEL included *Potamogeton* sp. (142), *Zannichellia palustris* (2), *Carex* triconvex-type (6), *Carex* biconvex-type (37), *Potentilla* sp. (10), *Ranunculus* sp. (32), *Scirpus* sp. (20) and *Armeria maritima* (11).

A small bulk sample collected from unit 5d (Fig. 3, log 4) in November 2012 yielded *Potamogeton* sp. (7), *Zannichellia palustris* (1), *Carex* triconvex-type (2), *Carex* biconvex-type (2), *Potentilla* sp. (1), *Ranunculus* sp. (2) and *Scirpus* sp. (1).

A further bulk sample collected from unit 5c (Fig. 3, log 4) in November 2012 yielded *Potamogeton* sp. ?natans (13), *Carex* triconvex-type (20), *Carex* biconvex-type (24), *Potentilla* sp. (6), Caryophyllaceae (1) and Cyperaceae (3).

It is not possible to say much about the palaeobotany from such a sparse species list. However, with that caveat, all the taxa recorded here are characteristic of cold-stage floras (Godwin, 1975; West, 2000). Aquatic environments are clearly common (and, in the case of unit 3a, dominant), as seen by the presence of *Potamogeton* sp., *Ranunculus* sp., *Zannichellia palustris* and *Scirpus* sp. The presence of *Carex* (both biconvex- and triconvex-type), which typically colonize damp ground on the edge of water bodies, grassland species such as *Potentilla* sp. and herbs such as *Armeria maritima* in unit 3a shows that a continuum of environments was present. *Armeria maritima* indicates high rates of evaporation, probably due to increased windiness (West, 2000).

## 3.2. Palaeozoology

### 3.2.1. Mollusca

Langford et al. (2007, unit F1) reported the molluscan fauna from a small bulk sample of unit 1c[WF] (Fig. 3, log 2): it was entirely fluvial in character (Table 2), with the exception of the single fragment of the terrestrial gastropod *Azeca goodalli*. *Valvata piscinalis*, the most abundant species in the sample, prefers relatively deep, moving water and is described by Meijer and Cleveringa (2009) as a fluvio-lacustrine species. Deep, moving water is also preferred by *Pisidium amnicum* and *Pisidium henslowanum*. *Pisidium subtruncatum* prefers running water and *Pisidium nitidum* well-oxygenated sediments; both avoid swampy environments and places prone to desiccation. *Bithynia tentaculata* also prefers deep, moving water but requires aquatic vegetation. The low number of *B. tentaculata* in the sample, compared with *V. piscinalis*, may indicate reworking from an earlier deposit, or that aquatic vegetation was rare, as suggested by the lack of Planorbidae in the sample. In contrast to the moving water preferences of the above, *Sphaerium corneum* and *Pisidium casertanum* can be found in a full range of aquatic habitats, including stagnant pools and ditches. The latter, together with *Galba truncatula*, an indicator of marsh or muddy bankside habitats, also can be found in habitats subject to drying out.

The fluvial species in this assemblage occur commonly throughout Europe at the present day, with *B. tentaculata* extending to western Siberia and Kashmir. They therefore can tolerate a wide range of temperature, with *P. nitidum* and *P. casertanum* today found at 490 m and over 1000 m altitude, respectively. Some restriction on geographical distribution, and hence climatic conditions, may be offered by the

presence of *P. henslowanum*, which at present does not reach the Arctic Circle, *S. corneum* and *V. piscinalis*, which are rare in northern Scandinavia, and *P. subtruncatum*, which at present is scarce in the Mediterranean region. There is every possibility that the fragment of *A. goodalli* was reworked from an earlier temperate deposit, because in continental Europe it is today found from central Germany to the Pyrenees, and it is widespread but sporadic in England at present, being rare in Scotland and western Wales (Kerney, 1999).

Preliminary molluscan data for unit 3a (Fig. 3, log 3) have *V. piscinalis*, *G. truncatula*, *S. corneum*, *P. casertanum* and *P. subtruncatum* (Table 2) in common with unit 1c[WF] and they therefore share the same ecological characteristics in terms of these species. In contrast, *Pupilla muscorum*, a dominant component of the unit 3a assemblage, is a terrestrial gastropod that favours dry, open, calcareous habitats; however, in Late Pleistocene glacial contexts it can be found in marshland deposits (Briant et al., 2004a). In contrast again, *Valvata cristata* and *Gyraulus laevis* prefer clean, quiet-water conditions. *Gyraulus crista* also prefers quiet-water conditions and *Anisus leucostoma* and *Pisidium obtusale* prefer standing or stagnant water away from the main channel. The former can tolerate habitats that dry out in the summer. *Radix balthica* inhabits small water bodies, including non-permanent pools. Overall, the molluscan assemblage represents a quiet-water setting distal to the main channel that periodically received an influx of floodwaters carrying species from the main channel and intervening marsh and terrestrial habitats. The presence of only *P. muscorum* amongst the land species indicates either a very impoverished land fauna or specific hydrodynamic conditions.

*Belgrandia marginata* is an exotic species that today inhabits pristine calcareous springs in northern Spain and southern France (Keen et al., 1999). This single specimen, like the *Bithynia* opercula, and possibly the *G. crista* and Cochlicopidae, has most probably been reworked from the earlier, temperate, MIS 7 sediments of unit 2 (Fig. 3, log 1; Langford et al., 2004a, 2007, this issue).

Climatically the Mollusca of unit 3a represent similar conditions to those of unit 1c[WF]. Although common in lowland settings of northwest Europe, *P. obtusale* also occurs at high altitudes (700 m) in the Scottish Highlands at present, and the northern limit may be reinforced by the presence of *A. leucostoma*, which at present does not occur above 63° latitude in Sweden. The significant presence of *P. muscorum* may be instructive from a climatic point of view because it is prevalent in Devensian cold-stage molluscan assemblages (Holyoak, 1982).

The ecological preferences of most species in the molluscan fauna of unit 5d (Fig. 3, log 4) are described above for units 1c[WF] and 3a. In addition, both *Planorbis planorbis* and *Pisidium milium* (Table 2) have a preference for quiet-water conditions, and both *Pisidium supinum* and *Pisidium moitessierianum* prefer slowly moving, well-oxygenated water bodies. The terrestrial gastropod *Vallonia pulchella* is a riverside species, found for example in water meadows and marshes. The molluscan assemblage as a whole represents a quiet-water setting with influxes of species from riverside habitats and from a slowly moving water body in the main channel. As in unit 1c[WF] the low percentage of *B. tentaculata* relative to *V. piscinalis* and opercula could represent reworking or a lack of aquatic vegetation, as suggested by the low percentages of Planorbidae. All of the species present in the unit 5d assemblage also are present in the earlier Ipswichian channel C assemblage (Fig. 2b; Langford et al., 2004b) and therefore the reworking of some specimens cannot be ruled out.

Climatically the unit 5d assemblage is similar to units 1c[WF] and 3a, but the presence of *P. supinum* could be of interest because in Europe today it occurs mainly in lowlands between the Alps and southern Scandinavia (to 60°N).

### 3.2.2. Beetles

The coleopteran fauna from a boulder-sized rip-up clast, in unit 1a (Fig. 3, log 1), of reworked laminated organic mud and silt with abundant wood fragments is small (27 MNI, 16 species; Table 3).

*Bembidion guttula* is a riparian species, usually associated with moist clay or clay-mixed soil with rich waterside vegetation (Lindroth, 1963; 1974), while *Helophorus orientalis* is associated with temporary, grassy pools. Its modern distribution covers distinctly northern areas of Russia and Siberia (south of the Arctic), whereas in southern Canada and northern USA it has a considerably more southern distribution (Angus, 1973). It is typical of cold, continental, tundra conditions, as is *Helophorus obscurellus*, a terrestrial species found under stones and vegetation in sandy places; today, it is distributed from Cape Kanin in northwest Russia, the mountains of central (Middle) Asia and the northern part of the Tibetan Plateau (R. Angus, pers. comm., 2013). There are no other aquatic species present. A small assemblage of rove beetles and weevils suggests wet, marshy conditions with sedge vegetation (*Carex* spp., *Juncus* spp.). *Platystethus cornutus* suggests exposed mud and sand (Koch, 1989). Drier, herb-vegetation is also indicated (e.g. *Cryptocephalus* sp., *Chaetocnema* sp), while the polyphagous *Otiorhynchus politus* is a montane to high alpine taxon (Koch, 1992) found in high regions of central Europe. Grazing animals may have been present (indicated by, e.g., *Aphodius* spp), while the rove beetle *Tachinus furcatus* indicates all types of rotting material, such as plant litter and moss. Today, this is an eastern species, found in the Russian Tuva Republic (M. Schülke, pers. comm., 2013), and the mountains of Mongolia, south of Ulan Bator, between 1150 and 2000 m a.s.l., where it can often be found in birch woodland (Ullrich, 1975). Taken together, this assemblage suggests a landscape of temporary pools fringed by wetland vegetation with areas of bare mud and sand. Drier, herb-vegetation probably characterized the areas further away from the site deposition. There are no species associated with trees. The low number of water beetles present is worth highlighting, especially as *H. orientalis* is typical of temporary rather than permanent pools. This suggests that conditions were dry and that there was not extensive winter snow melt that gradually melted over summer. Lack of moisture probably explains this situation, possibly the result of a prevailing easterly airstream, thus allowing species that today live in cold, continental areas of Siberia to thrive this far west (cf. Angus, 1973). In this context, it is important to note that this deposit includes four 'non-British' taxa (*H. obscurellus*, *H. orientalis*, *T. furcatus* and *O. politus*), all of which are typical of cold, dry, continental climatic conditions.

The beetle fauna of unit 1c[WF] (Fig. 3, log 2) reported in Langford et al. (2007, unit F1) was recovered from a sample that had already been sorted for molluscs. Two bulk samples specifically processed for insect fossils are reported here. Their richness compared with the previously reported fauna is undoubtedly a result of this different approach: 231 MNI were recovered from c. 82 Coleoptera taxa, of which 47 could be identified to the species level, and of these, 12 are no longer living in the British Isles (Table 3).

The assemblage is dominated by Carabidae (ground beetles), Staphylinidae (rove beetles) and aquatic taxa of the Dytiscidae (diving beetles), Hydraenidae (small aquatic beetles) and Hydrophilidae (water scavenger beetles) families – indicative of

marshy, shallow, or quiet-water habitats (e.g. *Helophorus* spp, *Nebrioporus depressus*, *Coelambus impressopunctatus*) – being well represented. Several species are typical of cold conditions, at least during the winter, such as *Colymbetes paykulli*, found in small stagnant water bodies, often in cold *Sphagnum* bogs or small stagnant water bodies in forests (Nisson and Holmer, 1995), and *Colymbetes dolobratus*, found in alpine and subalpine habitats, often at higher altitudes (above 1000 m), in pools usually rich in vegetation (Lindroth, 1973; Böcher, 1988). Its modern distribution is distinctly northern, including Greenland, Iceland, northern Scandinavia, northern Russia, northern Siberia, Alaska and Labrador; notably, the species hibernates in lakes that do not freeze to the bottom (Böcher, 1988). *Helophorus praenanus* is well known from Devensian and Wolstonian deposits (Angus, 1973). Its modern distribution in eastern Siberia is suggestive of quite warm summers and very cold winters (R. Angus, pers. comm., 2013). Mildly basic environmental conditions are indicated by the reed beetle *Plateumaris sericea*, the larvae of which spin cocoons in rhizomes and roots of *Typha latifolia* L., *Iris pseudacorus* L., *Schoenoplectus lacustris* L., *Bolboschoenus maritimus* L. and *Sparganium erectum* L. (Stainforth, 1944), as well as on *Carex* and *Nuphar* species (Bullock, 1993). *Macrolea appendiculata* indicates *Potamogeton* and *Myriophyllum* spp (Hyman 1992), habitats also suitable for *Notaris bimaculatus* and *N. aethiops*. Of particular note is the halotolerant *Ochthebius lenensis*, a beetle that is commonly associated with brackish, saltmarsh conditions (Hansen, 1987; Foster, 2000). Halotolerant taxa are able to survive in saline/brackish habitats, but are not exclusively saline obligates, with modern distributions most likely a reflection of relict habitats, differing dispersal abilities and an ability to exploit recently exposed soils and sediments. Several halotolerant species commonly occur in Late Glacial and interstadial deposits, probably reflecting cryoturbated or immature, soils or exposed clay habitats (Coope et al., 1961; P.C. Buckland, pers. comm., 2013). Brackish conditions could have occurred in pools developed on the bedrock (cf. Lewis et al., 2006): the underlying Oxford Clay (Jurassic) has suitable mineralogical content (Hudson and Martill, 1994).

Amongst the ground beetles are several that indicate open conditions, with a preference for sandy gravelly soil (*Notiophilus aquaticus*, *Clivina fossor*, *Dyschirius thoracicus*, *Patrobis assimilis*). Many beetles are typical of sandy bank and wet, river-side conditions (e.g. *Bembidion bipunctatum*, *Bembidion aeneum*, *B. guttula*), while *Dyschirius septentrionum* occurs in clayey or muddy sites with *Juncus*, *Carex*, *Equisetum* spp. (Lindroth, 1985). It is a distinctly northerly species, being found in Sweden, Norway, Finland and Russia. There are a wide range of species associated with rotting, organic litter debris (*Cercyon tristis*, *Omalium excavatum*, *Olophrum boreale*, *Eucnecosum brachypterum*, *Geodromicus kunzei*, *Platystethus cornutus* and *Tachinus furcatus*) indicating an abundance of wet litter and vegetation. Species associated with plants and grasslands are also relatively well-represented, with Curculionidae (weevils), Chrysomelidae (leaf beetles) and Scarabaeidae dung beetles. *Nephus bipunctatus* suggests shrubs and leaf litter (Koch, 1989), perhaps from dwarf birch: the arctic ladybird *Hippodamia arctica* is often found in *Betula nana*-rich *Empetrum* heath in northern Europe (Finland, Sweden) and the Caucasus (Brundin, 1934). Areas of grassland and dry heathland area are suggested by *Apion* spp., *Otiorhynchus politus* (Koch, 1992), *O. ovatus* – which is often found at heather roots and *Helianthemum* spp (Hoffman, 1950) – while *Strophosoma faber* is usually in species-rich grassland and heathland at the roots of *Rumex acetosella* L. (sheep's sorrel) and other heathland taxa (Hyman, 1992).

The assemblage as a whole suggests small water bodies colonized by plants such as *Potamogeton* or *Myriophyllum* and an abundance of marginal vegetation and build-up of wet litter dominated the local environment. Areas of grassland and dry heathland dominated the wider landscape, with perhaps occasional patches of shrubby dwarf birch. Small numbers of dung beetles suggest the presence of grazing animals in the wider landscape. Several cold-climate beetles, many of which are Asiatic in origin, suggest dry, continental conditions with winter temperatures that were cold, although not of truly arctic severity, whereas summers may have been relatively warmer.

The coleopteran fauna (Table 3) of unit 3a (Fig. 3, log 3) includes 185 MNI, across approximately 53 species. Carabidae, Hydraenidae, Staphylinidae and Curculionidae dominate the assemblage as a whole, suggesting marshy bankside habitats beside still, well-vegetated water habitats (e.g. *Ochthebius dilatatus*, *Helophorus grandis*, *Helophorus splendidus*, *Colymbetes dolobratus*). Areas of sandy, exposed places nearby are indicated (e.g. *Helophorus obscurellus*). Abundant vegetation and plant litter are indicated by the plant-eating weevils as well as the rove beetles *Pycnoglypta lurida*, *Olophrum fuscum*, *Eucnecosum brachypterum* and *Gymnusa variegata*, all of which are found in damp vegetation litter. Grazing animals are suggested by the comparatively high numbers of *Aphodius* spp. Dung also provides a food source along with other rotting plant litter for *Platystethus* spp., *Tachinus* spp. and *Anotylus nitidulus*. Dry places were available in the landscape (e.g. *Notiophilus aquaticus*, *Dyschirius thoracicus*, *Nethus (Scymnus) bipunctatus*, *Amara quenseli*, *Simplocaria semistriata*), with *Otiiorhynchus arcticus* being typical of fairly dry, mixed heath with *Empetrum* and *Vaccinium*. *Boreaphilus hennianganus* is found in areas of wet heath and grassland, in wet moss and under damp plant litter, often close to the snowline; today, it is considered a glacial relict in central Europe (Lohse, 1964). Of interest is *Anthicus ater*, which today is a species of the sandy seashore, found under rotting seaweed and vegetation, but it is not exclusively associated with coastal areas (Koch, 1989), as well as several halotolerant *Ochthebius* species (*O. dilatatus*, *O. lenensis*). As noted above, the presence of these halotolerant species does not necessarily imply brackish conditions.

As with unit 1c[WF], the beetle fauna indicates a marshy landscape of pools fringed by vegetation with areas of bare mud and sand, with no indication for the presence of trees, and areas of dry and wet heath. Grazing animals appear to have made good use of the landscape. Several beetles are indicative of very cold conditions (*Colymbetes dolobratus*, *Pycnoglypta lurida*, *Boreaphilus hennigianus* and *Helophorus obscurellus*). The cold stenotherm *Helophorus splendidus* is virtually confined to arctic coastal plains of Siberia and western Canada (Angus, 1973). It is likely that conditions are similar to those represented by the previous unit, although conditions in winter may have been more arctic in character.

A bulk sample of sandy organic silt weighing about 10 kg was taken from unit 5d (Fig. 3, log 4). Although the individual skeletal elements of the beetles were rather fragmentary their preservation was good, yielding an abundant assemblage of 252 MNI, across approximately 72 species (Table 3). The local environment was predominantly aquatic, reflecting the large numbers of *Helophorus* and Dytiscidae, suggesting a variety of open and vegetation-rich habitats. *Helophorus aspericollis* is found in some abundance and is today restricted to eastern Siberia and Mongolia, where it appears in shallow grassy pools (Angus, 1973). The pond could have been flooded occasionally because of the rare presence of the larvae of the caddisfly *Hydropsyche contubernalis*, which is a river species. The immediate surroundings

were probably largely made up of reedy vegetation (*Carex* or similar plants) but there was also some sandy bare ground where *Heterocerus* sp. could burrow. Rather clayey soils must also have been available for *Bembidion aeneum*. On the drier ground away from the water's edge, the vegetation was largely made up of weedy plants. The larvae of *Sitona* feed on the roots of various species of Papilionaceae. *Phaedon pyritosus* is a monophage feeding on *Ranunculus repens* L., while *Galeruca tanacetii* feeds on Compositae, mostly on *Tanacetum vulgare* L. (Koch, 1992). *Chrysolina marginata* is associated with yarrow, *Achillea millefolium* L., as well as sea plantain, *Plantago maritima* L. (Hyman, 1992). Dry conditions are indicated by *Chrysomela septentrionis*, which today lives in polar desert conditions in Russia (Makarova et al., 2007). The large number of dung beetle *Aphodius* spp. indicates large herbivorous mammals. *Thanatophilus dispar* is found in carcasses where it is probably a predator on other arthropods. Of some biogeographic note is the presence of the Tibetan dung beetle, *Aphodius holdereri*, which is today restricted to the Tibetan Plateau, where it can be found in yak dung. Modern specimens are found in a region underlain by permafrost, with both moist and dry substrates and patchy grassland (Morgan, 1997).

Climatically, this fauna indicates cold, dry conditions. The presence of a number of exclusively Asiatic species is noteworthy: the most abundant species, *Helophorus aspericollis* is now confined to eastern Siberia. The fauna as a whole suggests that the climate was very continental.

### 3.2.3. Ostracoda and Foraminifera

The ostracod fauna of unit 1a (Fig. 3, log 1) is freshwater in character and dominated by *Ilyocypris gibba* (41%; Table 4), which lives in shallow permanent water bodies with a muddy substrate. *Candona candida*, which prefers cool water (lakes as well as springs and ponds connected to springs), and has a high tolerance of eutrophication, is also numerous (34%). *Cycloocypris ovum* also has a significant presence (22%), while there are a few specimens of *Limnocythere inopinata* (2%) – both these species have a wide tolerance in almost all aquatic environments. The final species – *Leucocythere batesi* – is extinct, being known in cool/cold stages of the Pleistocene between the Hoxnian/Holsteinian ('Arctic Bed') and the Devensian/Weichselian (Whittaker and Horne, 2009).

As in unit 1a the ostracod fauna of unit 1c[WF] (Fig. 3, log 2) is dominated by *C. candida* (28%) and *I. gibba* (30%) (Table 4), with *C. ovum* again being a significant component (17%). Of the remaining four species, *Herpetocypris reptans* is present in significant numbers (17%), whereas *Candona neglecta* (5%), *Fabaeformiscandona caudata* (2%) and *Eucypris pigra* (1%) form minor components. Of these latter the ecology of *H. reptans* is perhaps the most well known, being found in permanent water bodies rich in vegetation with a muddy bottom. Limnocytherids, this time, are totally absent from the faunal assemblage.

The most interesting ostracod assemblage comes from unit 3a (Fig. 3, log 3), listed in Table 4. *Candona candida* and *I. gibba* are again present in significant numbers. In contrast *Cycloocypris* has not been identified to species level, being present but only in low numbers (3%). *Leucocythere batesi* is present, as in unit 1a, and as in unit 1c[WF] *H. reptans* and *C. neglecta* are present, the latter in significant numbers (10%). The importance of the fauna, however, lies in two factors: the strength of the cold/cool component and, uniquely in the present study, of a brackish component evidenced by the occurrence of *Cyprideis torosa* (6%) and several estuarine species of foraminifera. *Fabaeformiscandona levanderi* (6%), *Limnocytherina sanctipatricii* (13%), *Juxilyocypris schwarzbachi* and *Amploocypris*

*tonnensis* (3%) are all significant finds. *Fabaeformiscandona levanderi* is not part of the present British fauna and today it occurs mainly in northern and eastern Europe. *Limnocytherina sanctipatricii*, although part of the present-day fauna, is characterized by Meisch (2000) 'as [an] indicator of cold water'. Both *J. schwarzbachi* and *A. tonnensis* became extinct in Britain in the Devensian and are cold/cool indicators (Whittaker and Horne, 2009). Recently, Van der Meeren et al. (2009) have found *A. tonnensis* living in central Asia, suggesting a restriction to high-altitude, cold environments; the known Pleistocene records from western Europe, however, suggest a much wider distribution during cold periods. Today, it seems ecologically to be found mainly in shallow running waters.

It is true that *C. torosa* is sometimes found in inland lakes some distance from the sea, albeit saline and/or almost fresh water. However, also present in unit 3a are the estuarine foraminifera *Elphidium williamsoni*, *Elphidium macellum*, *Elphidium clavatum*, *Elphidium albiumbilicatum*, *Haynesina germanica*, the dwarfed form of *Ammonia batavus*, *Cassidulina reniformis* and *Elphidium* sp. Foraminifera do not live in freshwater. Moreover, *E. clavatum*, *E. albiumbilicatum*, and especially *C. reniformis* and the dwarfed *Ammonia*, are all indicative of cold/cool conditions. They are either reworked (as with the *C. torosa*) but from where (?), or this is clear evidence of a tidal connection through an estuary close by, or brought in by tidal surges at a time of high sea-level.

Unit 5d (Fig. 3, log 4) has an ostracod fauna characterized by *C. neglecta* (21%; Table 4), *F. levanderi* (23%), *C. ovum* (18%), *Ilyocypris monstifrica* (12%) and *H. reptans* (9%). The species *I. gibba* and *C. candida* are also present but in insignificant numbers, in contrast to the unit 1a, 1c[WF] and 3a assemblages. *Limnocythere inopinata* and *E. pigra* are also present, as in units 1a and 1c[WF], respectively, but again in low numbers. *Ilyocypris monstifrica* is unique to this assemblage, as are *Cypria ophthalmica* (5%), *Prionocypris zenkeri* (2%) and *Psychrodromus olivaceus* (5%). Meisch (2000) describes *I. monstifrica* as 'an active swimmer that prefers stagnant and slowly flowing muddy-bottomed waters where it is found moving above the substrate or amongst aquatic vegetation'. These sediments, perhaps particular to this site, were laid down in a slow-flowing, often stagnant water body, rich with vegetation.

#### 3.2.4. Vertebrates

A number of significant surface finds are associated with unit 5d, including a well-preserved right unciform and metapodial of *Coelodonta antiquitatis*, seven associated upper molars of *Equus ferus*, a left deciduous M4 of *Mammuthus primigenius* and three elephant rib midshaft fragments, and a lower molar of a large bovid. These large-vertebrate remains indicate a predominantly open environment with rich grazing.

#### 3.3. Palaeotemperature estimates

The coleopteran MCR and MOTR palaeotemperature ranges for TMAX July and TMIN January are shown in Table 5 and Fig. 6. Species used for the MOTR and their calibrated temperature ranges are provided in Table 6, and species used in each unit for the MCR are shown in Table 7. Among the ostracods *C. torosa* and *I. gibba* were omitted due to lack of calibration and taxonomic uncertainty respectively. *Juxilyocypris schwarzbachi* and *L. batesi* cannot be calibrated because they are extinct, but both are considered to be cold-climate indicators by association with other cold-climate fauna. *Amplocypris tonnensis*, also regarded as a cold-climate indicator,

has been calibrated but only on the basis of a very few records and when included it does not have a mutual range with all other taxa in the assemblage; accordingly it has been omitted from the MOTR application, but its significance as a cold-climate indicator is noted.

Also recorded in Fig. 6 are the numbers of species (NSPEC) used in each temperature reconstruction. Higher numbers of species used in an MCR reconstruction create more robust temperature reconstructions. Units 1c[WF], 3a and 5d have particularly high NSPEC values, indicating that a good proportion of the assemblage has been used in the MCR reconstruction. These indicate that the reconstructions associated with these units are probably more refined. Unit 1a, on the other hand, is based on just two taxa and this reconstruction should be treated with greater caution, representing a conservative estimate of temperatures. It is worth highlighting that several of the cold, continental taxa from this unit (discussed above) do not (at present) have MCR envelopes associated with them and thus could not be used in the temperature reconstruction. It is thus likely that unit 1a was associated with much cooler, continental conditions than the MCR might at first suggest. The TRANGE values for this unit hint at this high degree of continentality.

Also recorded in Fig. 6 for the coleopteran temperature reconstructions is the percentage overlap. With the exception of unit 1a, with 100% overlap, the other assemblages do not display 100% MCR overlap, varying between 72 and 88%. This means that there is a mixture of species with different climatic tolerances within these assemblages and/or the presence of several species with an envelope that requires further revision. It is likely that in this case both these comments hold true and certainly the latter in particular. With the exception of the case of *A. tonnensis* discussed above, all of the ostracod assemblages used in the MOTR analyses showed 100% overlap, that is they all had a mutual range, with no outliers.

The two methods yielded broadly consistent results for units 1a, 1c[WF] and 3a, permitting more tightly constrained palaeotemperature estimates to be derived from the overlapping or 'mutual mutual' ranges (in other words, the ranges of temperatures within which both the ostracod and coleopteran taxa could have coexisted). For unit 1a the present-day values for Whittlesey fall within the mutual mutual ranges. Substantially cooler than present-day climate is indicated for unit 1c[WF], by at least 3°C in both July and January. Somewhat cooler than present-day climate is indicated for unit 3a, by at least 1°C in July and at least 2°C in January.

For unit 5d, however, there are major differences between the palaeotemperature ranges derived from Coleoptera and Ostracoda, with no overlap. The coleopteran MCR results are indicative of summers at least 4°C cooler than today and harsh winters at least 15°C colder. The MOTR results, on the other hand, point to somewhat warmer climate and suggest a climatic amelioration during the infilling of the channel, with summers not dissimilar to today's (although with winters at least 2°C colder). Possible explanations for this discrepancy are discussed below.

## 4. Discussion

### 4.1. Palaeoecological synthesis

Cool/cold stage fossil assemblages are generally characterized by their restricted fauna/flora, mostly encompassing species tolerant of a broad temperature range, and by the occasional presence of exotic cold obligate species. Cool/cold climatic conditions are recorded, to a greater or lesser extent, by each of the unit 1a, 1c[WF], 3a and 5d fossil assemblages, but this is more apparent in the insect and ostracod faunas because they contain cold obligate species, except for the ostracod

fauna of unit 5d. In contrast to the beetle and ostracod faunas, and to many (e.g. West, 1991; Briant et al., 2004a; Lewis et al., 2006), but not all, of the Devensian/Weichselian cool/cold fossil assemblages reported, the pollen, plant macrofossil and molluscan assemblages of units 1a, 1c[WF], 3a and 5d do not include cold obligate species, albeit that their restricted assemblages do indicate cool or cold conditions.

Although the individual depositional settings are different, the sediments sampled from units 1a, 1c[WF], 3a and 5d were deposited under low-energy regimes; the assemblages are essentially freshwater in character, but unit 3a additionally has components suggestive of a brackish water, possibly estuarine, environment. This low-energy depositional environment is reflected by the palaeontological evidence, which largely indicates permanent and non-permanent quiet-water habitats rather than higher energy moving-water habitats. Essentially the different strands of palaeontological evidence broadly paint the same ecological picture for each of the fossil assemblages: a continuum from low-energy permanent to non-permanent aquatic habitats through marshland with associated waterside taxa, together with flood influxes of fluvial, riparian and ruderal taxa. Additionally, certain components of the ostracod assemblages in units 1c[WF] and 5d suggest the proximity of springs or spring-fed seepages.

An exception is the molluscan fauna of unit 1c[WF], which is more fluvial in character in contrast to the insect and ostracod faunas, and probably reflects flood influxes in a stabilized bar-top setting. Similarly there need be no conflict between the evidence for trees in the pollen data and for the lack of trees in the other lines of evidence, because there might have been only a sparse presence of trees at some distance from the channel in ameliorated pockets in the catchment, or the tree pollen could represent long-distance transport or, especially if accompanied by high values of pre-Quaternary palynomorphs from underlying bedrock, reworking of earlier deposits (e.g. West et al., 1999; Briant et al., 2004a).

This dominance of low-energy permanent and non-permanent aquatic habitats is also evident in the Lapwing Bed (Worsley et al., 1983) fossil assemblage, as well as at Latton (Lewis et al., 2006), Lynford (Boismier et al., 2012), Whitemoor Haye (Schreve et al., 2013) and Stanwick (Briant et al., 2008). In contrast, the fossil assemblage from the Balderton Sand and Gravel (Brandon and Sumbler, 1988) indicates a more open landscape in which aquatic habitats were available but they were neither extensive nor permanent. Interestingly, at Baston (Briant et al., 2004a) the data set from channels within the MIS 3 gravel body also represents a more open landscape, but that from ice-wedge casts represents aquatic habitats.

The dominance of low-energy aquatic habitats in cool/cold stage fossil assemblages should not be considered unusual because such habitats are found at the higher topographic levels of braided-stream environments away from the active channel belt, and thus have greater preservation potential; and if the active channel belt is downcutting such sequences may be preserved as terrace elements (Miall, 1977). Interpretation of such preserved sequences is not straightforward, however, as demonstrated by taphonomic studies on assemblages in different settings of modern braided stream environments (e.g. Briggs et al., 1990; West et al., 1993).

Of interest is the occurrence of *P. muscorum* in unit 3a, which generally represents drier terrestrial habitats but is occasionally found in marshland, and this seems to be especially so in Pleistocene stadial/interstadial assemblages, where it is often represented by a tall cylindrical form (see Seddon and Holyoak, 1985; Briant et al., 2004a; Boismier et al., 2012). To explain its frequent presence in Pleistocene

stadial/interstadial assemblages (Holyoak, 1982) it may be necessary to consider the manner in which organic material transported by floods would accumulate in such settings. In addition to fine-grained material in suspension, organic debris with a propensity to float, for example gastropods with small apertures (R. C. Preece, in West, 1991), including juveniles of species with wide apertures, is more likely to be carried to the higher topographic levels during floods. There also will be a tendency for size sorting with distance from the active channel. Thus this mechanism could account for the palaeoecological similarity of fossil assemblages in the different depositional settings (i.e. the deep channel of unit 5d, the shallow cut-and-fill channels of unit 3a and the bar-top settings of units 1a and 1c[WF]) and the frequent occurrences in Pleistocene stadial/interstadial assemblages of species with different habitat preferences (Holyoak, 1982).

Reworking of pre-existing deposits in fluvial environments presents problems for palaeoecological reconstructions (Holyoak, 1982; West et al., 1994; Briant et al., 2004b), and it is likely that the *B. tentaculata* shells and opercula (and possibly other specimens) present in the assemblages of units 1c[WF], 3a and 5d are reworked, as in the radiocarbon dated assemblage from Somersham (West et al., 1999). Thus, in addition to the vagaries of the time-transgressive nature of ecological assemblages (Begon et al., 1990) in response to complex climatic change (e.g. Johnsen et al., 2001; Hammer, 2006) and the limitations of dating techniques, establishing typical stadial and interstadial assemblages for the purposes of comparison and biostratigraphy is fraught with difficulty.

Of special interest is the fossil assemblage of unit 3a, with its implications for cold climate and high sea level. Although exposed Oxford Clay bedrock could provide the salinity requirements for the insect and ostracod species concerned, this would not account for the presence of foraminifera. Alternative proposals to account for this intriguing assemblage include: (i) saline conditions developed on exposed Oxford Clay supported the halotolerant insects (and ostracods), and the foraminifera (and ostracods) are reworked – but no foraminifera have as yet been found in the late MIS 7 channel B sediments; (ii) saline conditions developed on exposed Oxford Clay supported the halotolerant insects and ostracods, and the foraminifera were transported by wind; (iii) saline conditions developed on exposed Oxford Clay were contemporaneous with nearby estuarine conditions and the halotolerant ostracods and the foraminifera were transported on tidal surges; and (iv) the halotolerant insects and ostracods and the foraminifera are part of a nearby estuarine fauna. Presence of cold-indicator species in each of the insect, ostracod and foraminifera assemblages strongly suggests that these faunas were contemporaneous rather than being a mixture of contemporaneous and reworked taxa.

This apparent enigma may be reconcilable by comparison with evidence from elsewhere: Lefebvre (1993) noted cooling at the MIS 7–6 transition in the River Seine estuary prior to sea-level fall; Bates et al. (2000) noted cooling at Norton Farm (Fig. 1b) on the Sussex coast during the same transition, and similarly this was prior to glacially driven sea-level fall – the foraminifera faunas of Norton Farm and unit 3a are almost identical (Jones and Whittaker, 2010); on the Norfolk coast the Morton (Fig. 1b) raised beach has an OSL age-estimate that places it within the MIS 7–6 transition (Hoare et al., 2009).

#### 4.2. Palaeotemperature estimates

Pollen palaeotemperature reconstructions by Kolstrup (1980) for the LGM in The Netherlands provide an independent insight into the temperatures likely to be

experienced in lowland England during late Middle and Late Pleistocene stadials. At a latitude similar to that of the area of South East England and East Anglia, The Netherlands is also similar in size and shares a similar climate, albeit that The Netherlands experiences slightly more continental conditions (Hatch, in press). Nevertheless, the area of South East England and East Anglia is considered the most climatically continental in the UK (Mayes and Wheeler, 2013) and during glacial periods would be even more continental, thus validating comparison of the palaeotemperature records for the study site and The Netherlands

The mutual mutual palaeotemperature-estimate envelopes provided by the overlapping MCR and MOTR ranges for units 1a, 1c[WF] and 3a have minimum mean July values 1 to 3°C warmer than the LGM mean July temperature of +9 to +10°C in The Netherlands estimated by Kolstrup (1980); all three mean January palaeotemperature-estimate envelopes are consistent with the -8°C mean January temperature estimated by Kolstrup (1980). Climate during the deposition of unit 3a was cooler than today, by at least 1°C in July and at least 2°C in January; this is supported by the occurrence in this unit of three cold-climate indicators not included in the MOTR application (for reasons explained above): *L. batesi*, *J. schwarzbachii* and *A. tonnensis*.

Regarding the interesting disparity between the MCR and MOTR temperature estimates for unit 5d, comparison with literature data (Fig. 6) reveals that the unit 5d coleopteran temperature-estimate envelopes are similar to Lynford, Whitemoor Haye, Baston and Stanwick, as well as facies association Bb at Latton, but not to Upton Warren or facies association Ba at Latton. Consequently, according to this comparison, unit 5d could have been deposited early in MIS 3, or late in MIS 3. As noted in Fig. 6 the percentage overlap of species forming the coleopteran temperature reconstructions for unit 5d is 87.5%. A possible reason for this partial overlap could be the rapidly changing climate characteristic of MIS 3, thereby introducing a mixture of cooler and warmer taxa in the same deposit, such as at Upton Warren and Lynford. This lack of agreement also may be explicable by the fact that the ostracod sample was taken from a higher level (about 40 cm) in the Channel D sediments than the coleopteran sample, and separated from it by a lateral distance of a few metres, thus inferring that: (i) the infilling of channel D was episodic and possibly spanning more than one MIS 3 climatic episode; or (ii) that the more basal coleopteran sample is reflecting reworking of sediments from the underlying unit 5c, which contains evidence of cryogenic deformation in the form of ice-wedge casts (truncated by channel D; unpublished data) and has yielded a plant macrofossil assemblage indicative of cold conditions (see section 3.1.2). Marked episodic deposition is not apparent from the sedimentology, but discontinuities in such settings can be obscure (e.g. Keen et al., 1999; Langford and French, 1999). Neither are there any noticeable climatic alternations in the pollen profile, but as discussed above there is the problem of reworking of pollen, amongst other factors, within fluvial environments so that pollen spectra may not actually be representing the climatic conditions during sediment accumulation.

Climatically sensitive species also produce partial overlaps in the coleopteran temperature reconstructions for units 1c[WF] and 3a (Fig. 6). Apart from the reasons outlined above, this could be a function of incomplete knowledge of the temperature ranges of exotic species (see section 3.3), which could equally apply to unit 5d. As above, the sampling resolution may have been too coarse and thus the assemblage is in essence 'mixed', with both warmer and cooler elements being present, and with more than one climatic change encapsulated within the sampled deposits.

#### 4.3. Stratigraphical synthesis

Figure 7 provides a stratigraphical synthesis and a more detailed discussion follows. A minimum age of MIS 7 for unit 1a (and for unit 1b[WF]) is indicated by AAR age-estimate data for the overlying channel B sediments (log 1, Fig. 3; Penkman, 2005; Langford et al., 2007, this issue; Penkman et al., 2008, 2011), but the pollen assemblage of unit 1a suggests deposition within a cold stage, and the sedimentary characteristics of unit 1b indicate deposition within a cold-climate braided stream environment: thus a minimum age of MIS 8 is most likely. A maximum age of MIS 12 is indicated by the presence of Cretaceous material from the east of the site that was introduced into the area during the Anglian/Elsterian glacial stage.

A maximum age of MIS 8 for unit 1c[WF] is suggested by AAR data on *Bithynia* opercula found within the organic mud beds, and a minimum age of MIS 5c is suggested by optically stimulated luminescence (OSL) data for overlying units 5a and b (Fig. 3; Langford et al., 2007). A number of factors need to be taken into account in considering the probable age of unit 1c[WF]. (i) Temperate marine and estuarine ostracods and foraminifera record a probable flood event in the upper part of unit 3b (unpublished data), which incises both unit 1c[WF] and the late MIS 7 channel B. The high sea level that this implies and the temperate nature of the fauna therefore suggest a minimum age for unit 3b of MIS 5e and a maximum age of late MIS 7. (ii) A gravel with a similar clast-lithology assemblage (unit 1c[BF]; Fig. 3) has a minimum age of MIS 7 because it underlies channel B in Bradley Fen Quarry. (iii) No fragments of the robust bivalve *Corbicula fluminalis*, so common in units 2a and 2b of the channel B sediments, have so far been found reworked into the organic mud beds of unit 1c[WF], but this may be related to hydrodynamics (see above). Although we consider the exact age of unit 1c[WF] to remain uncertain, together these factors indicate a probable age of MIS 8, but an age early in MIS 7 cannot be ruled out.

A minimum age of MIS 6 is indicated for unit 3a because it is incised at its western edge by unit 3b, which has a minimum age of MIS 5e and a maximum age of late MIS 7 (see above). A single shell of *B. marginata* has been found in the molluscan assemblage of unit 3a (see above). As it is possible that this shell was reworked from the late MIS 7 channel B sediments, where the species is abundant throughout the sequence, the maximum age for unit 3a therefore also could be late MIS 7. The cold aspect indicated by the fossil assemblage (see above) therefore would suggest a MIS 6 age, but the implication for high sea level indicated by the ostracod and foraminifera faunas would seem to contradict this. Although an age at the MIS 7–6 transition is preferred (see section 4.1), there are two reasons for caution. First, unit 3b on this (north) side of the quarry (Figs 2b and 3) has not been investigated in detail and correlation with unit 3b on the south side of the quarry relies on a similar clast-lithology assemblage (unpublished data) and two-dimensional facies architecture observed during a reconnaissance survey (Langford, 2002). Second, the North Sea can be cold even during interglacials (Jones and Whittaker, 2010).

The presence of woolly rhinoceros in the cold-climate mammalian fauna of unit 5d restricts the age of the fauna to within MIS 8, late MIS 7 or MIS 3 (Langford et al., 2004b) because so far it has been recorded in Britain only at those times, but an age no older than MIS 6 is indicated for unit 5d because it is incised into cold-stage gravels that cut out the MIS 7 channel B. A maximum age of MIS 3 for unit 5d therefore is indicated, which is reinforced, on the basis of mammalian biostratigraphy

(Currant and Jacobi, 2001), by the presence of associated upper molars of horse at the contact between units 5c and 5d (Langford et al., 2004b). In addition, all British fossil records of the beetle *A. holdereri*, which was also found in this unit, are attributed to the mid-Devensian, dating between 54,000 and 26,000 years BP. Although some of these dates may be at the current resolution limit for radiocarbon dating, this does at least suggest that this unit is older than Late Devensian/Weichselian (MIS 2). Further work on dating the last glacial sediments from this sequence is planned by R. Briant.

## 5. Conclusions

A multidisciplinary study was undertaken of the palaeoecology of cool/cold stage fossil assemblages from different glacial stage deposits in a complex sequence of late Middle to Late Pleistocene deposits at Whittlesey, eastern England. The fossiliferous sediments investigated form part of the River Nene 1st Terrace.

Pollen, plant macrofossil, molluscan, coleopteran, ostracod, foraminifera and vertebrate data have been analysed, to a greater or lesser extent, for each fossil assemblage. Cool/cold climatic conditions are recorded, to a greater or lesser extent, in each fossil assemblage, but the presence of cold indicator species make this more apparent in the insect and ostracod faunas. The palaeontological data broadly present the same ecological picture for each fossil assemblage studied: a continuum from low-energy permanent to non-permanent aquatic habitats through marshland with associated waterside taxa, together with flood influxes of fluvial, riparian and ruderal taxa. This dominance of low-energy aquatic habitats reflects the greater preservation potential of such habitats found in the higher topographic levels of braided-stream environments, away from the active channel belt.

It is apparent from the rich coleopteran data that very similar and sometimes the same exotic cool/cold indicator species also appeared in pre-Ipswichian/Eemian cold stages and therefore assignment of particular exotic fauna to particular Devensian/Weichselian intervals should not be accepted uncritically. This also would be true for other lines of palaeontological evidence.

'Mutual mutual' temperature estimates from coleopterans and ostracods were ascertained for the three pre-Ipswichian/Eemian faunas and they indicate that minimum mean July temperatures were at least 1 to 3°C warmer at these times than during the LGM stadial in The Netherlands; however, the mean January temperature-estimate envelopes for these three faunas embrace the -8°C mean January temperature for the same location and period. At the MIS 7-6 transition the mean January temperature may have been at least 2°C lower than present. There is, however, a disparity between the coleopteran and ostracod temperature-estimates for the MIS 3 (Middle Devensian/Weichselian) fossil assemblage, which could be because the sampling procedure was too coarse and encompassed sediments representing separate climatic events during MIS 3. Comparison of the MIS 3 channel D coleopteran palaeotemperature estimates with those from other MIS 3 sites suggests an age early in MIS 3 or late in MIS 3.

Lack of numerical age-estimates prevents a robust stratigraphical interpretation. The youngest of the fossil assemblages, however, is assigned to the complex MIS 3 (Middle Devensian/Weichselian) interstadial, albeit on biostratigraphical grounds, whereas the youngest pre-Ipswichian/Eemian (MIS 5e) probably dates to the MIS 7-6 transition at a time when cooling preceded glacially driven sea-level fall. Of the other two cool/cold stage fossil assemblages, one probably dates to MIS 8, although a cool stage in early MIS 7 cannot be ruled out,

whereas the other has a minimum age of MIS 8 and a probable maximum age of MIS 10.

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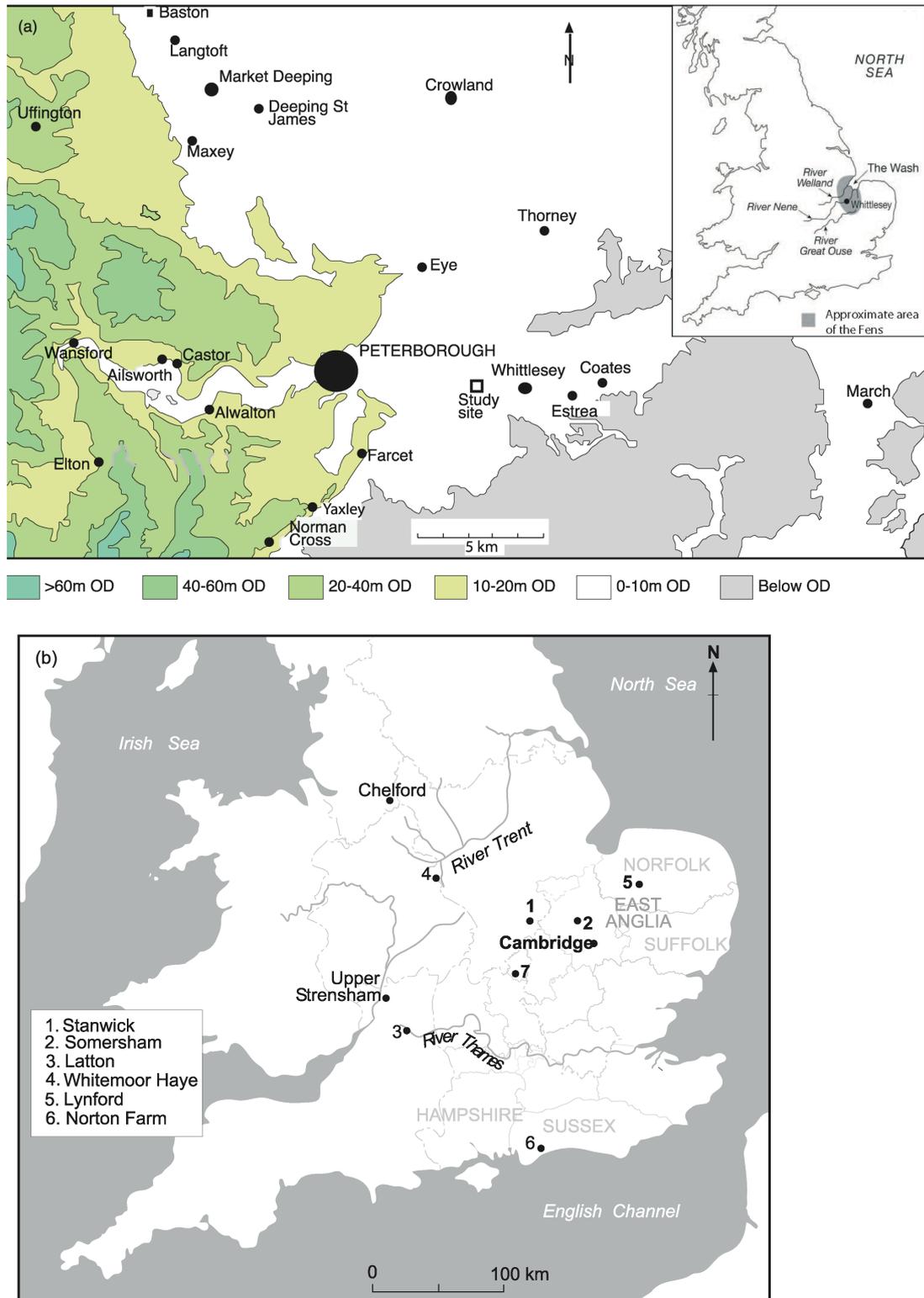
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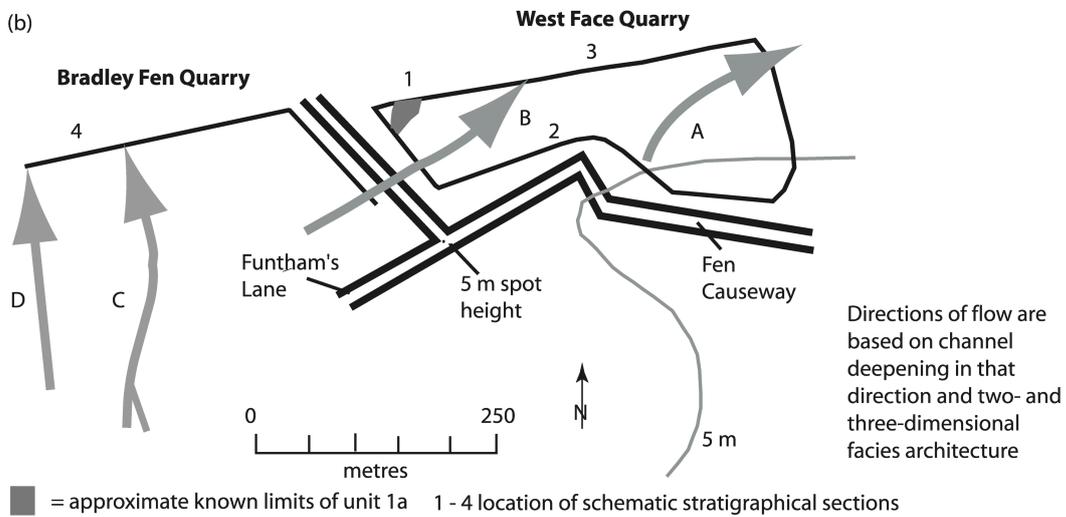
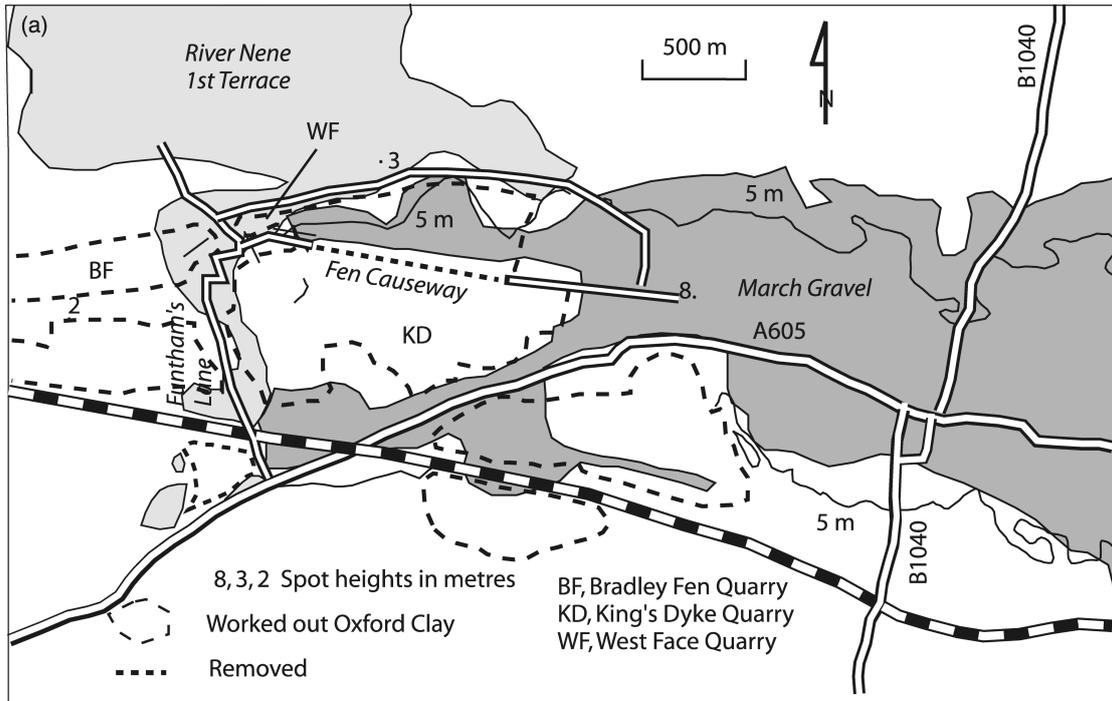
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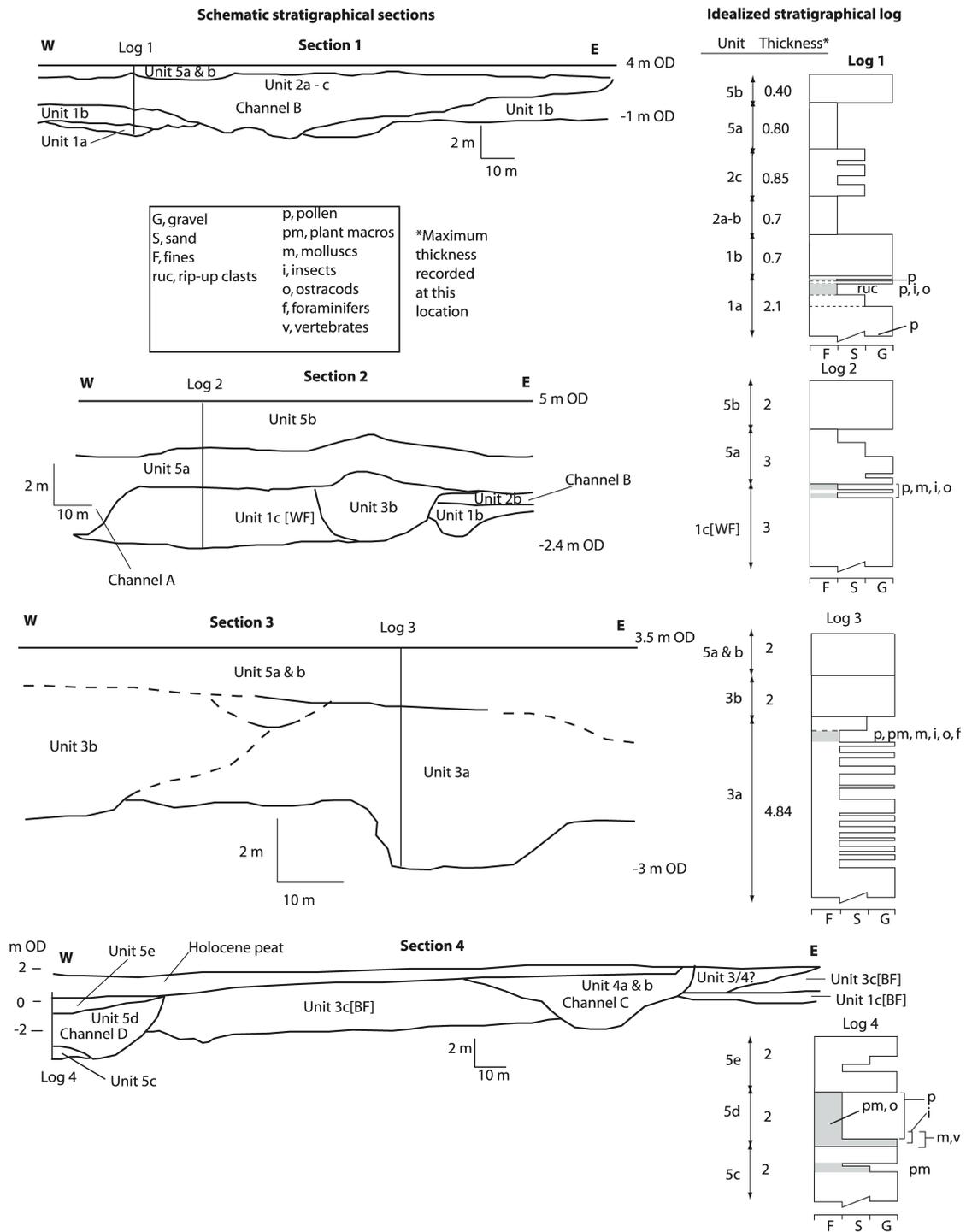
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**Fig. 1.** (a) Location of the study site within the East Anglian Fens, which encompasses the King’s Dyke (Langford et al., 2004c), West Face (informally referred to as Funtham’s Lane East by Langford (2002) and Langford et al. (2004a, 2007)) and Bradley Fen (Langford et al., 2004b) quarries. Produced in colour in the online version of this article. (Inset) The rivers Welland, Nene and Great Ouse that drain the Fens with outlets at The Wash. (b) Locations mentioned in the text.



**Fig. 2.** (a) Topography and Pleistocene geology at Whittlesey, eastern England. The Pleistocene deposits overlie the Peterborough Member of the Jurassic Oxford Clay. The March Gravel is a widespread marine deposit considered by the British Geological Survey (Horton, 1989) to be Ipswichian (MIS 5e) in age. (Based on BGS, 1984.) (b) Locations of channels A–D and sections 1–4.



**Fig. 3.** Schematic sketches of sections 1–4 showing the stratigraphical relationships among the different units and the locations of idealized logs 1–4, which also show maximum recorded thickness at the location of the log as well as the locations of the various samples.



**Fig. 4.** Photographs of unit 1a, 1c[WF], 3a and 5d sediments. Produced in colour in the online version of this article. (a) Sand lens (base of spade) and sampled organic mud clast (arrowed) in unit 1a. (b) Downslope transition to stratified gravels and diamictons in unit 1a; note the organic mud clast (arrowed) in the gravels of unit 1b. (c) Organic muds at the top of unit 1c[WF]. Samples were taken from the area within the box. (d) Unit 3a at log 3. Location of (e) is arrowed. (e) Close up on the upper contact of unit 3a and overlying sand. Bulk samples of the organic muds were taken from here. (f) Oxidized upper part of unit 5d with downward change to organic mud. (g) Gravel lag at base of unit 5d. Spade for scale in (a) to (d) is 90 cm long; scraper in (e) is about 23 cm long; staff in (d) and (f) is about 1.2 m long and in (g) about 70 cm of the staff is shown.

Bradley Fen A Section A Channel D Log A

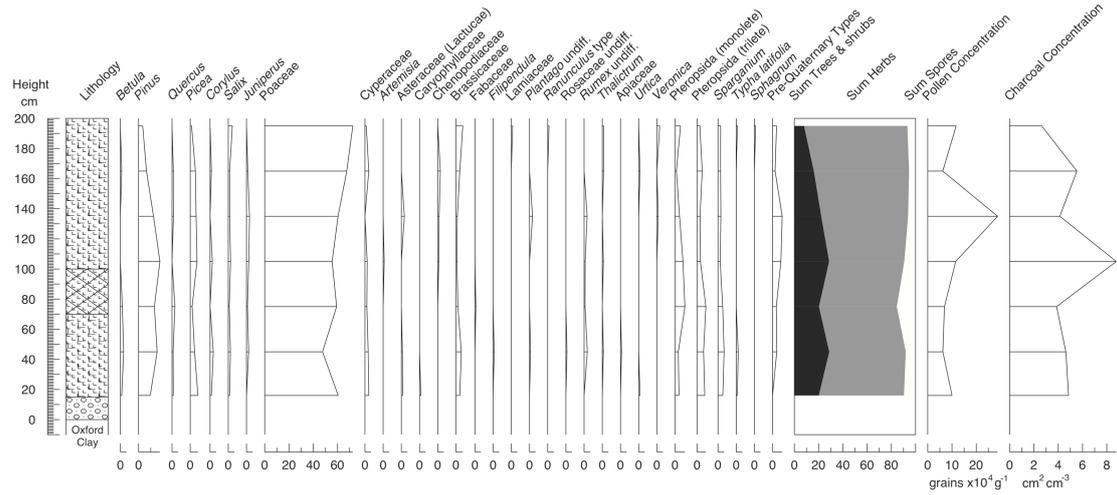
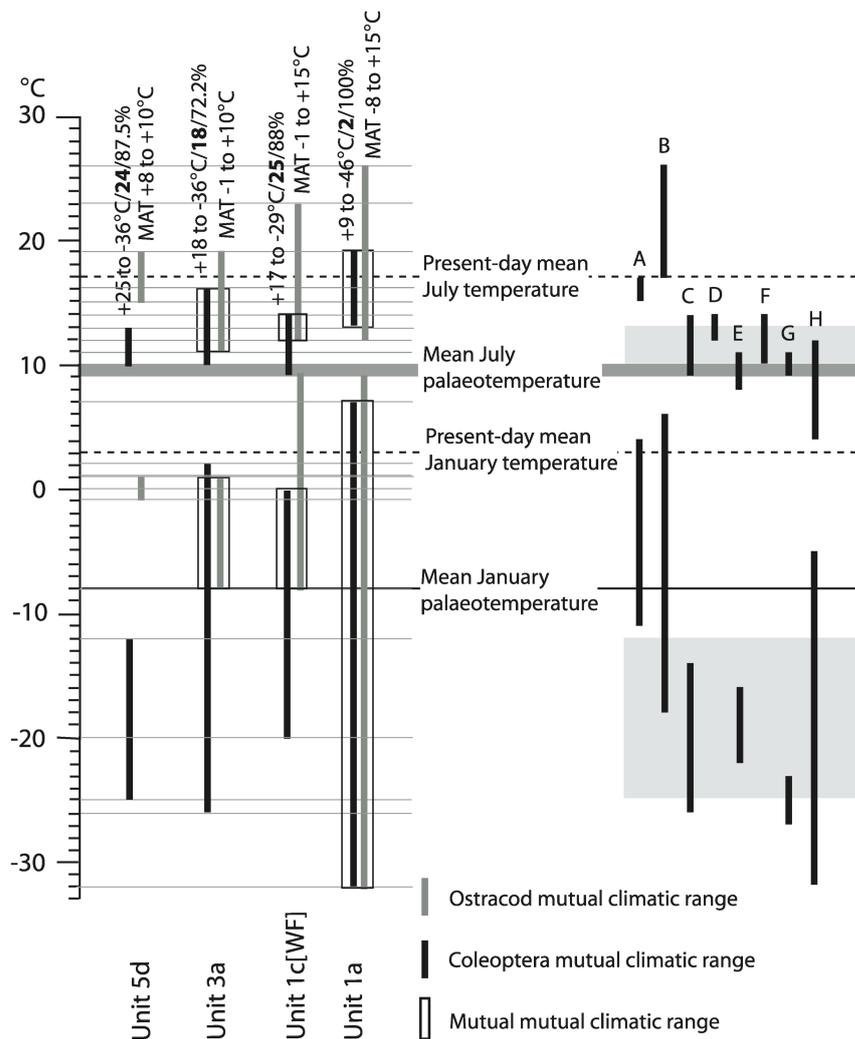


Fig. 5. Pollen diagram for unit 5d.



**Fig. 6.** Comparison of the coleopteran Mutual Climatic Range (MCR) and the Mutual Ostracod Temperature Range (MOTR) values for units 1a, 1c[WF], 3a and 5d. Minimum to maximum ranges are shown for January and July mean palaeotemperature estimates. It is important to note that the mean palaeotemperature estimate lies somewhere between the estimated ranges given, i.e. it could lie anywhere within that range. Mean annual palaeotemperature (MAT) estimates determined by the MOTR method are also provided. Data above the MCR ranges are TRANGE/NSPEC/overlap. Mean January ( $-8^{\circ}\text{C}$ ) and July ( $+9$  to  $+10^{\circ}\text{C}$ ) palaeotemperatures are from Kolstrup (1980). A, Upton Warren MCR data reported in Briant and Bateman (2009); B, Latton facies Ba MCR data (Lewis et al., 2006); C, Latton facies Bb MCR data (Lewis et al., 2006); D, Lynford MCR data, mean January palaeotemperature estimate  $\leq -15$  – dated by OSL to  $53.4 \pm 3.3$  to  $64.8 \pm 5.5$  ka (Boismier et al., 2012); E, Whitemoor Haye MCR data, dated by OSL to  $38 \pm 4$  ka (Schreve et al., 2013); F, Whitemoor Haye chironomid data (Schreve et al., 2013); G, Baston MCR data, dated by OSL to  $37.3 \pm 2.6$  ka (Briant et al., 2004a); Stanwick MCR data, dated by OSL to  $33.6 \pm 1.8$  ka (Briant et al., 2008). The light-grey shaded boxes show the MCR data for unit 5d.

Element	Significance	MIS	Unit 1a	Unit 1c[WF]	Unit 3a	Unit 5d
Holocene Peat	Provides minimum age for underlying units 3c[BF] and 5c-e[BF] and channel C	1				
		2				
		3				
		4				
Channel A	Dated by OSL. Provides minimum age for underlying unit 1c[WF], channel B, and units 3b and 3a	5a				
		5b				
		5c				
		5d				
Channel C	Biostratigraphically assigned to Ipswichian/Eemian. Provides minimum age for underlying unit 3c[BF]	5e				
Unit 3c[BF]	Cuts out channel B thus providing maximum ages for unit 3c[BF] and overlying channel C and units 5c-e[BF]					
Unit 3b[WF]	Cuts out channel B and units 3a and 1c[WF] thereby providing minimum ages for them. Contains evidence for high sea level so minimum age is 5e because it is overlain by channel A	6				
Channel B	Dated by AAR. Provides maximum age for unit 3b and channel A and minimum age for underlying units 1a and 1b	7				
		8				
		9				
		10				
		11				
Cretaceous clasts	Introduced from the east during the Anglian glaciation	12				

Preferred age
  Possible age range

**Fig. 7.** Stratigraphical synthesis showing the preferred ages and possible age ranges as well as details of age constraints: BF, Bradley Fen Quarry; WF, West Face Quarry.