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Evidence for the early onset of the Ipswichian thermal optimum: palaeoecology of Last Interglacial deposits at Whittlesey, eastern England

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Short title: Last Interglacial deposits at Whittlesey

†The late Professor Russell Coope wrote the initial draft of this article but his untimely death meant that he did not see its publication. His original text for the Coleoptera section has been retained unaltered as far as possible, except where new scientific insights could not justify such an approach.

Abstract: Fossiliferous deposits infilling a channel at Whittlesey, eastern England, are dated by amino acid racemization to the Last Interglacial, and pollen analysis indicates deposition in Ipswichian biozones Ip Ib and Ip IIb. Multidisciplinary palaeoenvironmental analyses of these deposits provide a rare insight into Ip Ib subzone conditions. Specifically, the Ip Ib deposits contain exotic thermophiles *Naias minor, Belgrandia marginata, Bembidion elongatum, Pelochares versicolor, Caccobius schreberi*, *Onthophagus massai* and *Emys orbicularis*, usually associated with Ip IIb. Combined palaeotemperature reconstructions based on beetle, ostracod and vertebrate assemblages of the Ip Ib deposits indicate that summers (mean July range +19 to +22°C) were at least 2°C warmer than at present, while winters (mean January air temperature range 0 to +7°C) were probably similar to those of today. These palaeotemperature ranges encompass those for Ip IIb deposits at Trafalgar Square (+20 to +21°C and +1.5 to +3°C), previously considered the only Ipswichian site to record temperatures significantly warmer than Holocene temperatures. Of particular significance is that thermal optimal conditions commenced in Ip Ib, rather than being confined to Ip IIb. This demonstrates rapid warming and biological response to early Ipswichian climate amelioration, which accords with the deep-sea Last Interglacial and European Eemian records.

As we face an immediate future of increasing global temperatures, more extreme weather events and higher sea levels (e.g. Crutzen & Stoermer, 2000; IPCC, 2014) it is important that we investigate Pleistocene interglacial deposits. These can provide insight into past natural climate change, including meaningful parameters to variables such as sea level and temperature, and spatial and temporal patterns within these (e.g. Petit *et al*., 2005; Abrantes *et al*., 2012). The Last Interglacial (LIG) stage, although not a direct analogue in terms of causal processes and their products, is appropriate for assessing the implications of anthropogenic climate change for the following reasons. First, it was a globally strong (warm) temperate period (Past Interglacials Working Group of PAGES, 2016) with higher temperatures and sea level interpreted from many records (e.g. Kukla *et al*., 2002; van Kolfschoten *et al*., 2003; Sánchez-Goñi *et al*., 2012). Second, there have been many studies of LIG deposits, regionally and globally, against which to compare research outcomes (e.g. West, 1957; Zagwijn, 1961; Shackleton, 1969; van Kolfschoten & Gibbard 2000; Lisiecki & Raymo, 2005). Third, there are many long records from a variety of depositional environments that span the entire interglacial stage (e.g. Andersen, 1966; Woillard, 1978; De Beaulieu & Reille, 1984; Mamakowa, 1989; Cramp & O'Sullivan, 1999; Rohling *et al*., 2015). Fourth, it is within the range of several absolute and relative dating techniques (e.g. Gascoyne *et al*., 1981, 1983; Bateman & Catt, 1996; McFarlane & Ford, 1998; Wastegård *et al*., 2005; Penkman *et al*., 2011; Sier *et al*., 2011, 2015; Abbott *et al*., 2013; Sier & Dekkers, 2013; Davies *et al*., 2014).

Although the LIG is broadly recognized as a period when climatic conditions were similar to today that occurred about 130 to 115 thousand years ago, corresponding to marine oxygen isotope substage (MIS) 5e (Fig. 1), it is in reality a complex entity. What emerges from the many studies of LIG deposits is a somewhat disparate picture of eustatic sea-level estimates, rates of sea-level rise, temperature estimates, commencement dates and durations, in both space and time at inter- and intrahemispheric scales (e.g. Shackleton, 1969; Broeker, 1998; Turner, 2000; Kukla *et al*., 2002; van Kolfschoten *et al*., 2003; Sier *et al*., 2011, 2015; Sánchez-Goñi *et al*., 2012; Long *et al*., 2015; Peeters *et al*., 2016). For example, the commencement of the southwest Europe LIG lags that of the global deep-sea record by 5000 years, and in turn is lagged by the northwest Europe LIG by a further 5000 years (Fig. 1; Shackleton, 1969; Shackleton *et al*., 2002, 2003; Lisiecki & Raymo, 2005; Sánchez-Goñi *et al*., 2012; Sier *et al*., 2015). It is possible that these spatial and temporal mismatches may be attributable partly to chronostratigraphical interpretation of LIG deposits being tied to a variety of age models or absolute dated sequences. For example, in Fig. 1, the ages of the top and base of sapropel S5 (a lithological marker of the eastern Mediterranean deep-sea record) are taken from Zeigler *et al*. (2010) and are based on precession tuning to U/Th dated caves in China. Shackleton *et al*. (2002, 2003), however, determined the ages of the top and base of the southwest Europe LIG in Fig. 1 by tying sea-level stillstands observed in core MD95-2042 to U/Th dated uplifted coral reefs. In addition, as noted by Turner (2000) and Shackleton (2002), there is a fundamental difference between the use of peaks and troughs in the MIS record for astronomical forcing and the determination of MIS boundaries on the rising and falling limbs of the peaks.

In Europe the LIG is referred to as the Eemian Interglacial, based on borehole evidence from the Amersfoot area in The Netherlands (Zagwijn, 1961). Significantly, the Blake Event (Fig. 1) identified by Sier *et al*. (2015) is dated by optically stimulated luminescence (OSL), which Peeters *et al*. (2016) combined with other OSL ages from different Dutch Eemian sequences to provide an absolute dated chronostratigraphy. Notwithstanding the error margins these data support a short duration and late commencement for the northwest Europe LIG (Fig. 1), in contrast to the southwest Europe and global LIGs (Shackleton *et al*., 2002, 2003; Lisiecki & Raymo, 2005).

In Britain, West (1957) first identified this period as the Ipswichian Interglacial, using palynostratigraphy to identify a series of pollen zones (Table 1) at the type-site of Bobbitshole (Ipswich, Suffolk; Fig. 2). Amino acid racemization (AAR) data confirm that the deposits at Bobbitshole are of LIG age (Penkman *et al*., 2013). A range of U/Th and luminescence age estimates have been published that place the Ipswichian Interglacial in the interval 130–115 ka (Fig. 1), but the error terms associated with these dates are too large to determine whether the interglacial here had an early or late commencement date. Thus, the Ipswichian and the Dutch Eemian can be only broadly correlated in terms of time.

A key problem in Britain is that there are only fragmentary Ipswichian records (Fig. 2b) and consequently pollen biozonation (Turner & West, 1968) is based on the combination of records at Bobbitshole (biozones I and II; West, 1957) and Wing (biozones II–IV; Hall, 1980) in Rutland (Fig. 2), the latter of which is not even securely dated to the LIG (Lewis *et al*., 2010). Indeed many sites early identified as

Ipswichian on the basis of pollen records have been conflated with those from the penultimate (MIS 7) interglacial (Sutcliffe, 1975, 1976; Shotton *et al*., 1983; Bridgland, 1994; Dixon, 1997; Turner, 2000; Thomas, 2001). In a comprehensive review, Lewis *et al*. (2010) recognized 38 sites that could be confidently assigned to the Ipswichian Interglacial (Fig. 2a), of which 22 are dated: mostly by amino acid racemization (AAR), with 10 sites by luminescence and/or U-series (Fig. 1). The remaining 16 are assigned on the basis of a characteristic mammalian fauna (the Joint Mitnor Cave Mammal Assemblage-Zone of Currant & Jacobi, 2001) that includes the hippopotamus, *Hippopotamus amphibious*, with fallow deer and/or straight-tusked elephant (Currant & Jacobi, 2001), and is U-series dated to 120 ± 6 ka from speleothem covering a *Hippopotamus*-bearing fauna at Victoria Cave (Gascoyne *et al*., 1981).

The vast majority of the Ipswichian sites recognized by Lewis *et al*. (2010) fall into the early temperate pollen biozone IIb (Table 1). Candy *et al*. (2016) used the data from five of these Ip IIb sites (Bobbitshole, Deeping St James (Keen *et al*., 1999), Swanton Morley (Phillips, 1976; Coxon *et al*., 1980), Tattershall Castle (Holyoak & Preece, 1985) and Trafalgar Square (Preece, 1999), together with data from Woolpack Farm (Gao *et al*., 2000), to assess how warm Britain was during the Ipswichian Interglacial, showing that only the sequence from Trafalgar Square convincingly demonstrates temperatures warmer than during the Holocene thermal optimum, though all are warmer than the present day.

This article presents the findings of a multidisciplinary study of the palaeoenvironment of Ipswichian deposits at Whittlesey [TL236980], eastern England (Fig. 2a; Langford *et al*., 2004b) that can be compared with the sites utilized by Candy *et al*. (2016). As with other Ipswichian sites (Fig. 2b) the palaeoenvironmental record at Whittlesey represents only a fragment of the LIG, but in contrast to most of these sites the data available offer a rare insight into the climatic and ecological conditions of Ipswichian biozone I. In particular, they shed light on the speed of establishment of thermal optimum conditions and the biological response to early Ipswichian climate amelioration, which were rapid in the deep-sea LIG (Fig. 1) and the northwest and southwest Europe LIGs (Zagwijn, 1961; Shackleton, 1969; Turner, 2002; Sánchez-Goñi *et al*., 2012; Sier *et al*., 2011, 2015). Our work at Whittlesey includes quantitative reconstructions of mean July and January air temperatures based on Coleoptera and Ostracoda, of significant value for palaeoclimate modelling, as well as qualitative interpretations of the palaeoecology and depositional environment that improve our understanding of Ipswichian biozonation and biostratigraphy. In addition, this study complements the palaeoecological and palaeotemperature studies of Langford *et al*. (2014a,b) on MIS 7 and cold-stage deposits at Whittlesey, and provides the first comprehensive multidisciplinary account of a fully fluvial Ipswichian deposit of the River Nene catchment.

Background

Geographical and geological contexts of the Whittlesey sedimentary succession

The fossiliferous sediments investigated here form part of the River Nene 1st Terrace (BGS, 1984; Horton, 1989; the Ecton Member of Maddy, 1999) and are located in Bradley Fen Quarry at Whittlesey, Cambridgeshire (Fig. 3a), where they unconformably overlie the Peterborough Member of the Jurassic Oxford Clay (Hudson & Martill, 1994) and underlie Holocene Peat (see Langford *et al*. (2004b, 2007, 2014a,b) for further details of the geographical and geological contexts). The late Middle to Late Pleistocene sedimentary succession at Whittlesey represents an important fluvial archive spanning more than half the post-Anglian (Elsterian/Mindel/MIS 12 glacial stages) to Holocene period (Langford *et al*., 2004a–c, 2007, 2014a,b). This complex sequence of deposits contains a number of fossiliferous beds, of both cool/cold or temperate-climate character, that together span at least the previous three glacial and two interglacial stages.

Four distinctive channel-fill sequences have been recognized (channels A–D; Fig. 3b) within the Whittlesey sequence. The palaeoecology of two of these (B and D) has been reported by Langford *et al*. (2014a,b) and age-estimate data for two of them (A and B) have been provided by Langford *et al*. (2007, 2014a): OSL dates indicate an age for channel A within MIS 5b–a; AAR assigns channel B to an age within the MIS 7 complex (Penkman, 2005). This multidisciplinary investigation concerns the palaeoenvironment of channel C (Fig. 3b), which the sedimentary succession (sequence stratigraphy) demonstrates post-dates channel B (MIS 7). Langford *et al.* (2004b) interpreted channel C as Ipswichian based on its multiproxy biostratigraphy, and this is now confirmed by new AAR data on the intra-crystalline protein fraction of *Bithynia tentaculata* opercula (Fig. 4; Supplementary Table S1).

Sedimentary context of channel C

A schematic sedimentary succession section and detailed sedimentary log (Fig. 5) show the relationship of the fossil-bearing sediments of channel C to other units within section A of the Bradley Fen Quarry. The sedimentary unit nomenclature used here is based on Langford *et al*. (2014b), with the exception of unit 3c (see below). Channel C comprises a lower muddy facies (unit 4a, 0–102 cm) and an upper pebbly gravel facies (unit 4b, 102–305 cm). Unit 4a occurs only in section A of Bradley Fen Quarry and during the early part of fieldwork was observed to thin and narrow towards temporary section C (Fig. 3b) above an undulating contact with the underlying bedrock Oxford Clay.

The sedimentology of channel C is rather complex, with the presence of fining upward cycles producing an interbedded character in both unit 4a and 4b. The fining upward sequence at the base (0–20 cm) may represent waning flow deposition associated with the initial incision event. Above this there is a further fining upward sequence ending in a bed of coarse to medium to silty sand. The coarsening upwards cycle above this probably represents a period of stability but with increasing energy levels over time, as the underlying silty sand and medium sand would be easily mobilized by higher energy flows or closely spaced flood events. Another waning-flow flood deposit (fining upwards sequence) is preserved between 63 and 96 cm, and the uppermost pebbly gravel in unit 4a probably also represents a flood deposit. Thus unit 4a appears to represent initial flood deposition, followed by a period of stable conditions but increasing flow energy over time, with a return to flooding events in the upper part.

The erosional contact between unit 4a and 4b is planar and upwardly concave, representing a hiatus of unknown duration. It was clear from temporary vertical sections C and E (Figs 3b, 5 and 6a) that unit 4b represents lateral and vertical aggradation on a bank-attached bar, with the low-angle stratification dipping to the east in section C and to the south in section E suggesting a point bar of a sinuous channel. Overall unit 4b tends to fine upwards. There is, however, no evidence for contemporaneous point-bar deposition during accumulation of unit 4a.

The facies architecture of unit 4b and the direction of deepening indicate that flow in channel C was towards the north, completely opposite to the direction of flow indicated in the underlying gravels of unit 3b (Fig. 6b). It has been argued (Langford, 2012) that this southerly direction of flow in unit 3c was in response to impoundment of The Wash during MIS 6 (Gibbard *et al*., 2009). The northward flow of channel C would therefore appear to be part of the readjustment of drainage back through The Wash. This drainage adjustment in MIS 6 and readjustment in MIS 5e has implications for the stratigraphical interpretation of unit 3c. Unit 3c comprises pockets of fossiliferous gravels, sands and silts and would appear to be the product of cohesive flow processes. *Corbicula fluminalis* shells are common in these fossiliferous pockets (see Fig. 8d) and microscopic observations revealed the presence of fragments of *Theodoxus danubialis*, indicating reworking of channel B deposits from the south to southeast quadrant with transport in a northerly to northwesterly direction. It is evident that unit 3c post-dates unit 3b and pre-dates unit 4b (Fig. 5), but it cannot be demonstrated unequivocally that it pre-dates unit 4a. Therefore, unit 3c could have been deposited by slope failure associated with the incision of unit 4a during the early Ipswichian, or following the MIS 6 drainage adjustment. The latter explanation is preferred here because MIS 6 epigenetic ice-wedge casts were present in the Bradley Fen and West Face quarries (HEL, pers. obs., 2001) and MIS 6 large-scale periglacial involutions occur in King's Dyke Quarry (Langford, 1999; Langford *et al*., 2004a), suggesting the likelihood of widespread slope failure caused by periglacial processes at this time.

Palaeobotany results

Pollen

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

Pollen and charcoal were analysed from five levels (15, 35, 67, 90 and 260 cm) within channel C (Figs 5 and 7). The basal part of the sequence is dominated by grass (Poaceae) pollen and pteropsid spores, with pine (*Pinus*) (20–30%) and birch (*Betula*) (5–10%). Other arboreal taxa present include oak (*Quercus*), which increases up-section, and willow (*Salix*), juniper (*Juniperus*), sea buckthorn (*Hippophaë*), ivy (*Hedera*) and holly (*Ilex*). A range of herbs and aquatic plants are also represented, including meadowsweet (*Filipendula*), bur-reed (*Sparganium*) and yellow water-lily (*Nuphar*). The sample at 260 cm was very different and contained a grass–hazel (Poaceae–*Corylus*) assemblage, with a little pine (*Pinus*), oak (*Quercus*) and herb pollen. Pollen concentrations were moderate at 20 000–30 000 grains per gram, and charcoal, although increasing from the base, was generally low (< 1 cm^2 cm^{-3}) suggesting only limited regional burning.

Plant macrofossils

The samples from unit 4a were residues from bulk samples collected for analysis of small vertebrates whereas the two samples from unit 4b were picked from samples collected for molluscan analysis. As the volumes of the original samples are not known, the counts in Supplementary Table S2 should be treated as abundance and presence/absence data only.

Two samples were analysed from each of units 4a and 4b (Supplementary Table S2). The samples from unit 4a contain a wider range of species than those from 4b, although the greater number of specimens from unit 4a should be noted. As would be expected from a deposit laid down within a fluvial setting, both units are dominated by plants indicating aquatic conditions, for example pond weed (*Potomageton* sp.) and horned pond weed (*Zannichellia palustris*), or waterside environments, particularly bulrush (*Scirpus maritimus*) and sedge (*Carex* sp.). The aquatics bur-reed (*Sparganium*) and yellow water-lily (*Nuphar*), detected in the pollen record, are also observed here. In contrast to the pollen record, however, the only tree species recorded is elm (*Ulmus*) in unit 4a. The paucity of tree macrofossils suggests that the wooded areas recorded in the pollen were at a significant distance from the river channel. There is some indication of drier ground adjacent to the channel during deposition of unit 4b, with the increased presence of the disturbed ground species of the blackberry family (*Rubus* sp.) and common knotgrass (*Polygonum aviculare*) and some decrease in aquatic species.

Palaeozoology results

Mollusca

Four samples of approximately 2 kg each were collected from section A by J. Merry for mollusc analyses [samples a (0–20 cm from base), b (20–40 cm from base), c (70–90 cm from base), d (2.6 m from base)]. The mollusc samples from unit 4b in section E were collected by D. H. Keen in 2002 and labelled in centimetre intervals from the base of the exposed section. These samples were crudely sieved through a 500 µm mesh and subsequently picked by HEL in 2014–2015. Samples were washed through 2 mm, 1 mm and 500 µm sieves and shells were picked by eye or under a binocular microscope at 10× 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. Environmental preferences and geographical distributions of the molluscs are based on Kerney (1999), Kerney & Cameron (1979) and Killeen *et al*. (2004).

As expected for a fluvial deposit, the molluscan fauna represents a diversity of riverine habitats (Supplementary Table S3). A substantial river is indicated by the dominance of *Valvata piscinalis* and *Bithynia tentaculata*, which prefer slow-moving water (Sparks, 1961). Together, they make up more than 50% of the assemblage in unit 4a, but this declines to above 30% in unit 4b. Other elements in the assemblage indicating a substantial, slow-moving river are *Unio tumidus*, *Pisidium supinum* and *Pisidium moitessierianum*, with the latter two increasing noticeably in unit 4b; *Pisidium amnicum*, indicative of a large body of moving water, also increases in unit 4b. *Hippeutis complanatus*, which also prefers slow-moving water, is present in unit 4a but absent in 4b. *Physa fontinalis*, *Ancylus fluviatilis* and *Pisidium henslowanum* are indicative of moving water, but the first two are present only at the base of unit 4a whereas the last has a significant presence only in unit 4b. The presence of only one specimen of *A. fluviatilis*, however, reinforces the impression of a substantial slow-moving water body, as this species prefers faster flowing habitats (Holyoak & Preece, 1985).

The presence of *V. piscinalis* and *B. tentaculata*, together with *Valvata cristata* and *P. supinum*, indicates that muddy substrate conditions were plentiful, although these declined in unit 4b. The presence of well-vegetated substrates is indicated by *V. cristata*, *B. tentaculata*, *P. fontinalis*, *Anisus vorticulus*, *Gyraulus laevis*, *Gyraulus crista*, *H. complanatus*, *Sphaerium corneum*, *Pisidium obtusale* and *Pisidium milium*, with indicators of these conditions peaking at above 45% in the middle of unit 4a and declining to below 15% in unit 4b. Such vegetation would have provided the organic debris required by *Pisidium nitidum* (Ellis, 1978), which can tolerate a variety of fluvial habitats.

Pisidium henslowanum prefers a coarse sandy or stony substrate (Boycott, 1936; Ellis, 1978). Other species that require a clean stony or sandy substrate include

G. laevis, *P. amnicum*, *A. fluviatilis*, *U. tumidus* and *P. moitessierianum*, with indicators of such conditions representing more than 30% of the assemblage in unit 4b compared with a maximum of 21% at the top of unit 4a.

Valvata cristata, *Radix balthica*, *G. laevis*, *G. crista*, *Acroloxus lacustris*, *S. corneum*, *P. obtusale* and *P. milium* prefer standing-water or quiet-water habitats. Indicators of these conditions peak at about 30% of the assemblage in the middle part of unit 4a but decline to less than 10% in unit 4b. Marsh and wetland species are represented by *Carychium minimum*, *Carychium tridentatum, Galba truncatula, Anisus leucostoma, A. vorticulus, Succinea putris, Vertigo antivertigo, Vallonia pulchella*, *Punctum pygmaeum* and *Euconulus* cf. *alderi*, with the latter also found in boggy woodland. Species such as *G. truncatula*, *R. balthica* and *A. leucostoma* are also found in marginal areas of the water body that are prone to drying out. Again, marsh and wetland conditions peaked in the middle part of unit 4a, represented by about 10% of the assemblage, and were less prevalent in unit 4b, represented by about 3% of the assemblage.

Amongst the remaining terrestrial species, *Aegopinella nitidula* is a shade-demanding species and *Cochlicopa* cf. *lubrica* requires damp, sheltered habitats, whereas *Pupilla muscorum* prefers dry grassland, although it also can be found in damp habitats; *Helicella itala itala* and *Truncatellina cylindrica* in unit 4b of section E are also indicative of dry habitats. Finally, *Belgrandia marginata* falls into the slum group recognized by Sparks (1961), and today inhabits pristine calcareous springs in northeast Spain and southern France (Keen *et al*., 1999).

Several trends are apparent from the above that may be important for palaeoenvironmental reconstruction. The numbers of *P. amnicum*, *P. supinum*, *P. henslowanum* and *P. moitessierianum* increase significantly in unit 4b compared with unit 4a, concomitant with a decrease in *V. piscinalis* and *B. tentaculata* and muddy substrate conditions, as well as an up-sequence increase in species preferring clean sandy or stony substrate conditions. The increase in *P. nitidum* in unit 4b is also consistent with these changing conditions given the catholic requirements of this species. Indicators of standing/quiet water and marsh/wetland habitats, as well as vegetated substrates, peak in the middle part of unit 4a and decline thereafter, and *P. muscorum, H. itala itala* and *T. cylindrica* hint at drier conditions during accumulation of unit 4b. Most noticeably, *B. marginata* shows a marked decrease up-sequence, which combined with increases in *P. supinum* and *P. henslowanum* could indicate decreasing alkalinity up-sequence – it should be noted, however, that *Chara* fragments dominate the < 2 mm fraction of samples from below 120 cm in section E.

Coleoptera

A single bulk sample of about 15 kg was obtained from the basal 10–62 cm sediments of unit 4a of channel C at Bradley Fen, section A. The sediment was grey silty clay with scattered plant fragments. The sample was washed over a sieve with a mesh aperture of 0.3 mm. The residue was then concentrated using the standard flotation technique and the insect fossils extracted using a binocular microscope (Coope, 1986). Specimens were identified by GRC who reported that on the whole the preservation was good though rather fragmentary. Taxonomy is based on Lucht (1987), as revised by Böhme (2005) and Gustafsson (2005). Counts indicate the minimum number of individuals (MNI) in the sample. Species habitat information was obtained from the BugsCEP database (Buckland & Buckland, 2012).

Altogether 123 coleopteran taxa were recognized of which 82 could be named to species or species group (Supplementary Table S4). An asterisk indicates those species not now living in the British Isles. This assemblage clearly represents species from a wide variety of habitats, probably swept together off the neighbouring landscape at times of flood. Insects from aquatic habitats dominate the assemblage, followed by species indicative of marshy ground. In the following account species are grouped according to their ecological preferences: aquatic habitats, marginal and hygrophilous habitats, drier habitats, tree-dependent species, dung community and saline habitats

The presence of running, well-oxygenated water is indicated by dryopid species that are found in stony or mossy riffles in clear rivers and streams, where they feed on algae and detritus. These include *Helichus substriatus, Stenelmis canaliculatus*, *Esolus parallelepipedus, Oulimnius tuberculatus, Oulimnius troglodytes, Limnius volckmari* and *Normandia nitens*. *Agabus guttatus* lives in springs and small rivulets (Nilsson & Holmen, 1995). *Ochthebius minimus* is found in all sorts of fresh water, both running and standing, and is usually abundant, as it is here, in shallow, standing water where there is vegetation (Hansen, 1987). Many species of *Hydraena* also live in clear running water. Since many of these species complete their life cycles almost entirely under water they indicate that the river was flowing throughout the year.

Standing-water habitats rich in vegetation are indicated by dytiscid species such as *Hydrovatus cuspidatus, Hydrotus inaequalis, Copelatus haemorrhoidalis, Agabus bipustulatus* and species of *Ilybius, Rhantus, Colymbetes* and *Dytiscus.* Most species of the Hydraenidae, and Hydrophilidae have predatory larvae but adults that live on decomposing vegetation. Significant species are *Limnebius aluta, Hydrochus* sp., *Helophorus* spp., *Coelostoma orbiculare, Cercyon sternalis*, *Hydrobius fuscipes, Limnoxenus niger, Anacaena globulus* and *Chaetarthria seminulum.*

Many of the phytophagous water beetles indicate the composition of the flora. *Macroplea appendiculata* lives principally on species of *Potamogeton* and *Myriophyllum*, and *Donacia versicolorea* is a monophage on *Potamonectes natans* (Koch, 1992). *Donacia dentata* feeds on *Sagittaria* and *Alisma*, while *D. semicuprea* feeds principally on the aquatic grass *Glyceria* (Koch, 1992). The minute weevil *Tanysphyrus lemnae* feeds on the duckweed *Lemna.*

Several of the predatory or general scavenging carabid species indicate marshy environments. These include relatively large numbers of *Bembidion assimile*, a species that lives beside eutrophic lakes or slowly moving rivers where there is luxuriant vegetation of *Carex, Phragmites* and similar plants (Lindroth, 1985). *Bembidion octomaculatum* often lives beside small ponds that dry up in the summer. It prefers muddy substrates where there is some shade (Lindroth, 1992). *Pterostichus vernalis* requires wet, rich soil, well vegetated with *Carex* where the surface is often moss covered. *Pterostichus aterrimus* and *Dyschirius aeneus* are also swamp species living where there is soft soil rich in humus with abundant vegetation, but where there are bare patches between the plants. *Bembidion biguttatum* inhabits wet places near to ponds or slowly moving water in moist meadow-like habitats. *Corlophus cassioides* is found typically in detritus in *Phragmites* swamps. Most of the small staphylinid species are also predators in accumulations of wet decaying vegetation, as are the hydrophilid species *Megasternum boletophagum* and *Anacaena globulus.*

Many of the phytophagous species feed on a variety of marsh plants. *Donacia sparganii, D. marginata, D. bicolor* and *D. thalassina* all feed on reedy plants such as *Sparganium* and *Carex*. *Donacia cinerea* feeds chiefly on *Typha, Phragmites, Sparganium* and *Carex. Plateumaris braccata* is a monophage, feeding almost exclusively on *Phragmites communis* (Koch, 1992). The weevils *Notaris scirpi, Limnobaris pilistriata* and *Thryogenes* also feed on a variety of reedy vegetation.

The larvae of *Pelochares versicolor* and *Limnichus pygmaeus* excavate burrows in wet soil where they feed on algae. Most species of *Trogophloeus* also feed on algae. The predators *Dyschirius aeneus* and *D. salinus* have been associated with this genus, upon which they are probably feeding.

Very few species in the assemblage live in drier habitats. The weevil *Otiorhynchus ovatus* is xerophilous and feeds on the leaves of a wide variety of herbaceous plants (Duff, 1993; Luff, 1996). Similarly, the larvae of the click beetle *Adelocera murina* feed on roots in meadowland. Species of *Sitona* feed on the roots of Papilionaceae. The carabid *Zabrus tenebrioides* is chiefly a vegetarian, feeding on seeds of various grasses. The larvae, however, will readily eat animal matter (Lindroth, 1992). Species of *Phalacrus* feed on smutted inflorescences of various grasses (Thompson, 1958).

Several species of weevil are dependent on trees. *Rhamphus pulicarius* is polyphagous, feeding on the leaves of *Salix, Betula, Populus* and *Myrica* (Morris, 1993). Two species are exclusively restricted to *Quercus*. The larvae of *Rhynchaenus quercus* mine the leaves of oaks and those of *Curculio venosus* develop inside acorns (Koch, 1992). *Melolontha melolontha* feeds on leaves of various deciduous trees, frequently on oaks (Koch, 1989).

Of particular significance in this assemblage are the dung beetles of the family Scarabaeidae: *Copris lunaris, Caccobius schreberi, Onthophagus massai* (we continue to use this name despite its debated taxonomic status – see the Biostratigraphy section of the Discussion), *Aphodius erraticus* and *Heptaulacus sp.* are all obligate dung feeders. *Caccobius schreberi* is found on dry, sandy warm slopes and banks, especially associated with cattle and horses and has a distinctly thermophilic distribution, being abundant in central and southern Europe, avoiding alpine and northerly areas (Koch, 1989). *Onthophagus massai* is endemic in Sicily, a subspecies that replaces *Onthophagus fracticornis* forms at altitude (Baraud, 1977). *Pleurophorus caesus* burrows in rather dry sandy soils often under decaying vegetation or dry cow dung. Their presence suggests that large herbivorous mammals were using the area to feed. Their dung must have been deposited on dry, sandy land for both them and their larvae to be able to feed and develop. Most histerids are found in dung and carrion where they are predators on maggots and beetle larvae. It is interesting to note therefore that *Dermestes murinus* feeds on the dried flesh of desiccated carcases (Duff, 1993).

Several species are typical of saline habitats. Thus, *Dyschyrius salinus* occurs exclusively on seashores and inland only in saline habitats (Lindroth, 1992). *Bembidion minimum* and *Bembidion fumigatum* are also predominantly halophilous, though occasionally they have been found away from saline habitats (Lindroth, 1974; Lott, 2003). Although some other species in this assemblage are salt tolerant they are not exclusive indicators of saline conditions.

Ostracoda

Two small samples in pollen tubes (BFC/01 and BFC/02) were collected from the same location as the Coleptera sample (10–63 cm from the base) and the residue from the latter was also processed for ostracod analysis (Supplementary Table S5). The samples were first 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 µm 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.

Extra-well-preserved ostracod material, including many carapaces, from the ‘insect sample’ of unit 4a has enabled accurate identification of the *Herpetocypris* and *Potamocypris* species. Using a revision of European *Herpetocypris* by Gonzales Mozo *et al*. (1996) that illustrates (by scanning electron microscopy – SEM) valve and carapace features as well as appendages, it has been possible to identify, with some confidence, the species in unit 4a as *Herpetocypris helenae* G.W. Müller. This is on the basis of carapace shape and morphology of the marginal zone in the left valve (specifically the inner list). Interestingly, therefore, it is not *H. reptans* (Baird), which, where *Herpetocypris* occurs in both fossil and recent UK sites, is reported almost ubiquitously. Instead, it belongs to the *H. chevreuxi–helenae–intermedia* lineage of Gonzales Mozo *et al.* (1996), and of these three, it best corresponds to *H. helenae*, which has more elongate valves, a greater separation of the left valve inner list from the outer margin, and a correspondingly more pronounced overlap anteriorly and posteriorly. Its modern distribution is still poorly known, although it has been reported previously in England as *H. palpiger* Lowndes, 1932 (a junior synonym). It has no previous Pleistocene fossil record (Meisch, 2000), but this is most likely due to misidentification.

The ‘Coleoptera sample’ from unit 4a has also enabled two species of

Potamocypris to be identified following SEM images of, valve and carapace morphology (Meisch, 1984). Finally, where there are more than one candonid species in a sample, it has not been possible to assign their respective juveniles with any confidence. They are therefore listed separately as *Candona* spp. (indet. juveniles).

Systematic treatment otherwise follows Meisch (2000), as do, for the most part, the environmental preferences.

The ostracod fauna is characterized by *Herpetocypris helenae, Cypridopsis vidua* and *Potamocypris* spp. In the sediment samples (BFC/01 and BFC/02) these make up about 70–80% of the fauna; even in the 'insect sample' concentrate, where candonids occur in greater numbers, they still make up almost 50%. *Herpetocypris helenae* has relatively long swimming setae on the antennae, so it can swim (as opposed to *H. reptans*, e.g., which cannot), although it undoubtedly spends most of its time on the bottom or on plants. It prefers small (even stagnant) water bodies, swamps and slow-flowing streams and rivers, with lots of vegetation. *Cypridopsis vidua* likes all permanent water bodies with rich, shady vegetation (especially *Chara* mats) and is an active swimmer. Both species of *Potamocypris* in the samples, unfortunately, have a poorly known ecology, due to previous misidentification (Meisch, 2000), but the more common *P. similis* appears to prefer muddy bottoms of weedy ponds and slow-flowing streams, whereas *P. fallax* inhabits springs and seeps. *Herpetocypris helenae* and *C. vidua*, as well as the candonids (*Candona* and *Pseudocandona* species), can also tolerate low brackish conditions (< 3 or 4‰).

Vertebrates

Three bulk samples were examined from the basal 50 cm of unit 4a and are treated as one for the purpose of the results presented below. Samples were washed through a 500 µm sieve, the dry residue graded through 2 mm, 1 mm and 500 µm and any microvertebrate teeth and bone fragments picked from under a low-power binocular microscope.

The three samples have yielded a combined total of 402 small bone fragments and teeth (Supplementary Table S6), representing a variety of small mammal, reptile, amphibian, fish and bird taxa, in addition to a single rib fragment of an indeterminate cervid-sized large mammal. Of the 402 small bone fragments and teeth, 77 of them are too comminuted or lacking in diagnostic surface features so as to be undetermined even to Class level. The material is uniformly stained a dark brown to black colour, with tooth enamel varying from black to blue-grey, and frequent dark orange sediment adhering. The bones and teeth are well preserved, with the fish remains spectacularly so; several fish vertebrae still retain the full length of the vertebral spines, and cyprinid pharyngeal bones with teeth still *in situ* are present within the sample, as are several fragile fish-scale fragments. Remains of terrestrial vertebrates are equally well preserved, for example a wood mouse maxilla with teeth *in situ*. No signs of predator damage or digestion are apparent on the small vertebrate remains, with the exception of a small and partial bird humerus that has some evidence of pitting and corrosion to the proximal end, consistent with digestion by an avian predator.

Fish dominate the identifiable remains of the assemblage (72% of the assemblage), followed by small mammals (25%), herpetofauna (2%) and birds (< 1%). In terms of environmental significance, the fish assemblage is characterized by the presence of cyprinid (carp family) species and their associated predator, the pike (*Esox lucius*). Within the cyprinids, remains of roach (*Rutilus rutilus*), rudd (*Scardinius erythopthalmus*) and tench (*Tinca tinca*) have been identified, all of which are native to Britain today. Also present is the European pond terrapin (*Emys orbicularis*), which today occurs no closer to Britain than central France (Fritz & Laufer, 2007). The assemblage also contains a number of the characteristic vertebrae of the European eel (*Anguilla anguilla*). This species is facultatively catadromous, inhabiting fresh, brackish and coastal waters but migrating to pelagic marine waters to breed (Wheeler, 1969). Under natural conditions, it therefore occurs only in water bodies that are connected to the sea.

Adjacent to the water body, the small mammals (bank vole, wood mouse, common shrew) and herpetofauna (grass snake, frog or toad and undetermined newt) indicate a mosaic of rough, damp grass, bushy scrub and deciduous woodland (Arnold & Burton, 1980; Corbet & Harris, 1991).

Discussion

Depositional environment

The sedimentology of unit 4a is reminiscent of the infilling of an avulsion-abandoned channel (Toonen *et al*., 2012), with initial deep incision, up to a minimum depth of 3.7 m, from a surface height of at least 2 m OD at the top of unit 3c to –1.7 m OD into the bedrock Oxford Clay. The basal fining upward sequence (0–40 cm) appears to represent the waning flow deposits of the avulsion event, the energy of which was sufficient to move cobbles as bedload. The molluscan evidence suggests, however, that energy reduced rapidly following incision. At the time of incision and start of aggradation (the basal 20 cm) the riverine environment provided a suitable habitat for the spring dweller *B. marginata* to flourish, but above 20 cm the numbers of *B. marginata* dramatically declined. The coleopteran and ostracod samples included material from the upper part of the basal 20 cm, and spring dwellers (*A. guttatus* and *P. fallax* respectively) were also recorded in their assemblages. For the basal 20 cm of the succession, the molluscan assemblage indicates that standing/quiet-water and clear-water conditions, as well as sandy/stony substrates, were rare within the immediate catchment and that marsh and wet grassland would have been common nearby.

The remainder of the basal fining upward sequence (i.e. above 20 cm) and the following coarsening upward sequence (the plant macrofossil, coleopteran, ostracod and vertebrate assemblages largely represent this part of the sedimentary succession) appear to reflect a period of stability that provided good preservation potential for the contained fossil fauna. Pollen data indicate a decrease in Poaceae at this level and an overall increase in herbs at the expense of trees and shrubs and spores. Plant macrofossil evidence indicates a number of species were present that prefer marginal swamp and fen conditions.

Molluscan data indicate a reduction in numbers from moving-water habitats, an increase in those preferring standing/quiet-water and that marsh and wet grassland habitats were common. It therefore appears that the sudden reduction in *B. marginata* numbers coincided with a rising water table and reduction in the potential for subaerial springs to form.

Amongst the Coleoptera the presence of both running-water and still-water species suggests that the river meandered along its course, alternating between riffles and pools. The preponderance of both carnivores and phytophages beetle species that live exclusively in hygrophilous eutrophic fen vegetation indicates that marginal swamp habitats were widespread and likely covered large areas of the river floodplain. Very few species in the assemblage live in drier habitats, suggesting these represent a very small proportion of the landscape habitat. Based on modern fossil beetle analogue work that examined ecological catchments (Smith *et al*., 2010), it is

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likely that these drier ecosystems were located very close to the deposit, probably within < 100 m at most, perhaps on drier banks and disturbed places.

Of significance in the ostracod fauna is the large numbers of whole adult carapaces as well as valves of juvenile instars, indicating that the fauna is *in situ* and has undergone only minimal transport and size-sorting. The assemblage appears to represent a sluggish or even a stagnant watercourse, with particularly rich vegetation (including charophytes).

The fish remains were from species that inhabit lowland, nutrient-rich, slow-flowing water bodies with dense, submerged vegetation (Wheeler, 1969). The exceptional state of preservation of both fish and terrestrial vertebrate material attests to a very gentle depositional environment within the channel, and suggests that the specimens were not transported any significant distance prior to deposition.

The presence of *D. salinus*, *B. minimum* and *B. fumigatum* in the beetle fauna strongly suggest nearby saline habitats, which is supported by pollen evidence for *Hippophaë* and plant macrofossil evidence for *S. maritimus*. The presence of the reed beetle *P. braccata* is also interesting in this respect because it is often associated with *Phragmites* growing in brackish waters in slow-moving rivers and estuaries (Hyman 1992). The fauna also includes species that are entirely typical of freshwater habitats and it is possible that the river channel was close to the uppermost tidal limit at this time. However, although some of the ostracods present can tolerate slightly saline conditions, estuarine species such as *C. torosa* are absent from the assemblage, suggesting a near-coastal rather than upper estuarine environment.

The upper part of unit 4a appears to represent successive flood deposits, coinciding with an increase in molluscs with a preference for moving-water habitats. There is also a slight increase in molluscs preferring clear-water conditions and sandy/stony substrates, as well as those preferring dry conditions. Pollen data indicate an expansion in trees and herbs, and there is also a sharp increase in charcoal concentration suggesting greater potential for natural fires under drier conditions.

Unit 4a probably represents the infilling of an avulsion-abandoned channel that subsequently may have been a backwater to the main channel, or a largely inactive channel. There may be a significant hiatus between unit 4a and 4b, but the increased molluscan signal for moving-water conditions at the top of unit 4a may indicate that the main channel was again nearby. Hence the succession from unit 4a to 4b may have resulted from minor channel migration over a short period. In contrast, unit 4b represents deposition as a lateral accretion sequence in the main channel of a sinuous river. The molluscan data for unit 4b indicate an increase in numbers of those with a preference for moving-water habitats and an expansion of clear-water conditions and sandy/stony substrates at the expense of those preferring standing/quiet-water habitats. Significantly, the pollen data indicate the presence of hazel in unit 4b, whereas it was absent in unit 4a, with an expansion of Poaceae, *Plantago lanceolata* and Pteropsida, and continued presence of *Nuphar*. There is a notable difference in the composition of the molluscan assemblage at the very top of unit 4b in section E, where the percentage of terrestrial species increases to 45%, which probably represents filling of the channel rather than a climatic signal. The corresponding plant macrofossil data indicate an increase in *Rubus* and *P. aviculare*, which prefer dry disturbed ground habitats, compared with unit 4a. The channel cannot have been completely infilled at this time though, because aquatic species such as *Z. palustris* and the damp-ground species *S. maritimus* were also recorded at the top of unit 4b.

Palaeoclimate

The presence of pollen of ivy, holly and yellow water-lily in channel C indicates fully temperate conditions. Climatically, all the species observed in the plant macrofossil data also are consistent with the interpretation of interglacial conditions, with particular evidence of warm conditions also indicated by the presence of yellow water-lily as well as brittle naiad (*Naias minor*). The number of species represented in the molluscan assemblage of channel C and the presence of the thermophile *B. marginata* suggest full interglacial conditions. It is clear from the coleopteran fauna that the sediments of unit 4a were deposited in fully temperate interglacial conditions, and this is particularly reinforced by the presence of thermophiles such as *B. elongatum, P. versicolor, C. schreberi* and *O. massai*, all of which today live across areas of central and southern Europe, avoiding northern Europe. There are no beetle taxa associated with alpine conditions. Both the ostracod and vertebrate fauna of unit 4a indicate fully temperate conditions, and in particular the co-abundance of bank vole and woodmouse is considered a characteristic feature of British interglacials.

Quantitative palaeotemperature reconstructions based on the coleopteran, ostracod and vertebrate assemblages of unit 4a confirm fully interglacial temperate conditions. The coleopteran Mutual Climatic Range (MCR) method (Atkinson *et al.*,

1987) uses the BugsMCR function of the BugsCEP database (Buckland & Buckland, 2012), to calculate T_{max} (mean July air temperature) and T_{min} (mean January air temperature) for each sample investigated: T_{range} 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 & Mezquita, 2008; Horne *et al*., 2012) likewise reconstructs mean January and mean July air temperatures. For the MOTR the most up-to-date published calibrations were used (Horne *et al*., 2012).

Twenty-nine species in the coleopteran assemblage were used to obtain the temperature reconstruction using the MCR database (see Supplementary Table S4). They give the following palaeotemperature values with 100% overlap of the climatic ranges of the species utilized:

mean July temperature lay within the range +17°C and +24°C
mean January temperature lay within the range −7°C and +7°C

Since several of the more southern species, which today live in central and southern Europe (e.g. *B. elongatum, O. massai, P. versicolor*) are not present on the MCR database, it is highly likely that the actual temperatures were closer to the higher limit of the MCR ranges.

Seven ostracod species were included in the MOTR reconstructions: no calibrations are currently available for *H. helenae*, *P. fallax* and *P. similis*. The MOTR results are:

mean July air temperature lay within the range: +12 to +22°C;
mean January air temperature lay within the range: −10 to +7°C.

Comparison of the coleopteran MCR and MOTR results shows that they are consistent with each other; a refined result can therefore be obtained from the ‘mutual mutual’ ranges from the two methods (as described by Langford *et al*., 2014a):

mean July air temperature lay within the range +17 to +22°C;
mean January air temperature lay within the range −7 to +7°C.

Further refinement is possible, taking account of vertebrate threshold temperatures. Rudd spawn in April–July, when temperatures rise above 15°C, and tench spawn in water temperatures above 19°C. The presence of pike implies winter water temperatures above freezing (Wheeler, 1969). Additionally, *E. orbicularis* requires minimum summer temperatures of 18°C in order to incubate its eggs, implying elevated summer temperatures (Stuart, 1979; Coxon *et al*., 1980). These data together indicate minimum summer temperatures of +19°C and winter temperatures above 0°C. It must be noted that these are water temperatures, which in sheltered conditions may well have been buffered against extremes of air temperature; nevertheless these thresholds fall within the 'mutual mutual' ranges determined by the coleopteran MCR and MOTR methods and it can be suggested, therefore, that mean air temperatures were likely as follows:

mean July air temperature lay within the range +19 to +22°C;
mean January air temperature lay within the range 0 to +7°C.

The present-day equivalent values for Whittlesey are July +17°C and January +3°C. We conclude that while winter temperatures may well have been similar to those of today, summer temperatures were at least 2°C warmer.

Coope (2010) applied MCR analysis to eight Ip IIb sites, including Bobbitshole, Deeping St James, Shropham, Trafalgar Square and Woolpack Farm, and his calculated mean July temperature of 20°C and mean January temperature of 0°C are consistent with the ranges determined for unit 4a. Candy *et al*. (2016) concluded that the thermal optimum of the Ipswichian (Ip II) was of relatively short duration (<1200 years) and reported only one of ten British Ipswichian sites as recording temperatures significantly warmer than Holocene temperatures: Trafalgar Square at +20 to +21°C (July) and +1.5 to +3°C (January). Our new reconstruction for Whittlesey adds a second such site.

These quantified palaeotemperature ranges are supported by the temperature requirements of some of the plant species represented within the fossil assemblage. For example, it has been suggested that ivy will not tolerate an average of less than −1.5°C for the coldest month (Iversen, 1944; West, 1957; Barber & Brown, 1987; Keen *et al*., 1999). Other species present that have been regularly seen in other Ipswichian deposits (Phillips, 1974), such as yellow water-lily and brittle naiad, suggest summer temperatures warmer than today during accumulation of unit 4a. In addition, molluscan species *B. marginata, H. itala itala*, *T. cylindrica, P. moitessierianum*, *A. vorticulus* and *P. supinum* as well as coleopteran species *B. elongatum, P. versicolor, C. schreberi*, *O. massai*, *B. octomaculatum, Z. tenebrioides,* *C. lunaris* and *P. caesus* suggest warmer summers and a more continental climate during the infilling of channel C than experienced in eastern England at the moment.

Biostratigraphy

Although the presence of *B. marginata* and absence of *C. fluminalis* seen here has been considered to provide biostratigraphical evidence for assignment to the Ipswichian Interglacial (Keen, 1990; Preece, 1995), such a situation also could arise due to differences in sedimentary facies (Langford *et al*., 2014a) or the reworking of older material into younger deposits (West *et al*., 1994; Dixon, 1997; Boreham, 2002; Briant *et al*., 2004). In the case of the robust bivalve *C. fluminalis* the potential for reworking and subsequent preservation is particularly high (e.g. Fig. 8). In the present context it is instructive to consider that somewhere downstream of channel C, north of section A, there may be a deposit preserved that contains elements of the reworked fauna of unit 3c, including *C. fluminalis*, secondarily reworked into unit 4a or 4b, or both, containing *B. marginata*. The biostratigraphical use of the presence of *B. marginata* with presence or absence of *C. fluminalis* therefore should be applied with caution (West *et al*., 1994).

Sparks (in Phillips, 1976) considered that the combined presence of *B. marginata*, *V. enniensis, A. vorticulus* and *G. laevis*, all in significant numbers, were characteristic of the Ipswichian Interglacial. At least three of these species do occur in the channel C counts (Supplementary Table S3). In addition, Dixon (1997) noted that *H. complanatus*, *Sphaerium* (*Acroluxus*) *lacustre* and *P. personatum* (rare or absent in channel C) occurred at many Ipswichian sites, and in combination with *B. marginata* and *V. enniensis* could be considered as characteristic of this interglacial. It should be noted, however, that none of these species is restricted to Ipswichian deposits, and that they can be found in combination in interglacial deposits of different ages.

Orthophagus massai, *C. schreberi*, *B. elongatum* and *C. lunaris* are among the 13 most common exotic beetle species found at Ipswichian sites (Walkling, 1996). Of particular interest is the presence of *O. massai*, which so far has been found only as a fossil in up to at least seven Ipswichian Interglacial deposits, including unit 4a. Although we have continued to use the name *O. massai*, its taxonomic status is debated. *Orthophagus massai* is likely a subspecies or a genetically distinct Sicilian population of *O. francticornis* that are going through genetic speciation, probably due to genetic isolation. This is based on modern genetic and morphological research of four different Italian populations of *O. fracticornis* (Pizzo *et al*., 2011). Here, we feel that it is important to distinguish this morphotype from *O. fracticornis*, being a much smaller type and likely to be an insular variety, based on modern studies and therefore likely of interest around species insularity in MIS 5e. Moreover, as genetic studies have been undertaken on only modern specimens we cannot explore the relationship between the modern specimens of *O. massai* and those found in the fossil record, which may still represent a different species. Morphological and genetic work on the fossil specimens would need to be undertaken to be clear on this attribution. The late Professor Coope distinguished these two varieties in the fossil record and so in the context of Ipswichian biostratigraphy we have retained these identifications.

Other exotic species within the channel C assemblage, or species not commonly present in England today, that are common at other Ipswichian sites include *N. minor*, *Nuphar*, *T. cylindrica*, *A. vorticulis*, *P. moitessierianum* and *E. orbicularis*, but again these are not biostratigraphically diagnostic for the British late Middle to Late Pleistocene. The presence of water vole (*Arvicola terrestris cantiana*) indicates an age no older than MIS 13, but unfortunately the single complete molar present is not one that is suitable for calculation of the enamel differentiation ratio. Otherwise, there is nothing in the small vertebrate assemblage that is age-diagnostic, since all taxa are regular components of British late Middle and Late Pleistocene interglacials.

Ipswichian biozonation and onset of the thermal optimum

It appears that unit 4a of channel C represents the pre-temperate zone (pollen biozone I; Turner & West, 1968) of an interglacial. This is interpreted as an ostensibly open grassland environment with scattered boreal woodland and light-demanding shrubs such as juniper and sea buckthorn. Locally, tall-herb, bank-side and marginal vegetation is also indicated, surrounding open water up to ca. 2 m deep. There are clear signs of impending early temperate conditions, with an up-section increase of oak and the presence of yellow water-lily. In contrast, it appears that unit 4b represents full early temperate (pollen biozone II) conditions with the development of hazel–oak woodland. Taken together, the pollen evidence suggests that the sediments of channel C were deposited during the earlier stages of an interglacial period. In addition, the pollen data represent accumulation from the wider catchment, including plants growing in dry land habitats away from the river, rather than representing an insular hydroseral succession that might occur in response to channel cut-off.

Of the sites identified by Lewis *et al*. (2010) as being reliably Ipswichian in age, only Bobbitshole and Swanton Morley have pollen data representing Ip I. At Bobbitshole biozone Ip Ib is characterized by *Betula–Pinus* forest, with *Ulmus* starting to expand and *Quercus* and *Acer* first appearing (West, 1957, 1980). The same characteristic tree pollen spectrum for this biozone was also evident at Swanton Morley (Phillips, 1976; Coxon *et al*., 1980). The pollen assemblage for unit 4a matches that for Ip Ib at both Bobbitshole and Swanton Morley. All species present in the pre-temperate substage molluscan assemblage at Bobbitshole (marked by an asterisk in Supplementary Table S3) are also present in unit 4a, with the exception of *Zonitoides nitidus* (O. F. Müller 1774), which is recorded as common in biozone Ip Ia (Sparks, 1957). The presence of *C. minimum*, *P. vorticulis*, *H. complanatus* and *A. lacustris* was considered by Sparks (1957) to support the warm climate conditions indicated by the appearance of thermophilous tree species in pollen biozone Ip Ib. There are, unfortunately, no molluscan or coleopteran data available from Swanton Morley for this biozone so comparison is not possible.

The rich multidisciplinary records for the Deeping St James (Keen *et al*., 1999), Woolpack Farm (Gao *et al*., 2000), Swanton Morley (Phillips, 1976; Coxon *et al*., 1980), Tattershall Castle (Holyoak & Preece, 1985) and Trafalgar Square (Preece, 1999) sites, although fragmentary, provide detailed insight into pollen biozone Ip IIb, which is considered to represent the thermal optimum. The temperate (Ip II) pollen spectrum and molluscan assemblage of unit 4b are also similar to the records from these sites, as well as Bobbitshole (Sparks, 1957; West, 1957), and therefore can be assigned to pollen biozone IIb.

The surprising feature of unit 4a (Ip Ib) here at Whittlesey is that it records many of the exotic thermophilous species listed in Supplementary Table S7 that indicate optimum thermal conditions in pollen biozone Ip IIb. This suggests that for the first time we have evidence of the onset of the Ipswichian thermal optimum in the pre-temperate zone, thereby indicating much more rapid biological response to climatic amelioration. This is markedly earlier than recorded at Bobbitshole, where the onset of the thermal optimum is only securely evidenced in pollen biozone Ip IIb, with merely ambiguous palaeobotanical evidence for possible early onset of the thermal optimum in the pre-temperate biozone. Supplementary Table S7 shows that at

Whittlesey, unit 4a records 17 thermophilous species from biozone Ip Ib, whereas Bobbitshole records only eight. Early onset of the thermal optimum is also hinted at in the coleopteran and molluscan assemblages and quantitative paleotemperature reconstructions at Shropham (Walkling, 1996; Dixon, 1997), but without supporting pollen biozonation data cannot be compared effectively with unit 4a. At Swanton Morley, Coxon *et al*. (1980) report the only Ip IIa temperate vertebrate fauna to date, which they consider supports palaeobotanical data that indicate rapid climate amelioration in the interglacial (Phillips, 1974; Stuart, 1976). This temperate vertebrate fauna resembles those of Ip IIb. The small-vertebrate assemblage from unit 4a at Whittlesey (Supplementary Table S6) is similar to this, including the presence of *E. obicularis*. Together the records from these sites demonstrate that rapid biological response to climate amelioration was underway well before Ip IIb. If indeed the Ipswichian Interglacial does correlate with the northwest Europe LIG, however, transition from pollen biozones Ip Ia–Ip IIb (E1–E3) may have taken place over just a few centuries (Sier *et al*., 2015).

Conclusions

A comprehensive, multidisciplinary, palaeoenvironmental investigation of a fossiliferous channel fill (channel C) at Whittlesey, eastern England, has been undertaken. Amino acid age estimates indicate deposition of channel C during the LIG stage, and all lines of palaeoenvironmental evidence indicate fully temperate conditions. Sedimentologically the infill of channel C comprises two fluvial deposits: the infill of an abandoned anastomosed channel at the base (unit 4a), overlain by upward and laterally accreting, interbedded gravels and sandy silts displaying low-angle stratification (unit 4b). Pollen analysis indicates deposition of unit 4a in pollen biozone Ip 1b and unit 4b in Ip IIb. The palaeoecological evidence from channel C indicates the presence of a large, slow-moving water body similar to British lowland rivers today, which had access to the sea and was not frozen over during winter months. Although some beetle and plant species present have a preference for saline and brackish habitats, the ostracod evidence indicates a near-coastal site rather than upper estuarine. Stable, low-energy conditions are indicated by the species present between 20 and approximately 60 cm from the base of unit 4a, which coincided with a rising water table and a reduction in habitat suitable for *B. marginata*.

Quantified palaeotemperature reconstructions based on the beetle, ostracod and vertebrate assemblages indicate that mean July air temperature during deposition of unit 4a lay within the range +19 to +22°C and mean January air temperature lay within the range 0 to +7°C, indicating that winters were probably similar to those of today but summers were significantly warmer. These palaeotemperature ranges encompass those for Ip IIb deposits at Trafalgar Square (+20 to +21°C and +1.5 to +3°C) reported by Candy *et al*. (2016) and add a second site in support of their conclusion that mean July temperatures during the Ipswichian thermal optimum were significantly higher than Holocene temperatures so far recorded. Exotic thermophile species present in both units likewise suggest warmer summers and a more continental type of climate. These species include the plant *N. minor,* mollusc *B. marginata,* beetles *B. elongatum, P. versicolor, C. schreberi* and *O. massai*, and the reptile *E. orbicularis*. Of these, only *O. massai* may have biostratigraphic significance. Particularly significant is the presence of these thermophiles at the commencement of the interglacial, in the deposits of Ipswichian biozone Ip Ib (unit 4a), in contrast to many other sites where they occur only in biozone Ip IIb. The floral and faunal evidence from unit 4a therefore establishes the onset of the Ipswichian thermal optimum in the pre-temperate substage, earlier than traditionally thought, and indicates a rapid biological response to climate amelioration.

An important recent review of British LIG sites identified that less than one-third could be securely assigned to the Ipswichian Interglacial based on age estimates and/or a characteristic mammalian fauna that included *Hippopotamus* (Lewis *et al.,* 2010). Only a few of those sites have a record of the pre-temperate, late temperate or post-temperate substages and among those only Bobbitshole and Swanton Morley have records of the Ipswichian pre-temperate zone. Their records support the evidence from unit 4a that rapid biological response to climate amelioration was underway before Ip IIb, but that evidence is not as strong as at Whittlesey.

Early onset of the Ipswichian thermal optimum does, however, accord with other LIG records, such as the global MIS 5e (Lisiecki & Raymo, 2005), the Dutch Eemian (Zagwijn, 1961) and the southwest Europe LIG (Shackleton, 1969; Sánchez-Goñi *et al*., 1999). This accordance is not without its problems though, because the date of commencement of the LIG has been found to be different for each of these records (Fig. 1). These different LIG commencement dates, if valid, raise the question as to whether there are some Ipswichian Interglacial sites that correlate with the northwest Europe LIG (late commencement) and some with the southwest Europe LIG (early commencement)?

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Figure captions

Fig. 1. Last Interglacial chronostratigraphy: marine oxygen isotope, Blake Event, sapropel and Eemian biozone data from Sier *et al*. (2015). The LR04 curve is the stacked record of Lisiecki & Raymo (2005) and represents a global record from deep-sea cores, and the marine isotope stages (MIS) displayed below are related to this. The onset of the 'global' Eemian is tied to the onset of sapropel S5 of the eastern Mediterranean. The MD95-2042 curve is the benthic record off the Iberian coast (Sanchez-Goñi *et al*., 1999) and represents the Eemian of southwest Europe. The Eemian of northwest Europe is from a fluvial record at Rutten in the Dutch 'type-site' area (Sier *et al*., 2015). Onset of both the northwest and southwest Europe Eemian is tied to the onset of the magnetic Blake Event, which here is depicted for the northwest Eemian. British U-series data are from Gascoyne *et al*. (1983), Jones & Keen (1993), McFarlane & Ford (1998), Bowen (1999) and Lewis *et al*. (2010); the solid grey line labelled Dutch Eemian in the thermoluminescence data indicates the range of median data for 21 individual dates and the dashed line indicates 1σ SD (Peeters *et al*., 2016). British luminescence data are from Keen *et al*. (1999), Gao *et al*. (2000), Holyoak & Preece (1985) and Preece *et al*. (1990).

Fig. 2. (**a**) British Ipswichian sites: sites identified by Lewis *et al*. (2010) are shown as circles – filled circles represent sites where the Ipswichian deposit has been numerically dated and others represent those assigned by mammalian biostratigraphy, some of which may be constrained by age estimates from overlying and/or underlying deposits; other sites of interest mentioned in the text are shown as open squares and the study site by a filled square. (**b**) Pollen-zone ranges at selected Ipswichian sites (black bars) and of Wing (grey bar), which is of uncertain age.

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Fig. 3. (**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 to be Ipswichian (MIS 5e) in age. (Based on BGS, 1984.) (**b**) Locations of channels A–D and sections A, C and E.

Fig. 4. Comparison of amino acid racemization data determined following standard procedures (Penkman *et al*., 2008, 2013) for three *Bithynia* opercula from mollusc sample b, unit 4a, compared with AAR data for other UK Ipswichian sites (Penkman

et al., 2011). Free amino acid (FAA) versus total hydrolysable amino acid (THAA) D/Ls indicate that the Bradley Fen material is consistent with correlation with the Ipswichian.

Fig. 5. Schematic diagram of the sedimentary succession in section A, Bradley Fen and detailed logs A and E from sections A and E respectively. Note the exaggerated vertical scale for section A.

Fig. 6. (**a**) Unit 4b at the western end of section C in Bradley Fen Quarry (see Fig. 4) comprises the low-angle cross-stratified beds beneath the staff (1.2 m long) that dip to the east. (**b**) Large-scale planar cross-beds in unit 3b in a perpendicular section immediately south of section C. The spade is 90 cm long.

Fig. 7. Pollen diagram for unit 4a and 4b in section A, Bradley Fen.

Fig. 8. Comparison of *Corbicula fluminalis* shells equivalent in age to MIS 7 from different units at Whittlesey (a–e) and from Somersham (f): (a) from large-scale sand lens in unit 2b (West Face Quarry); (b) from muddy gravel facies in unit 2a (West Face Quarry); (c) from subhorizontally stratified gravels in unit 2b (West Face Quarry); (d) from gravel pocket in unit 3c (Bradley Fen Quarry); (e) from sand and gravel lens at the top of unit 3b of Langford *et al*. (2014b) in West Face Quarry (unit F2 in Langford *et al*., 2007); (f) from section SBK at Somersham (West *et al*., 1994). The shells in (a)–(c) are from primary contexts in channel B (Langford *et al*., 2014a), with those in (b) the oldest. At the right-hand end of (c) the specimen beneath is part of a conjoined shell. The shells in (b) and (c) have experienced post-depositional subaerial weathering, but still during MIS 7. Those in (e) were reworked from channel B some time between MIS 7 and MIS 5b: note that two have Fe staining that occurred prior to reworking (i.e. during MIS 7), but two do not. Those in (d) were reworked from channel B in Bradley Fen probably some time in MIS 6 (see text), after sediments of channel B had been subjected to a temperate weathering phase and subsequent cold-stage cryogenic processes. In (f) the shells are believed to have been reworked from pre-existing temperate deposits during the last cold stage (Devensian/Weichselian).

Table 1. *Ipswichian and Eemian pollen biozonation*

Pollen zonation scheme of Jessen & Milthers (1928) applied by West (1957) to Bobbitshole		Pollen biozonation		
		Ipswichian (Turner & West 1968)		Eemian (Zagwin, 19
		Ip IV	Post-temperate sustage: *Pinus–Betula* with *Carpinus*	E6b E6a
		Ip III	Late temperate substage: *Carpinus–Pinus* with *Betula*, *Alnus*, *Quercus* and *Corylus*	E5
f	*Quercus* + *Pinus* + *Corylus*, with its base where *Corylus* starts to increase	Ip IIb	Early temperate substage: *Pinus–Quercus–Corylus* with *Betula–Alnus–Acer–Tilia–Taxus*	E4b E4a
e	*Pinus* (dominant) + *Betula* + *Quercus* + *Ulmus*, with its base where *Quercus* starts to increase	Ip IIa	Early temperate substage: *Pinus–Quercus* with *Betula–Alnus–Fraxinus*	E3b E3a
d	*Betula* (dominant) + *Pinus* + *Ulmus*, with its base positioned where *Pinus* and *Ulmus* start to increase and *Betula* starts to decline	Ip Ib	Pre-temperate substage: *Pinus–Betula* with *Ulmus–Quercus–Acer*	E2b E2a
c	*Betula* (dominant) + *Pinus*	Ip Ia	Pre-temperate substage: *Pinus*	E1

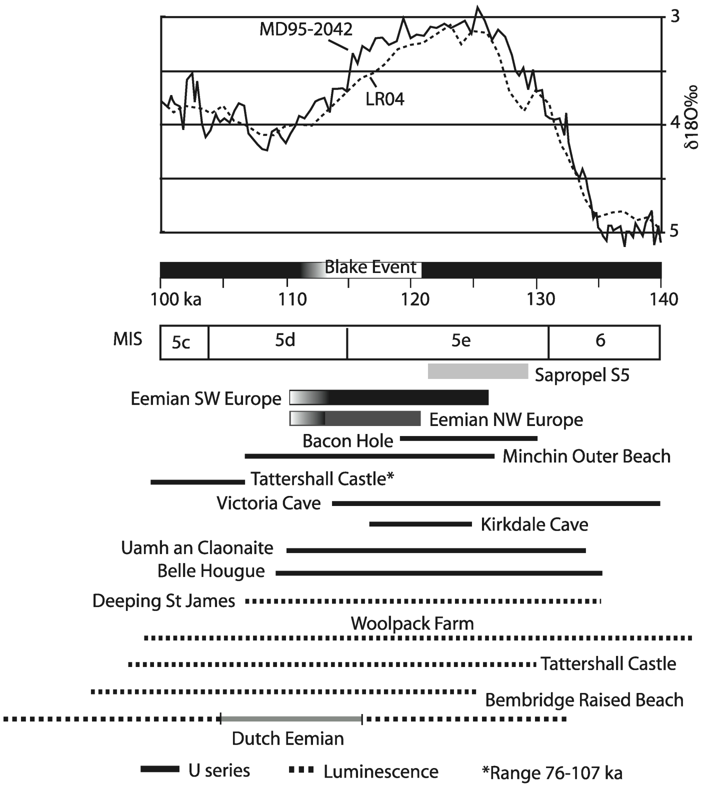

MD95-2042
LR04
3
4
5
δ18O‰
Blake Event
100 ka
110
120
130
140
MIS
5c
5d
5e
6
Sapropel S5
Eemian SW Europe
Eemian NW Europe
Bacon Hole
Minchin Outer Beach
Tattershall Castle*
Victoria Cave
Kirkdale Cave
Uamh an Claonaite
Belle Hougue
Deeping St James
Woolpack Farm
Tattershall Castle
Bembridge Raised Beach
Dutch Eemian
U series
Luminescence
*Range 76-107 ka

Figure 1


(a)
Kirkdale Cave
Sewerby
Victoria Cave
Little Syke,
Stubton Gorse Pond,
Stubton Moor Farm,
Fulbeck Airfield
Cresswell Crags,
Mother Grundy's Parlour
Kirkby on Bain,
Tattershall Castle
Elder Bush
Cave
Swanton
Morley
Boulton Moor
Allenton
Itteringham
Deeping St James
Saham
Toney
Coston
Shropham
Wing
Study site
Chatteris, Block Fen
Woolpack Farm
Old Fallow Farm
Little Comberton
Eckington
Cropthorne
New Inn
Bobbitshole
Marsworth
Upper Channel
Jaywick
Sands
Eynsham
Dorchester-
on-Thames
East Mersea
Restaurant
Site
Ravenscliffe Cave
Brentford
Bacon Hole,
Minchin Hole Outer Beach
Trafalgar Square
Stone Point
Honiton
Pennington
Bembridge
Newtown
Joint Mitnor Cave
Portland East
Eastern Tors Quarry Cave

Figure 2a

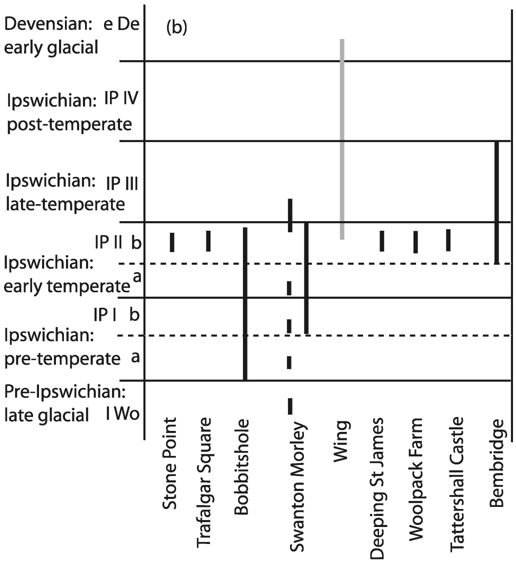
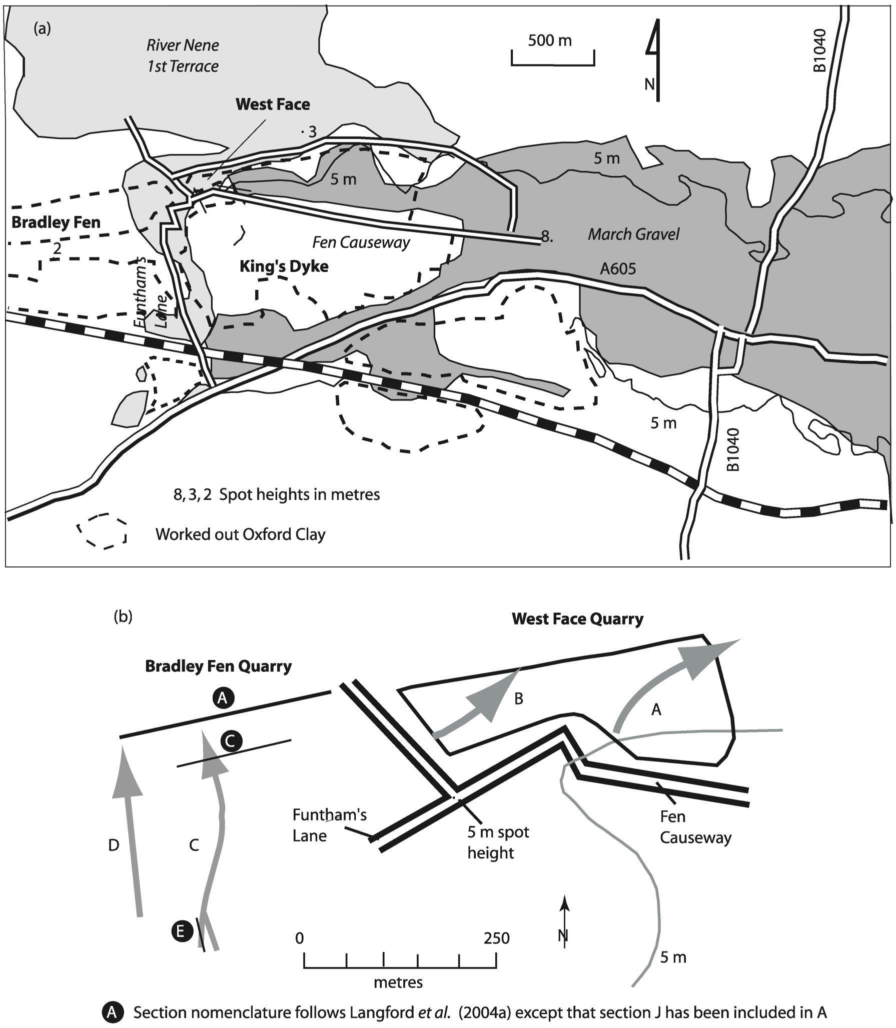

(b)
Devensian: e De
early glacial
Ipswichian: IP IV
post-temperate
Ipswichian: IP III
late-temperate
IP II b
Ipswichian:
early temperate a
IP I b
Ipswichian:
pre-temperate a
Pre-Ipswichian:
late glacial I Wo
Stone Point
Trafalgar Square
Bobbitshole
Swanton Morley
Wing
Deeping St James
Woolpack Farm
Tattershall Castle
Bembridge

Figure 2b



Ⓐ Section nomenclature follows Langford *et al.* (2004a) except that section J has been included in A

A = early Devensian channel (Langford *et al*., 2007)

B = MIS 7 channel (Langford *et al*., 2014a)

C = Ipswichian channel

D = MIS 3 channel (Langford *et al*., 2014b)

Figure 3

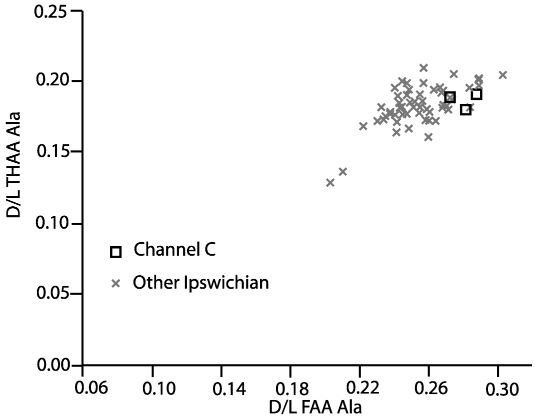

0.25
0.20
0.15
0.10
0.05
0.00
D/L THAA Ala
0.06
0.10
0.14
0.18
0.22
0.26
0.30
D/L FAA Ala
Channel C
Other Ipswichian

Figure 4

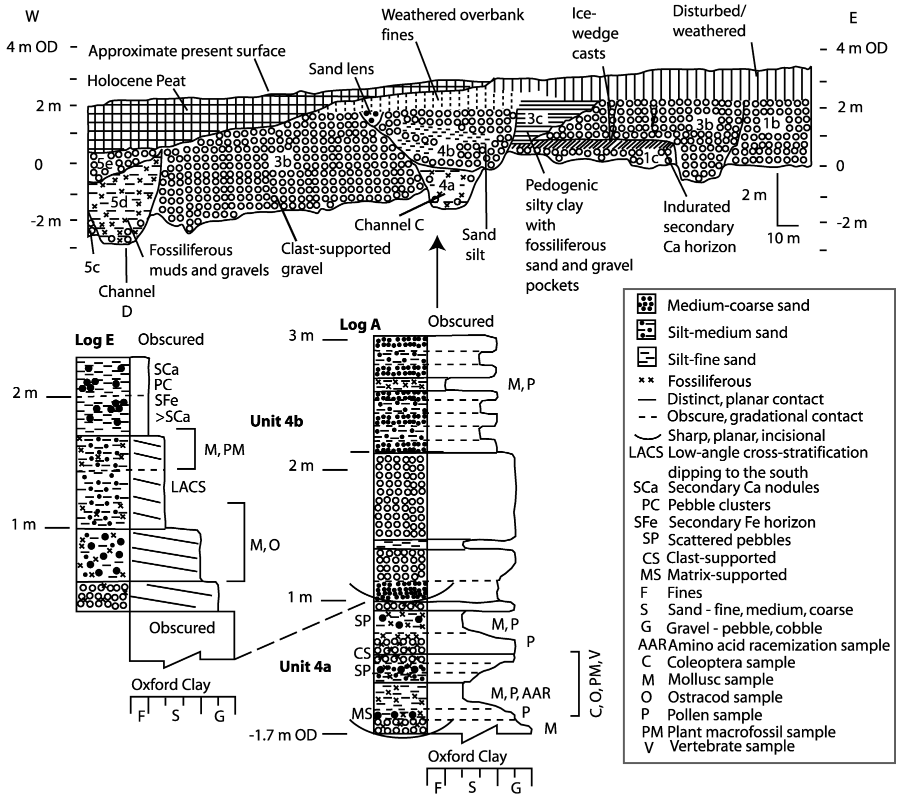

W
E
4 m OD
2 m
0
-2 m
4 m OD
2 m
0
-2 m
Approximate present surface
Holocene Peat
Sand lens
Weathered overbank fines
Ice-wedge casts
Disturbed/ weathered
3c
3b
1b
1c
4b
4a
3b
5d
5e
5c
Channel D
Fossiliferous muds and gravels
Clast-supported gravel
Channel C
Sand silt
Pedogenic silty clay with fossiliferous sand and gravel pockets
Indurated secondary Ca horizon
2 m
10 m
Log E
Obscured
SCa
PC
SFe
>SCa
M, PM
LACS
M, O
2 m
1 m
Obscured
Oxford Clay
F
S
G
Unit 4b
Unit 4a
Log A
Obscured
3 m
2 m
1 m
-1.7 m OD
M, P
M, P
P
SP
CS
SP
MS
M, P, AAR
P
M
C, O, PM, V
Oxford Clay
F
S
G
Medium-coarse sand
Silt-medium sand
Silt-fine sand
Fossiliferous
Distinct, planar contact
Obscure, gradational contact
Sharp, planar, incisional
LACS Low-angle cross-stratification dipping to the south
SCa Secondary Ca nodules
PC Pebble clusters
SFe Secondary Fe horizon
SP Scattered pebbles
CS Clast-supported
MS Matrix-supported
F Fines
S Sand - fine, medium, coarse
G Gravel - pebble, cobble
AAR Amino acid racemization sample
C Coleoptera sample
M Mollusc sample
O Ostracod sample
P Pollen sample
PM Plant macrofossil sample
V Vertebrate sample

Figure 5

Figure 6a

Figure 6b

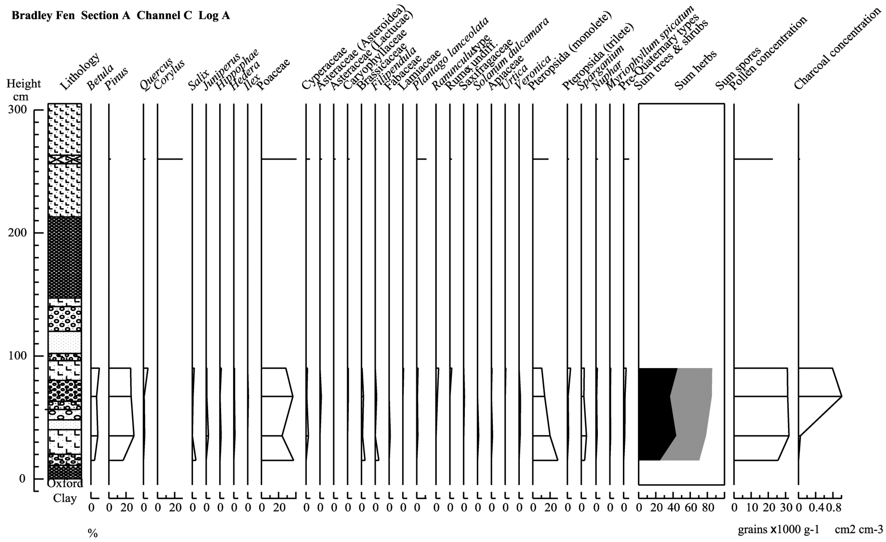

Bradley Fen Section A Channel C Log A
Height cm
Lithology
Betula
Pinus
Quercus
Corylus
Salix
Juniperus
Hippophae
Hedera
Ilex
Poaceae
Cyperaceae
Asteraceae (Asteroidea)
Asteraceae (Lactucae)
Caryophyllaceae
Brassicaceae
Filipendula
Fabaceae
Lamiaceae
Plantago lanceolata
Ranunculus-type
Rumex undiff.
Saxifragaceae
Solanum dulcamara
Apiaceae
Urtica
Veronica
Pteropsida (monolete)
Pteropsida (trilete)
Sparganium
Nuphar
Myriophyllum spicatum
Pre-Quaternary types
Sum trees & shrubs
Sum herbs
Sum spores
Pollen concentration
Charcoal concentration
300
200
100
0
Oxford Clay
0 20 40 60 80
0 10 20 30
0 0.4 0.8
%
grains x1000 g-1
cm2 cm-3

Figure 7

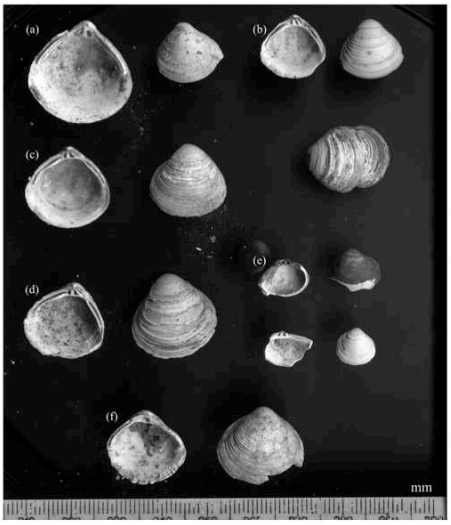


Figure 8

Supplementary material

Table S1. *Amino acid data on opercula of* Bithynia tentaculata *from unit 4a of channel C at Bradley Fen, Whittlesey determined following standard procedures (Hill, 1965; Sykes* et al.*, 1995; Kaufman & Manley, 1998; Penkman, 2005; Preece & Penkman, 2005; Langford* et al.*, 2007; Penkman* et al.*, 2008a, 2008b, 2011, 2013)*†

NEaar number	Sample name	Asx D/L	Glx D/L	Ser D/L	Ala D/L	Val D/L
9516bF	BFBto493-1bF	0.643 ± 0.001	0.209 ± 0.008	0.931 ± 0.005	0.275 ± 0.001	0.159 ± 0.001
9516bH*	BFBto493-1bH*	0.519 ± 0.000	0.131 ± 0.001	0.596 ± 0.012	0.182 ± 0.003	0.097 ± 0.000
9517bF	BFBto493-2bF	0.646 ± 0.001	0.194 ± 0.010	0.989 ± 0.001	0.286 ± 0.002	0.162 ± 0.003
9517bH*	BFBto493-2bH*	0.520 ± 0.000	0.139 ± 0.000	0.642 ± 0.006	0.191 ± 0.018	0.101 ± 0.000
9518bF	BFBto493-3bF	0.641 ± 0.001	0.184 ± 0.001	0.962 ± 0.000	0.265 ± 0.013	0.152 ± 0.002
9518bH*	BFNto493-3bH*	0.520 ± 0.000	0.137 ± 0.000	0.625 ± 0.003	0.189 ± 0.002	0.098 ± 0.001

†Error terms represent one standard deviation about the mean for the duplicate analyses for an individual sample. Each sample was bleached (b), with the free amino acid fraction signified by 'F' and the total hydrolysable fraction by 'H*'.

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Table S2. *Plant macrofossil analysis for residue from vertebrate sample (10–63 cm from base) of unit 4a (section A) and residue of mollusc samples from unit 4b (section E) of channel C in Bradley Fen, Whittlesey**

Ecology	Taxon	Plant part	Section A: unit 4a		Section E: unit 4b	
			Sample A	Sample B	Sample 150–165 cm	Sample 165–180 cm
Woodland and shade tolerant	*Ulmus* sp.	Bud	–	3	–	–
Shrubs and terrestrial plants	*Cerastium arvense*	Seed	–	3	–	–
	Rubus sp.	Seed	–	1	1	3
	Polygonum aviculare	Seed	–	–	–	3
Waterside and damp ground	*Eleocharis* cf. *palustris*	Nutlet	–	7	–	–
	Ranunculus sp.	Achene	7	5	2	30
	Scirpus maritimus.	Nutlet	200	58	–	7
	Sparganium erectum	Fruitstone	12	1	–	–
	Sparganium minimum	Fruitstone	3	–	–	–
	Saponaria officinalis	Seed	–	2	–	–
	Carex sp(p).	Biconvex nutlet	1	1	7	1
	Carex sp(p).	Trigonous nutlet	5	24	–	–
	Potentilla sp.	Seed	7	4	–	1
Aquatic	*Hydrocotyle vulgaris*	Bract	2	1	–	–
	Potamogeton sp.	Fruit	191	200	7	–
	Nymphaea sp.	Seed	4	1	–	–
	Nuphar sp.		1	–	–	–
	Naias minor	Seed	–	29	–	–
	Menyanthes trifoliata	Seed	2	–	–	–

	Ceratophyllum demersum	Seed	14	3	–	–
	Zannichellia palustris	Fruit	–	7	3	38
Other	Undetermined taxon	Budscales	–	1	–	–
	Other		–	29 *Chara* oospores 6 ostracods	–	Fish tooth

*The counts should be treated as abundance/presence/absence data only since volumes of original sample are not consistent and often not known, because all samples were residues from other fossil analyses and not all the residue was processed.

Table S3. *Molluscan analysis of samples from channel C in sections A and E of Bradley Fen, Whittlesey. The nomenclature used by J. Merry (Langford et al., 2004) has been updated, where appropriate, in accordance with the revision of Mollusca by Anderson (2008)*

Taxa[a]	Section A samples†				Section E samples from unit 4b					
	Unit 4a			Unit 4b	Depth from base (cm)					
	a	b	c	d	60–75§	75–90	90–105	105–120	150–165	165–180
Freshwater										
Valvata cristata O. F. Müller 1774*	4	28	25	16	30	10	3	1		
Valvata piscinalis (O. F. Müller 1774)*	213	183	227	157	236	89	193	141	56	21
Belgrandia marginata (Michaud 1831)	133	13	11	2	14	17	12	2		1
Bithynia tentaculata (Linnaeus 1758)*	162	106	74	30	33	34	30	27	19	16
Bithynia opercula	74	117	53	82	67	164	82	19	35	34
Physa fontinalis (Linnaeus 1758)	3									
Radix balthica (Linnaeus 1758)*	12	22	13	4	7	11	3	18	19	7
Galba truncatula (O. F. Müller 1774)	3	2	3	5	3	6	3	2		
Lymnaeidae										2
Planorbidae	1	18	17	7	1					
Anisus leucostoma (Millet 1813)	1	12	8		2	1	1			
Anisus vorticulus (Troschel 1834)*	8	12	1		1	3	2			
Gyraulus laevis (Alder 1838)	3	74	81	20					3	
Gyraulus laevis (Alder 1838)/*Planorbis planorbis* (Linnaeus 1758)‡					30	88	24	17	35	28
Gyraulus crista (Linnaeus 1758)*	13	21	6	1	17	29	15	4	2	1
Hippeutis complanatus (Linnaeus 1758)*	3	5								
Ancylus fluviatilis O. F. Müller 1774	1									
Acroloxus lacustris (Linnaeus 1758)*		1								
Unio tumidus Retzius 1788		1	1							
Unio cf. *pictorum* (Linnaeus 1758)										3 (juveniles)
Unio sp.	1	2	8	1					1	
Anodonta sp.	1	1								
Corbicula cf. *fluminalis* (O. F. Müller 1774)				1						
Sphaerium corneum (Linnaeus 1758)*	2			1						
Pisidium amnicum (O. F. Müller 1774)	7	9	7	18	3	10	6	4		
Pisidium casertanum (Poli 1791)										1
Pisidium obtusale (Lamarck 1818)	1									
Pisidium milium Held 1836*	1									

Pisidium subtruncatum Malm 1855		1	1		1		1			1
Pisidium supinum A. Schmidt 1851			6	39	2	6	1			
Pisidium henslowanum (Sheppard 1823)		12	17	56	25	29	32	22	31	8
Pisidium nitidum Jenyns 1832*	29	17	26	84	42	30	46	35	25	15
Pisidium moitessierianum Paladilhe 1866		1	8	94	7	2	6	20	36	4
Pisidium spp.	11	8		27	55	107	61	16	10	2
Total	687	666	593	645	576	636	521	328	272	144
Total minus *Bithynia* opercula counts	613	549	540	563	509	472	439	309	237	110
Terrestrial										
Carychium minimum O. F. Müller 1774*	1	1								
Carychium tridentatum (Risso 1826)		1	1				1	1		
Succinea/*Oxyloma* sp.	6	3	7	10	2				4	
Cochlicopa cf. *lubrica* (O. F. Müller 1774)	1					1			5	6
Cochlicopa sp.	2		1		1	1				
Truncatellina cylindrica (A. Férussac 1807)										1
Vertigo antivertigo (Draparnaud 1801)	2	2								
Vertigo pygmaea (Draparnaud 1801)								1	1	
Vertigo sp.						1		1	1	
Pupilla muscorum (Linnaeus 1758)		1	8	7	3	7	4	3	4	13
Vallonia costata (O. F. Müller 1774)					3	6	2			4
Vallonia pulchella (O. F. Müller 1774)	2		1	5					1	13
Vallonia excentrica Sterki 1893	1	1		2						
Vallonia spp.	9	2	18	23	19	21	22	18	13	49
Punctum pygmaeum (Draparnaud 1801)*	2									1
Aegopinella nitidula (Draparnaud 1805)	11	1								
Oxychilus sp.							1			1
Derocerus/Limax	1		2	3						
Euconulus cf. *alderi* (O. F. Müller 1774)	1									
Helicella itala itala (Linnaeus 1758)					1		1		1	3
Troculus hispida				3						
Cepaea sp.					1				4	2
Helicidae				2				2		
Total	40	12	39	54	30	37	31	24	34	93
Total freshwater and terrestrial minus opercula	653	561	579	617	539	509	470	333	271	203
Percentage of terrestrial	6.13	2.14	6.74	8.75	5.57	7.27	6.60	7.21	12.55	45.81

*Present at Bobbitshole (Sparks, 1957).

†Samples a–d of section A were not available for verifying species identification and so this list differs from that in Langford *et al*. (2004) as follows: *V. macrostoma* counts have been included in the *V.*

piscinalis counts; *A. vortex* counts have been deleted; *S. putris* has been included in *Succinea*/*Oxyloma* sp.; *C. nitens* has been included in *Cochlicopa* sp.; *V. enniensis* has been included in *Vallonia* spp.

‡Juvenile *G. laevis* and *P. planorbis* are difficult to distinguish from each other, with the latter being consistently present in small numbers in all samples of section E (R. C. Preece, pers. comm., August 2015).

§Includes a small barnacle fragment of indeterminate age.

References

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Sparks, B.W. 1957 The non-marine Mollusca of the interglacial deposits at Bobbitshole, Ipswich. *Philosophical Transactions of the Royal Society of London*, **8241**, 33–44.

Table S4. *Coleopteran analysis for a bulk sample from 10 to 63 cm from base of unit 4a of channel C in Bradley Fen, Whittlesey*

Family	Genera/species	MNI
Carabidae	*Carabus* sp.	1
	Dyschirius salinus Schaum.	2
	Dyschirius aeneus (Dej.)†	1
	Dyschirius globosus (Hbst.)†	9
	Tachys bistriatus (Duft.)	1
	*Bembidion properan*s (Steph.)†	1
	Bembidion elongatum Dej.*	2
	Bembidion fumigatum (Duft.)†	2
	Bembidion assimile Gyll.†	6
	Bembidion minimum (F.)†	2
	Bembidion doris (Panz.) †	1
	Bembidion octomaculatum (Goeze)†	5
	Bembidion biguttatum (F.)†	1
	Bembidion aeneum Germ.	1
	Pterostichus vernalis (Panz.)†	1
	Pterostichus nigrita (Payk.)†	1
	*Pterostichus aterrimu*s (Hbst.)†	1
	Zabrus tenebrioides (Goeze)†	1
	Amara sp.	1
Haliplidae	*Haliplus* sp.	1
Dytiscidae	*Hydrovatus cuspidatus* (Kunze)	1
	Hygrotus inaequalis (F.)†	2
	Hydroporus sp.	2
	Copelatus haemorrhoidalis (F.)†	1
	Agabus guttatus (Payk.P)	1
	Agabus bipustulatus (L.)†	1
	Ilybius sp.	1
	Rhantus sp.	1
	Colymbetes sp.	1
	Dytiscus sp.	1
Gyrinidae	*Gyrinus* sp.	1
Hydraenidae	*Hydraena* sp.	30
	Ochthebius minimus (F.)†	22
	Limnebius truncatellus (Thunb.)†	1
	Limnebius aluta Bedel	5
	Hydrochus sp.	4

	Helophorus aquaticus (L.)	1
	Helophorus misc small spp.	5
Hydrophilidae	*Coelostoma orbiculare* (F.)†	1
	Cercyon pygmaeus (Illiger)	1
	Cercyon sternalis Shp.	13
	Megasternum boletophagum (Marsh.)†	1
	Hydrobius fuscipes (L.)†	3
	Limnoxenus niger (Zachach)	2
	Anacaena globulus (Payk.)	4
	Laccobius sp.	1
	Chaetarthria seminulum (Hbst.)†	1
Histeridae	*Acritus homoeopathicus* Woll.	1
	Hister (sensu lato) sp.	2
Colonidae	*Colon* sp.	1
Orthoperidae	*Corylophus cassidoides* (Marsh.)	3
Sphariidae	*Sphaerius acaroides* Waltl	2
Ptiliidae	*Ptenidium* sp.	4
	Acrotrichis sp.	1
Staphylinidae	*Micropeplus staphylinoides* (Marsh.)	1
	Lesteva longelytrata (Goeze)†	1
	Carpelimus spp.	8
	Anotylus rugosus (F.)†	1
	Anotylus sculpturatus Grav.†	1
	Platystethus cornutus (Grav.)	1
	Platystethus nitens (Sahlb.)†	1
	Stenus spp.	4
	Paederus sp.	1
	Xantholinus sp.	1
	Philonthus spp	2
	Tachyporus sp.	1
	Tachinus sp.	1
	Alaeocharinae Gen. et sp. indet.	3
Pselaphidae	*Bryaxis* sp.	2
	Pselaphaulax dresdensis (Hbst.)	6
	Pselaphus heisei Hbst.	1
Elateridae	*Agrypnus murina* (L.)	1
	Gen. et sp, indet.	2
Buprestidae	*Agrilus* sp.	1
Helodidae	Gen. et sp. indet.	2

Dryopidae	*Pomatinus substriatus* (Müll.)	7
	Dryops sp.	4
	Stenelmis canaliculata (Gyll.)	3
	Esolus parallelepipedus (Müll.)	1
	Oulimnius tuberculatus (Müll.)	6
	Oulimnius troglodytes (Gyll.)	19
	Limnius cf volckmari (Panz.)	1
	Normandia nitens (Er.)	19
Georyssidae	*Georissus crenulatus* (Rossi)	1
Dermestidae	*Dermestes murinus* L.	1
Byrrhidae	*Pelochares versicolor* (Waltl)*	1
	Limnichus pygmaeus (Duft.)	3
Cryptophagidae	*Atomaria cf mesomela* (Hbst.)	1
Phalacridae	*Phalacrus* sp.	1
Lathridiidae	*Corticarina* sp.	2
Endomychidae	*Sphaerosoma* sp.	1
	Copris lunaris (L.)†	1
Scarabaeidae	*Caccobius schreberi* (L.)*†	2
	Onthophagus massai Baraud*	2
	Aphodius erraticus (L.)†	2
	Aphodius spp.	4
	Heptaulacus sp.	1
	Pleurophorus caesus (Creutz.)	1
	Melolontha melolontha (L.)	1
Chrysomelidae	*Macroplea appendiculata* (Panz.)	1
	Donacia dentata Hoppe	1
	Donacia versicolorea (Brahm)	1
	Donacia semicuprea Panz.	1
	Donacia sparganii Ahr.	1
	Donacia marginata Hoppe	1
	Donacia bicolor Zschach	4
	Donacia thalassina Germ.	2
	Donacia cinerea Hbst.	1
	Plateumaris braccata (Scop.)	2

*Species not now living in the British Isles.

†Species used for palaeotemperature reconstruction.

Table S5. *Ostracod analysis for samples from 10 to 63 cm above base of unit 4a of channel C in Bradley Fen, Whittlesey*

Species	Sample					
	BFC/01*		BFC/02†		Insect residue‡	
	Count	%	Count	%	Count	%
Herpetocypris helenae G.W. Müller	6c, 11v (23)	46	1c, 5v (7)	18	7c, 21v (35)	8
Cypridopsis vidua (O.F. Müller)	5c, 3v (13)	26	4c, 2v (10)	25	51c, 4v (106)	25
Candona candida (O.F. Müller)	2v (2)	4	1c, 2v (4)	10	17c, 14v (48)	11
Candona neglecta Sars			1v (1)	3	7c, 6v (20)	5
Candona sp. (indet. juveniles)			2c, 2v (6)	15	27c, 17v (71)	17
Pseudocandona rostrata (Brady & Norman)					22c, 3v (47)	11
Potamocypris similis G.W. Müller	2c, 2v (6)	12	4c, 1v (9)	23	22c, 7v (51)	12
Potamocypris fallax Fox					7v (7)	< 2
Ilyocypris inermis Kaufmann					1c, 2v (4)	< 1
Cyclocypris ovum (Jurine)					8c (16)	4
Darwinula stevensoni (Brady & Robertson)	2c, 2v (6)	12	3v (3)	6	6c, 8v (20)	5
Total number of specimens in sample	50		40		425	

*From 42 g of dry residue.

†From 54 g of dry residue.

‡Residue from insect sample (from 30 g of dry residue, half the residue).

Table S6. *Vertebrate analysis for samples from 10 to 63 cm from base of unit 4a of channel C in Bradley Fen, Whittlesey, showing numbers of identified specimens (NISP) and minimum numbers of individuals (MNI) for herpetofauna, birds and mammals.*

Taxon	NISP	MNI
Anguilla anguilla L., 1758, European eel	5	–
Esox lucius L., 1758, pike	8	–
Scardinius erythropthalmus (l., 1758), rudd	12	–
Rutilus rutilus (L., 1758), roach	3	–
Tinca tinca, tench	1	–
Cyprinidae sp.(p.), carp family	35	–
Pisces spp., undetermined fish	170	–
Triturus sp., undetermined newt	1	1
Anura sp.(p.), undetermined frog or toad	3	1
Emys orbicularis L., 1758, European pond terrapin	1	1
Natrix natrix (L., 1758), grass snake	1	1
Aves sp., undetermined bird	1	1
Sorex araneus L., 1758, common shrew	3	1
Insectivora sp., undetermined insectivore	1	1
Myodes glareolus (Schreber, 1780), bank vole	7	1
Arvicola terrestris cantiana Hinton, 1910, water vole	2	1
Apodemus sylvaticus (L., 1758), wood mouse	6	3
Microtus sp.(p.), undetermined vole	21	2
Microtinae sp(p.), undetermined vole	17	–
Rodentia spp., undetermined rodent	35	–
Undetermined small mammal	77	–
Undetermined large mammal	1	1
Undetermined bone fragments, small	9	–

Table S7. *Thermophile species in channel C and at other Ipswichian sites according to pollen biozonation*

Flora/fauna	Thermophile species	Bradley Fen		Bobbitshole		Swanton Morley			Deeping St James	Woolpack Farm	Tattershall Castle	Trafalgar Square
		I	II	I	II	I	II	III	II	II	II	II
Pollen	*Hedera*	Y			Y		Y	Y	Y			
	Nuphar	Y	Y	Y	Y	Y		Y	Y	Y	Y	
	Ilex	Y			Y			Y	Y		Y	
	Carpinus							Y				
Plant macrofossils	*Naias minor*	Y			Y		Y		Y			Y
	Trapa natans L.						Y					Y
	Salvinia natans			Y			Y		Y			
	Acer cf. *monspessulanum*				Y		Y	Y		Y	Y	Y
	Sambucus nigra						Y	Y		Y		
	Mentha aquatica			Y								
	Myosoton aquaticum			Y								
	Najas marina			Y	Y							
	Oenanthe aquatica			Y								
	Potamogeton cf. *densus*			Y								
	Cladium mariscus				Y		Y					
	Hydrocharis morsus-ranae			?	Y		Y					
	Lemna cf. *minor*				Y							
Mollusca	*Belgrandia marginata*	Y			Y		Y		Y	Y	Y	Y
	*Cochlicopa niten*s								Y	Y	Y	
	Vallonia enniensis				Y		Y		Y	Y	Y	
	Potomida littoralis									Y		Y
	Clausilia cf. *pumila*								Y	Y		Y
	Truncatellina cylindrica		Y							Y	Y	Y
	Discus ruderatus								Y		Y	
	Anisus (Planorbis) vorticulis	Y	Y	Y	Y		Y		Y	Y	Y	Y
	Helicella itala itala		Y								Y	Y
	Pisidium moitessierianum	Y	Y		Y				Y	Y	Y	Y
	Pisidium supinum	Y	Y		Y					Y		Y

Coleoptera	*Onthophagus massai*	Y				Y	Y		Y
	Caccobius schreberi	Y	Y			Y	Y		Y
	Onthophagus furcatus					Y	Y		Y
	Oniticellus fulvus						Y		Y
	Onthophagus vacca						Y	Y	Y
	Rhyssemus germanus						Y		Y
	Drepanocerus						Y		Y
	Heptaulacus cf. pirazzolii					Y	Y		
	Bembidion elongatum	Y				Y		Y	Y
	Oodes gracilis		Y			Y		Y	Y
	Cybister lateralimarginatus		Y			Y			Y
	Rhysodes sulcatus					Y			Y
	Valgus hemipterus		Y			Y			
	Melanotus niger								
	Aphodius carpetanus						Y		
	Bembidion octomaculatum	Y				Y			Y
	Hydrophilus caraboides					Y			Y
	Hydrous piceus					Y			Y
	Pelochares versicolor	Y							
	Cercyon sternalis					Y	Y		
	Zabrus tenebrioides	Y					Y		
	Copris lunaris	Y					Y	Y	Y
	Pleurophorus caesus	Y				Y			Y
Vertebrates	*Palaeoloxodon antiquus*			Y		Y	Y		Y
	Hippopotamus amphibius			Y	Y				Y
	Dama dama			Y		Y	Y		Y
	Emys orbicularis	Y		Y					
	Crocuta crocuta			Y					Y
	Bos primigenius			Y	Y		Y		Y
	Panthero leo								Y
	Stephanorhinus hemitoechus								Y
	Ursus arctos						Y		Y