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

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26 Short title: Last Interglacial deposits at Whittlesey

27
28 †The late Professor Russell Coope wrote the initial draft of this article but his
29 untimely death meant that he did not see its publication. His original text for the
30 Coleoptera section has been retained unaltered as far as possible, except where new
31 scientific insights could not justify such an approach.

32
33 **Abstract:** Fossiliferous deposits infilling a channel at Whittlesey, eastern England,
34 are dated by amino acid racemization to the Last Interglacial, and pollen analysis

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

51

51 As we face an immediate future of increasing global temperatures, more extreme
52 weather events and higher sea levels (e.g. Crutzen & Stoermer, 2000; IPCC, 2014) it
53 is important that we investigate Pleistocene interglacial deposits. These can provide
54 insight into past natural climate change, including meaningful parameters to variables
55 such as sea level and temperature, and spatial and temporal patterns within these (e.g.
56 Petit *et al.*, 2005; Abrantes *et al.*, 2012). The Last Interglacial (LIG) stage, although
57 not a direct analogue in terms of causal processes and their products, is appropriate
58 for assessing the implications of anthropogenic climate change for the following
59 reasons. First, it was a globally strong (warm) temperate period (Past Interglacials
60 Working Group of PAGES, 2016) with higher temperatures and sea level interpreted
61 from many records (e.g. Kukla *et al.*, 2002; van Kolfschoten *et al.*, 2003; Sánchez-
62 Goñi *et al.*, 2012). Second, there have been many studies of LIG deposits, regionally
63 and globally, against which to compare research outcomes (e.g. West, 1957; Zagwijn,
64 1961; Shackleton, 1969; van Kolfschoten & Gibbard 2000; Lisiecki & Raymo, 2005).
65 Third, there are many long records from a variety of depositional environments that
66 span the entire interglacial stage (e.g. Andersen, 1966; Woillard, 1978; De Beaulieu &
67 Reille, 1984; Mamakowa, 1989; Cramp & O'Sullivan, 1999; Rohling *et al.*, 2015).
68 Fourth, it is within the range of several absolute and relative dating techniques (e.g.
69 Gascoyne *et al.*, 1981, 1983; Bateman & Catt, 1996; McFarlane & Ford, 1998;
70 Wastegård *et al.*, 2005; Penkman *et al.*, 2011; Sier *et al.*, 2011, 2015; Abbott *et al.*,
71 2013; Sier & Dekkers, 2013; Davies *et al.*, 2014).

72 Although the LIG is broadly recognized as a period when climatic conditions
73 were similar to today that occurred about 130 to 115 thousand years ago,
74 corresponding to marine oxygen isotope substage (MIS) 5e (Fig. 1), it is in reality a
75 complex entity. What emerges from the many studies of LIG deposits is a somewhat
76 disparate picture of eustatic sea-level estimates, rates of sea-level rise, temperature
77 estimates, commencement dates and durations, in both space and time at inter- and
78 intrahemispheric scales (e.g. Shackleton, 1969; Broecker, 1998; Turner, 2000; Kukla *et*
79 *al.*, 2002; van Kolfschoten *et al.*, 2003; Sier *et al.*, 2011, 2015; Sánchez-Goñi *et al.*,
80 2012; Long *et al.*, 2015; Peeters *et al.*, 2016). For example, the commencement of the
81 southwest Europe LIG lags that of the global deep-sea record by 5000 years, and in
82 turn is lagged by the northwest Europe LIG by a further 5000 years (Fig. 1;
83 Shackleton, 1969; Shackleton *et al.*, 2002, 2003; Lisiecki & Raymo, 2005; Sánchez-
84 Goñi *et al.*, 2012; Sier *et al.*, 2015). It is possible that these spatial and temporal

85 mismatches may be attributable partly to chronostratigraphical interpretation of LIG
86 deposits being tied to a variety of age models or absolute dated sequences. For
87 example, in Fig. 1, the ages of the top and base of sapropel S5 (a lithological marker
88 of the eastern Mediterranean deep-sea record) are taken from Zeigler *et al.* (2010) and
89 are based on precession tuning to U/Th dated caves in China. Shackleton *et al.* (2002,
90 2003), however, determined the ages of the top and base of the southwest Europe LIG
91 in Fig. 1 by tying sea-level stillstands observed in core MD95-2042 to U/Th dated
92 uplifted coral reefs. In addition, as noted by Turner (2000) and Shackleton (2002),
93 there is a fundamental difference between the use of peaks and troughs in the MIS
94 record for astronomical forcing and the determination of MIS boundaries on the rising
95 and falling limbs of the peaks.

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

105 In Britain, West (1957) first identified this period as the Ipswichian
106 Interglacial, using palynostratigraphy to identify a series of pollen zones (Table 1) at
107 the type-site of Bobbitshole (Ipswich, Suffolk; Fig. 2). Amino acid racemization
108 (AAR) data confirm that the deposits at Bobbitshole are of LIG age (Penkman *et al.*,
109 2013). A range of U/Th and luminescence age estimates have been published that
110 place the Ipswichian Interglacial in the interval 130–115 ka (Fig. 1), but the error
111 terms associated with these dates are too large to determine whether the interglacial
112 here had an early or late commencement date. Thus, the Ipswichian and the Dutch
113 Eemian can be only broadly correlated in terms of time.

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

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

131 The vast majority of the Ipswichian sites recognized by Lewis *et al.* (2010)
132 fall into the early temperate pollen biozone IIb (Table 1). Candy *et al.* (2016) used the
133 data from five of these Ip IIb sites (Bobbitshole, Deeping St James (Keen *et al.*,
134 1999), Swanton Morley (Phillips, 1976; Coxon *et al.*, 1980), Tattershall Castle
135 (Holyoak & Preece, 1985) and Trafalgar Square (Preece, 1999), together with data
136 from Woolpack Farm (Gao *et al.*, 2000), to assess how warm Britain was during the
137 Ipswichian Interglacial, showing that only the sequence from Trafalgar Square
138 convincingly demonstrates temperatures warmer than during the Holocene thermal
139 optimum, though all are warmer than the present day.

140 This article presents the findings of a multidisciplinary study of the
141 palaeoenvironment of Ipswichian deposits at Whittlesey [TL236980], eastern England
142 (Fig. 2a; Langford *et al.*, 2004b) that can be compared with the sites utilized by Candy
143 *et al.* (2016). As with other Ipswichian sites (Fig. 2b) the palaeoenvironmental record
144 at Whittlesey represents only a fragment of the LIG, but in contrast to most of these
145 sites the data available offer a rare insight into the climatic and ecological conditions
146 of Ipswichian biozone I. In particular, they shed light on the speed of establishment of
147 thermal optimum conditions and the biological response to early Ipswichian climate
148 amelioration, which were rapid in the deep-sea LIG (Fig. 1) and the northwest and
149 southwest Europe LIGs (Zagwijn, 1961; Shackleton, 1969; Turner, 2002; Sánchez-
150 Goñi *et al.*, 2012; Sier *et al.*, 2011, 2015). Our work at Whittlesey includes
151 quantitative reconstructions of mean July and January air temperatures based on
152 Coleoptera and Ostracoda, of significant value for palaeoclimate modelling, as well as

153 qualitative interpretations of the palaeoecology and depositional environment that
154 improve our understanding of Ipswichian biozonation and biostratigraphy. In
155 addition, this study complements the palaeoecological and palaeotemperature studies
156 of Langford *et al.* (2014a,b) on MIS 7 and cold-stage deposits at Whittlesey, and
157 provides the first comprehensive multidisciplinary account of a fully fluvial
158 Ipswichian deposit of the River Nene catchment.

159

160 **Background**

161 ***Geographical and geological contexts of the Whittlesey sedimentary succession***

162 The fossiliferous sediments investigated here form part of the River Nene 1st Terrace
163 (BGS, 1984; Horton, 1989; the Ecton Member of Maddy, 1999) and are located in
164 Bradley Fen Quarry at Whittlesey, Cambridgeshire (Fig. 3a), where they
165 unconformably overlie the Peterborough Member of the Jurassic Oxford Clay
166 (Hudson & Martill, 1994) and underlie Holocene Peat (see Langford *et al.* (2004b,
167 2007, 2014a,b) for further details of the geographical and geological contexts). The
168 late Middle to Late Pleistocene sedimentary succession at Whittlesey represents an
169 important fluvial archive spanning more than half the post-Anglian
170 (Elsterian/Mindel/MIS 12 glacial stages) to Holocene period (Langford *et al.*, 2004a–
171 c, 2007, 2014a,b). This complex sequence of deposits contains a number of
172 fossiliferous beds, of both cool/cold or temperate-climate character, that together span
173 at least the previous three glacial and two interglacial stages.

174 Four distinctive channel-fill sequences have been recognized (channels A–D;
175 Fig. 3b) within the Whittlesey sequence. The palaeoecology of two of these (B and D)
176 has been reported by Langford *et al.* (2014a,b) and age-estimate data for two of them
177 (A and B) have been provided by Langford *et al.* (2007, 2014a): OSL dates indicate
178 an age for channel A within MIS 5b–a; AAR assigns channel B to an age within the
179 MIS 7 complex (Penkman, 2005). This multidisciplinary investigation concerns the
180 palaeoenvironment of channel C (Fig. 3b), which the sedimentary succession
181 (sequence stratigraphy) demonstrates post-dates channel B (MIS 7). Langford *et al.*
182 (2004b) interpreted channel C as Ipswichian based on its multiproxy biostratigraphy,
183 and this is now confirmed by new AAR data on the intra-crystalline protein fraction
184 of *Bithynia tentaculata* opercula (Fig. 4; Supplementary Table S1).

185

186 ***Sedimentary context of channel C***

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

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

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

216 The facies architecture of unit 4b and the direction of deepening indicate that
217 flow in channel C was towards the north, completely opposite to the direction of flow
218 indicated in the underlying gravels of unit 3b (Fig. 6b). It has been argued (Langford,
219 2012) that this southerly direction of flow in unit 3c was in response to impoundment
220 of The Wash during MIS 6 (Gibbard *et al.*, 2009). The northward flow of channel C

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

238

239 **Palaeobotany results**

240 **Pollen**

241 Volumetric 1 cm³ pollen samples were prepared using the standard hydrofluoric acid
242 technique, and counted for pollen using a high-power stereo microscope at ×400
243 magnification, with ×1000 used for critical determinations.

244 Pollen and charcoal were analysed from five levels (15, 35, 67, 90 and
245 260 cm) within channel C (Figs 5 and 7). The basal part of the sequence is dominated
246 by grass (Poaceae) pollen and pteropsid spores, with pine (*Pinus*) (20–30%) and birch
247 (*Betula*) (5–10%). Other arboreal taxa present include oak (*Quercus*), which increases
248 up-section, and willow (*Salix*), juniper (*Juniperus*), sea buckthorn (*Hippophaë*), ivy
249 (*Hedera*) and holly (*Ilex*). A range of herbs and aquatic plants are also represented,
250 including meadowsweet (*Filipendula*), bur-reed (*Sparganium*) and yellow water-lily
251 (*Nuphar*). The sample at 260 cm was very different and contained a grass–hazel
252 (Poaceae–*Corylus*) assemblage, with a little pine (*Pinus*), oak (*Quercus*) and herb
253 pollen. Pollen concentrations were moderate at 20 000–30 000 grains per gram, and

254 charcoal, although increasing from the base, was generally low ($< 1 \text{ cm}^2 \text{ cm}^{-3}$)
255 suggesting only limited regional burning.

256

257 ***Plant macrofossils***

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

263 Two samples were analysed from each of units 4a and 4b (Supplementary
264 Table S2). The samples from unit 4a contain a wider range of species than those from
265 4b, although the greater number of specimens from unit 4a should be noted. As would
266 be expected from a deposit laid down within a fluvial setting, both units are
267 dominated by plants indicating aquatic conditions, for example pond weed
268 (*Potamogeton* sp.) and horned pond weed (*Zannichellia palustris*), or waterside
269 environments, particularly bulrush (*Scirpus maritimus*) and sedge (*Carex* sp.). The
270 aquatics bur-reed (*Sparganium*) and yellow water-lily (*Nuphar*), detected in the pollen
271 record, are also observed here. In contrast to the pollen record, however, the only tree
272 species recorded is elm (*Ulmus*) in unit 4a. The paucity of tree macrofossils suggests
273 that the wooded areas recorded in the pollen were at a significant distance from the
274 river channel. There is some indication of drier ground adjacent to the channel during
275 deposition of unit 4b, with the increased presence of the disturbed ground species of
276 the blackberry family (*Rubus* sp.) and common knotgrass (*Polygonum aviculare*) and
277 some decrease in aquatic species.

278

279 **Palaeozoology results**

280 ***Mollusca***

281 Four samples of approximately 2 kg each were collected from section A by J. Merry
282 for mollusc analyses [samples a (0–20 cm from base), b (20–40 cm from base), c (70–
283 90 cm from base), d (2.6 m from base)]. The mollusc samples from unit 4b in section
284 E were collected by D. H. Keen in 2002 and labelled in centimetre intervals from the
285 base of the exposed section. These samples were crudely sieved through a 500 μm
286 mesh and subsequently picked by HEL in 2014–2015. Samples were washed through
287 2 mm, 1 mm and 500 μm sieves and shells were picked by eye or under a binocular

288 microscope at 10× magnification. The total counts of species follow the conventions
289 of Sparks (1964), where each gastropod apex counts as one individual and each intact
290 bivalve hinge counts as half an individual. The taxonomy follows Kerney (1999),
291 Killeen *et al.* (2004) and Cameron (2008) for current British species and Gittenberger
292 *et al.* (1998) for species no longer found in Britain. Environmental preferences and
293 geographical distributions of the molluscs are based on Kerney (1999), Kerney &
294 Cameron (1979) and Killeen *et al.* (2004).

295 As expected for a fluvial deposit, the molluscan fauna represents a diversity of
296 riverine habitats (Supplementary Table S3). A substantial river is indicated by the
297 dominance of *Valvata piscinalis* and *Bithynia tentaculata*, which prefer slow-moving
298 water (Sparks, 1961). Together, they make up more than 50% of the assemblage in
299 unit 4a, but this declines to above 30% in unit 4b. Other elements in the assemblage
300 indicating a substantial, slow-moving river are *Unio tumidus*, *Pisidium supinum* and
301 *Pisidium moitessierianum*, with the latter two increasing noticeably in unit 4b;
302 *Pisidium amnicum*, indicative of a large body of moving water, also increases in unit
303 4b. *Hippeutis complanatus*, which also prefers slow-moving water, is present in unit
304 4a but absent in 4b. *Physa fontinalis*, *Ancylus fluviatilis* and *Pisidium henslowanum*
305 are indicative of moving water, but the first two are present only at the base of unit 4a
306 whereas the last has a significant presence only in unit 4b. The presence of only one
307 specimen of *A. fluviatilis*, however, reinforces the impression of a substantial slow-
308 moving water body, as this species prefers faster flowing habitats (Holyoak & Preece,
309 1985).

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

319 *Pisidium henslowanum* prefers a coarse sandy or stony substrate (Boycott,
320 1936; Ellis, 1978). Other species that require a clean stony or sandy substrate include

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

324 *Valvata cristata*, *Radix balthica*, *G. laevis*, *G. crista*, *Acroloxus lacustris*, *S.*
325 *corneum*, *P. obtusale* and *P. milium* prefer standing-water or quiet-water habitats.
326 Indicators of these conditions peak at about 30% of the assemblage in the middle part
327 of unit 4a but decline to less than 10% in unit 4b. Marsh and wetland species are
328 represented by *Carychium minimum*, *Carychium tridentatum*, *Galba truncatula*,
329 *Anisus leucostoma*, *A. vorticulus*, *Succinea putris*, *Vertigo antivertigo*, *Vallonia*
330 *pulchella*, *Punctum pygmaeum* and *Euconulus cf. alderi*, with the latter also found in
331 boggy woodland. Species such as *G. truncatula*, *R. balthica* and *A. leucostoma* are
332 also found in marginal areas of the water body that are prone to drying out. Again,
333 marsh and wetland conditions peaked in the middle part of unit 4a, represented by
334 about 10% of the assemblage, and were less prevalent in unit 4b, represented by about
335 3% of the assemblage.

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

343 Several trends are apparent from the above that may be important for
344 palaeoenvironmental reconstruction. The numbers of *P. amnicum*, *P. supinum*, *P.*
345 *henslowanum* and *P. moitessierianum* increase significantly in unit 4b compared with
346 unit 4a, concomitant with a decrease in *V. piscinalis* and *B. tentaculata* and muddy
347 substrate conditions, as well as an up-sequence increase in species preferring clean
348 sandy or stony substrate conditions. The increase in *P. nitidum* in unit 4b is also
349 consistent with these changing conditions given the catholic requirements of this
350 species. Indicators of standing/quiet water and marsh/wetland habitats, as well as
351 vegetated substrates, peak in the middle part of unit 4a and decline thereafter, and *P.*
352 *muscorum*, *H. itala itala* and *T. cylindrica* hint at drier conditions during
353 accumulation of unit 4b. Most noticeably, *B. marginata* shows a marked decrease up-
354 sequence, which combined with increases in *P. supinum* and *P. henslowanum* could

355 indicate decreasing alkalinity up-sequence – it should be noted, however, that *Chara*
356 fragments dominate the < 2 mm fraction of samples from below 120 cm in section E.

357

358 ***Coleoptera***

359 A single bulk sample of about 15 kg was obtained from the basal 10–62 cm sediments
360 of unit 4a of channel C at Bradley Fen, section A. The sediment was grey silty clay
361 with scattered plant fragments. The sample was washed over a sieve with a mesh
362 aperture of 0.3 mm. The residue was then concentrated using the standard flotation
363 technique and the insect fossils extracted using a binocular microscope (Coope,
364 1986). Specimens were identified by GRC who reported that on the whole the
365 preservation was good though rather fragmentary. Taxonomy is based on Lucht
366 (1987), as revised by Böhme (2005) and Gustafsson (2005). Counts indicate the
367 minimum number of individuals (MNI) in the sample. Species habitat information
368 was obtained from the BugsCEP database (Buckland & Buckland, 2012).

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

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

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

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

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

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

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

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

434 Several species of weevil are dependent on trees. *Rhamphus pulicarius* is
435 polyphagous, feeding on the leaves of *Salix*, *Betula*, *Populus* and *Myrica* (Morris,
436 1993). Two species are exclusively restricted to *Quercus*. The larvae of *Rhynchaenus*
437 *quercus* mine the leaves of oaks and those of *Curculio venosus* develop inside acorns
438 (Koch, 1992). *Melolontha melolontha* feeds on leaves of various deciduous trees,
439 frequently on oaks (Koch, 1989).

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

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

462

463 ***Ostracoda***

464 Two small samples in pollen tubes (BFC/01 and BFC/02) were collected from the
465 same location as the Coleoptera sample (10–63 cm from the base) and the residue from
466 the latter was also processed for ostracod analysis (Supplementary Table S5). The
467 samples were first dried in an oven and then soaked in hot water for several hours,
468 with a little sodium carbonate added to aid breakdown. Washing took place through a
469 75 µm sieve with hand-hot water, before the remaining residues were decanted back
470 to their bowls for drying in the oven. Their identification and environmental
471 preferences are based on Meisch (2000) and other sources listed in the text.

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

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

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

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

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

511

512 **Vertebrates**

513 Three bulk samples were examined from the basal 50 cm of unit 4a and are treated as
514 one for the purpose of the results presented below. Samples were washed through a
515 500 µm sieve, the dry residue graded through 2 mm, 1 mm and 500 µm and any
516 microvertebrate teeth and bone fragments picked from under a low-power binocular
517 microscope.

518 The three samples have yielded a combined total of 402 small bone fragments
519 and teeth (Supplementary Table S6), representing a variety of small mammal, reptile,
520 amphibian, fish and bird taxa, in addition to a single rib fragment of an indeterminate
521 cervid-sized large mammal. Of the 402 small bone fragments and teeth, 77 of them
522 are too comminuted or lacking in diagnostic surface features so as to be undetermined
523 even to Class level. The material is uniformly stained a dark brown to black colour,

524 with tooth enamel varying from black to blue-grey, and frequent dark orange
525 sediment adhering. The bones and teeth are well preserved, with the fish remains
526 spectacularly so; several fish vertebrae still retain the full length of the vertebral
527 spines, and cyprinid pharyngeal bones with teeth still *in situ* are present within the
528 sample, as are several fragile fish-scale fragments. Remains of terrestrial vertebrates
529 are equally well preserved, for example a wood mouse maxilla with teeth *in situ*. No
530 signs of predator damage or digestion are apparent on the small vertebrate remains,
531 with the exception of a small and partial bird humerus that has some evidence of
532 pitting and corrosion to the proximal end, consistent with digestion by an avian
533 predator.

534 Fish dominate the identifiable remains of the assemblage (72% of the
535 assemblage), followed by small mammals (25%), herpetofauna (2%) and birds
536 (< 1%). In terms of environmental significance, the fish assemblage is characterized
537 by the presence of cyprinid (carp family) species and their associated predator, the
538 pike (*Esox lucius*). Within the cyprinids, remains of roach (*Rutilus rutilus*), rudd
539 (*Scardinius erythrophthalmus*) and tench (*Tinca tinca*) have been identified, all of which
540 are native to Britain today. Also present is the European pond terrapin (*Emys*
541 *orbicularis*), which today occurs no closer to Britain than central France (Fritz &
542 Laufer, 2007). The assemblage also contains a number of the characteristic vertebrae
543 of the European eel (*Anguilla anguilla*). This species is facultatively catadromous,
544 inhabiting fresh, brackish and coastal waters but migrating to pelagic marine waters to
545 breed (Wheeler, 1969). Under natural conditions, it therefore occurs only in water
546 bodies that are connected to the sea.

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

551

552 **Discussion**

553 ***Depositional environment***

554 The sedimentology of unit 4a is reminiscent of the infilling of an avulsion-abandoned
555 channel (Toonen *et al.*, 2012), with initial deep incision, up to a minimum depth of
556 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
557 the bedrock Oxford Clay. The basal fining upward sequence (0–40 cm) appears to

558 represent the waning flow deposits of the avulsion event, the energy of which was
559 sufficient to move cobbles as bedload. The molluscan evidence suggests, however,
560 that energy reduced rapidly following incision. At the time of incision and start of
561 aggradation (the basal 20 cm) the riverine environment provided a suitable habitat for
562 the spring dweller *B. marginata* to flourish, but above 20 cm the numbers of *B.*
563 *marginata* dramatically declined. The coleopteran and ostracod samples included
564 material from the upper part of the basal 20 cm, and spring dwellers (*A. guttatus* and
565 *P. fallax* respectively) were also recorded in their assemblages. For the basal 20 cm of
566 the succession, the molluscan assemblage indicates that standing/quiet-water and
567 clear-water conditions, as well as sandy/stony substrates, were rare within the
568 immediate catchment and that marsh and wet grassland would have been common
569 nearby.

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

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

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

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

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

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

603 The presence of *D. salinus*, *B. minimum* and *B. fumigatum* in the beetle fauna
604 strongly suggest nearby saline habitats, which is supported by pollen evidence for
605 *Hippophaë* and plant macrofossil evidence for *S. maritimus*. The presence of the reed
606 beetle *P. braccata* is also interesting in this respect because it is often associated with
607 *Phragmites* growing in brackish waters in slow-moving rivers and estuaries (Hyman
608 1992). The fauna also includes species that are entirely typical of freshwater habitats
609 and it is possible that the river channel was close to the uppermost tidal limit at this
610 time. However, although some of the ostracods present can tolerate slightly saline
611 conditions, estuarine species such as *C. torosa* are absent from the assemblage,
612 suggesting a near-coastal rather than upper estuarine environment.

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

619 Unit 4a probably represents the infilling of an avulsion-abandoned channel
620 that subsequently may have been a backwater to the main channel, or a largely
621 inactive channel. There may be a significant hiatus between unit 4a and 4b, but the
622 increased molluscan signal for moving-water conditions at the top of unit 4a may
623 indicate that the main channel was again nearby. Hence the succession from unit 4a to
624 4b may have resulted from minor channel migration over a short period. In contrast,

625 unit 4b represents deposition as a lateral accretion sequence in the main channel of a
626 sinuous river. The molluscan data for unit 4b indicate an increase in numbers of those
627 with a preference for moving-water habitats and an expansion of clear-water
628 conditions and sandy/stony substrates at the expense of those preferring
629 standing/quiet-water habitats. Significantly, the pollen data indicate the presence of
630 hazel in unit 4b, whereas it was absent in unit 4a, with an expansion of Poaceae,
631 *Plantago lanceolata* and Pteropsida, and continued presence of *Nuphar*. There is a
632 notable difference in the composition of the molluscan assemblage at the very top of
633 unit 4b in section E, where the percentage of terrestrial species increases to 45%,
634 which probably represents filling of the channel rather than a climatic signal. The
635 corresponding plant macrofossil data indicate an increase in *Rubus* and *P. aviculare*,
636 which prefer dry disturbed ground habitats, compared with unit 4a. The channel
637 cannot have been completely infilled at this time though, because aquatic species such
638 as *Z. palustris* and the damp-ground species *S. maritimus* were also recorded at the
639 top of unit 4b.

640

641 ***Palaeoclimate***

642 The presence of pollen of ivy, holly and yellow water-lily in channel C indicates fully
643 temperate conditions. Climatically, all the species observed in the plant macrofossil
644 data also are consistent with the interpretation of interglacial conditions, with
645 particular evidence of warm conditions also indicated by the presence of yellow
646 water-lily as well as brittle naiad (*Naias minor*). The number of species represented in
647 the molluscan assemblage of channel C and the presence of the thermophile *B.*
648 *marginata* suggest full interglacial conditions. It is clear from the coleopteran fauna
649 that the sediments of unit 4a were deposited in fully temperate interglacial conditions,
650 and this is particularly reinforced by the presence of thermophiles such as *B.*
651 *elongatum*, *P. versicolor*, *C. schreberi* and *O. massai*, all of which today live across
652 areas of central and southern Europe, avoiding northern Europe. There are no beetle
653 taxa associated with alpine conditions. Both the ostracod and vertebrate fauna of unit
654 4a indicate fully temperate conditions, and in particular the co-abundance of bank
655 vole and woodmouse is considered a characteristic feature of British interglacials.

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

659 1987) uses the BugsMCR function of the BugsCEP database (Buckland & Buckland,
660 2012), to calculate T_{\max} (mean July air temperature) and T_{\min} (mean January air
661 temperature) for each sample investigated: T_{range} determines the level of
662 continentality. The MCR method enables reconstructions of the thermal
663 palaeoclimates to be quantified using carnivorous and scavenging beetle species with
664 food requirements that are independent of particular macrophytes or terrestrial plants.
665 The Mutual Ostracod Temperature Range (MOTR) method (Horne, 2007; Horne &
666 Mezquita, 2008; Horne *et al.*, 2012) likewise reconstructs mean January and mean
667 July air temperatures. For the MOTR the most up-to-date published calibrations were
668 used (Horne *et al.*, 2012).

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

673 mean July temperature lay within the range +17°C and +24°C
674 mean January temperature lay within the range -7°C and +7°C

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

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

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

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

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

689 Further refinement is possible, taking account of vertebrate threshold
690 temperatures. Rudd spawn in April–July, when temperatures rise above 15°C, and
691 tench spawn in water temperatures above 19°C. The presence of pike implies winter

692 water temperatures above freezing (Wheeler, 1969). Additionally, *E. orbicularis*
693 requires minimum summer temperatures of 18°C in order to incubate its eggs,
694 implying elevated summer temperatures (Stuart, 1979; Coxon *et al.*, 1980). These
695 data together indicate minimum summer temperatures of +19°C and winter
696 temperatures above 0°C. It must be noted that these are water temperatures, which in
697 sheltered conditions may well have been buffered against extremes of air temperature;
698 nevertheless these thresholds fall within the ‘mutual mutual’ ranges determined by the
699 coleopteran MCR and MOTR methods and it can be suggested, therefore, that mean
700 air temperatures were likely as follows:

701 mean July air temperature lay within the range +19 to +22°C;

702 mean January air temperature lay within the range 0 to +7°C.

703 The present-day equivalent values for Whittlesey are July +17°C and January +3°C.

704 We conclude that while winter temperatures may well have been similar to those of
705 today, summer temperatures were at least 2°C warmer.

706 Coope (2010) applied MCR analysis to eight Ip IIb sites, including
707 Bobbitshole, Deeping St James, Shropham, Trafalgar Square and Woolpack Farm,
708 and his calculated mean July temperature of 20°C and mean January temperature of
709 0°C are consistent with the ranges determined for unit 4a. Candy *et al.* (2016)
710 concluded that the thermal optimum of the Ipswichian (Ip II) was of relatively short
711 duration (<1200 years) and reported only one of ten British Ipswichian sites as
712 recording temperatures significantly warmer than Holocene temperatures: Trafalgar
713 Square at +20 to +21°C (July) and +1.5 to +3°C (January). Our new reconstruction for
714 Whittlesey adds a second such site.

715 These quantified palaeotemperature ranges are supported by the temperature
716 requirements of some of the plant species represented within the fossil assemblage.
717 For example, it has been suggested that ivy will not tolerate an average of less than
718 -1.5°C for the coldest month (Iversen, 1944; West, 1957; Barber & Brown, 1987;
719 Keen *et al.*, 1999). Other species present that have been regularly seen in other
720 Ipswichian deposits (Phillips, 1974), such as yellow water-lily and brittle naiad,
721 suggest summer temperatures warmer than today during accumulation of unit 4a. In
722 addition, molluscan species *B. marginata*, *H. itala itala*, *T. cylindrica*, *P.*
723 *moitessierianum*, *A. vorticulus* and *P. supinum* as well as coleopteran species *B.*
724 *elongatum*, *P. versicolor*, *C. schreberi*, *O. massai*, *B. octomaculatum*, *Z. tenebrioides*,

725 *C. lunaris* and *P. caesus* suggest warmer summers and a more continental climate
726 during the infilling of channel C than experienced in eastern England at the moment.

727

728 **Biostratigraphy**

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

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

751 *Orthophagus massai*, *C. schreberi*, *B. elongatum* and *C. lunaris* are among the
752 13 most common exotic beetle species found at Ipswichian sites (Walkling, 1996). Of
753 particular interest is the presence of *O. massai*, which so far has been found only as a
754 fossil in up to at least seven Ipswichian Interglacial deposits, including unit 4a.
755 Although we have continued to use the name *O. massai*, its taxonomic status is
756 debated. *Orthophagus massai* is likely a subspecies or a genetically distinct Sicilian
757 population of *O. francicornis* that are going through genetic speciation, probably due
758 to genetic isolation. This is based on modern genetic and morphological research of

759 four different Italian populations of *O. fracticornis* (Pizzo *et al.*, 2011). Here, we feel
760 that it is important to distinguish this morphotype from *O. fracticornis*, being a much
761 smaller type and likely to be an insular variety, based on modern studies and therefore
762 likely of interest around species insularity in MIS 5e. Moreover, as genetic studies
763 have been undertaken on only modern specimens we cannot explore the relationship
764 between the modern specimens of *O. massai* and those found in the fossil record,
765 which may still represent a different species. Morphological and genetic work on the
766 fossil specimens would need to be undertaken to be clear on this attribution. The late
767 Professor Coope distinguished these two varieties in the fossil record and so in the
768 context of Ipswichian biostratigraphy we have retained these identifications.

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

779

780 ***Ipswichian biozonation and onset of the thermal optimum***

781 It appears that unit 4a of channel C represents the pre-temperate zone (pollen biozone
782 I; Turner & West, 1968) of an interglacial. This is interpreted as an ostensibly open
783 grassland environment with scattered boreal woodland and light-demanding shrubs
784 such as juniper and sea buckthorn. Locally, tall-herb, bank-side and marginal
785 vegetation is also indicated, surrounding open water up to ca. 2 m deep. There are
786 clear signs of impending early temperate conditions, with an up-section increase of
787 oak and the presence of yellow water-lily. In contrast, it appears that unit 4b
788 represents full early temperate (pollen biozone II) conditions with the development of
789 hazel–oak woodland. Taken together, the pollen evidence suggests that the sediments
790 of channel C were deposited during the earlier stages of an interglacial period. In
791 addition, the pollen data represent accumulation from the wider catchment, including

792 plants growing in dry land habitats away from the river, rather than representing an
793 insular hydrosere succession that might occur in response to channel cut-off.

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

809 The rich multidisciplinary records for the Deeping St James (Keen *et al.*,
810 1999), Woolpack Farm (Gao *et al.*, 2000), Swanton Morley (Phillips, 1976; Coxon *et*
811 *al.*, 1980), Tattershall Castle (Holyoak & Preece, 1985) and Trafalgar Square (Preece,
812 1999) sites, although fragmentary, provide detailed insight into pollen biozone Ip IIb,
813 which is considered to represent the thermal optimum. The temperate (Ip II) pollen
814 spectrum and molluscan assemblage of unit 4b are also similar to the records from
815 these sites, as well as Bobbitshole (Sparks, 1957; West, 1957), and therefore can be
816 assigned to pollen biozone IIb.

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

826 Whittlesey, unit 4a records 17 thermophilous species from biozone Ip Ib, whereas
827 Bobbitshole records only eight. Early onset of the thermal optimum is also hinted at in
828 the coleopteran and molluscan assemblages and quantitative paleotemperature
829 reconstructions at Shropham (Walkling, 1996; Dixon, 1997), but without supporting
830 pollen biozonation data cannot be compared effectively with unit 4a. At Swanton
831 Morley, Coxon *et al.* (1980) report the only Ip IIa temperate vertebrate fauna to date,
832 which they consider supports palaeobotanical data that indicate rapid climate
833 amelioration in the interglacial (Phillips, 1974; Stuart, 1976). This temperate
834 vertebrate fauna resembles those of Ip IIb. The small-vertebrate assemblage from unit
835 4a at Whittlesey (Supplementary Table S6) is similar to this, including the presence of
836 *E. obicularis*. Together the records from these sites demonstrate that rapid biological
837 response to climate amelioration was underway well before Ip IIb. If indeed the
838 Ipswichian Interglacial does correlate with the northwest Europe LIG, however,
839 transition from pollen biozones Ip Ia–Ip IIb (E1–E3) may have taken place over just a
840 few centuries (Sier *et al.*, 2015).

841

842 **Conclusions**

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

859 Quantified palaeotemperature reconstructions based on the beetle, ostracod
860 and vertebrate assemblages indicate that mean July air temperature during deposition
861 of unit 4a lay within the range +19 to +22°C and mean January air temperature lay
862 within the range 0 to +7°C, indicating that winters were probably similar to those of
863 today but summers were significantly warmer. These palaeotemperature ranges
864 encompass those for Ip IIb deposits at Trafalgar Square (+20 to +21°C and +1.5 to
865 +3°C) reported by Candy *et al.* (2016) and add a second site in support of their
866 conclusion that mean July temperatures during the Ipswichian thermal optimum were
867 significantly higher than Holocene temperatures so far recorded. Exotic thermophile
868 species present in both units likewise suggest warmer summers and a more
869 continental type of climate. These species include the plant *N. minor*, mollusc *B.*
870 *marginata*, beetles *B. elongatum*, *P. versicolor*, *C. schreberi* and *O. massai*, and the
871 reptile *E. orbicularis*. Of these, only *O. massai* may have biostratigraphic
872 significance. Particularly significant is the presence of these thermophiles at the
873 commencement of the interglacial, in the deposits of Ipswichian biozone Ip Ib (unit
874 4a), in contrast to many other sites where they occur only in biozone Ip IIb. The floral
875 and faunal evidence from unit 4a therefore establishes the onset of the Ipswichian
876 thermal optimum in the pre-temperate substage, earlier than traditionally thought, and
877 indicates a rapid biological response to climate amelioration.

878 An important recent review of British LIG sites identified that less than one-
879 third could be securely assigned to the Ipswichian Interglacial based on age estimates
880 and/or a characteristic mammalian fauna that included *Hippopotamus* (Lewis *et al.*,
881 2010). Only a few of those sites have a record of the pre-temperate, late temperate or
882 post-temperate substages and among those only Bobbitshole and Swanton Morley
883 have records of the Ipswichian pre-temperate zone. Their records support the evidence
884 from unit 4a that rapid biological response to climate amelioration was underway
885 before Ip IIb, but that evidence is not as strong as at Whittlesey.

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

893 northwest Europe LIG (late commencement) and some with the southwest Europe
894 LIG (early commencement)?

895

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903

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1277

1277 **Figure captions**

1278

1279 **Fig. 1.** Last Interglacial chronostratigraphy: marine oxygen isotope, Blake Event,
1280 sapropel and Eemian biozone data from Sier *et al.* (2015). The LR04 curve is the
1281 stacked record of Lisiecki & Raymo (2005) and represents a global record from deep-
1282 sea cores, and the marine isotope stages (MIS) displayed below are related to this. The
1283 onset of the ‘global’ Eemian is tied to the onset of sapropel S5 of the eastern
1284 Mediterranean. The MD95-2042 curve is the benthic record off the Iberian coast
1285 (Sanchez-Goñi *et al.*, 1999) and represents the Eemian of southwest Europe. The
1286 Eemian of northwest Europe is from a fluvial record at Rutten in the Dutch ‘type-site’
1287 area (Sier *et al.*, 2015). Onset of both the northwest and southwest Europe Eemian is
1288 tied to the onset of the magnetic Blake Event, which here is depicted for the northwest
1289 Eemian. British U-series data are from Gascoyne *et al.* (1983), Jones & Keen (1993),
1290 McFarlane & Ford (1998), Bowen (1999) and Lewis *et al.* (2010); the solid grey line
1291 labelled Dutch Eemian in the thermoluminescence data indicates the range of median
1292 data for 21 individual dates and the dashed line indicates 1 σ SD (Peeters *et al.*, 2016).
1293 British luminescence data are from Keen *et al.* (1999), Gao *et al.* (2000), Holyoak &
1294 Preece (1985) and Preece *et al.* (1990).

1295 **Fig. 2. (a)** British Ipswichian sites: sites identified by Lewis *et al.* (2010) are shown as
1296 circles – filled circles represent sites where the Ipswichian deposit has been
1297 numerically dated and others represent those assigned by mammalian biostratigraphy,
1298 some of which may be constrained by age estimates from overlying and/or underlying
1299 deposits; other sites of interest mentioned in the text are shown as open squares and
1300 the study site by a filled square. **(b)** Pollen-zone ranges at selected Ipswichian sites
1301 (black bars) and of Wing (grey bar), which is of uncertain age.

1302 **Fig. 3. (a)** Topography and Pleistocene geology at Whittlesey, eastern England. The
1303 Pleistocene deposits overlie the Peterborough Member of the Jurassic Oxford Clay.
1304 The March Gravel is a widespread marine deposit considered by the British
1305 Geological Survey to be Ipswichian (MIS 5e) in age. (Based on BGS, 1984.) **(b)**
1306 Locations of channels A–D and sections A, C and E.

1307 **Fig. 4.** Comparison of amino acid racemization data determined following standard
1308 procedures (Penkman *et al.*, 2008, 2013) for three *Bithynia* opercula from mollusc
1309 sample b, unit 4a, compared with AAR data for other UK Ipswichian sites (Penkman

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1310 *et al.*, 2011). Free amino acid (FAA) versus total hydrolysable amino acid (THAA)
1311 D/Ls indicate that the Bradley Fen material is consistent with correlation with the
1312 Ipswichian.

1313 **Fig. 5.** Schematic diagram of the sedimentary succession in section A, Bradley Fen
1314 and detailed logs A and E from sections A and E respectively. Note the exaggerated
1315 vertical scale for section A.

1316 **Fig. 6. (a)** Unit 4b at the western end of section C in Bradley Fen Quarry (see Fig. 4)
1317 comprises the low-angle cross-stratified beds beneath the staff (1.2 m long) that dip to
1318 the east. **(b)** Large-scale planar cross-beds in unit 3b in a perpendicular section
1319 immediately south of section C. The spade is 90 cm long.

1320 **Fig. 7.** Pollen diagram for unit 4a and 4b in section A, Bradley Fen.

1321 **Fig. 8.** Comparison of *Corbicula fluminalis* shells equivalent in age to MIS 7 from
1322 different units at Whittlesey (a–e) and from Somersham (f): (a) from large-scale sand
1323 lens in unit 2b (West Face Quarry); (b) from muddy gravel facies in unit 2a (West
1324 Face Quarry); (c) from subhorizontally stratified gravels in unit 2b (West Face
1325 Quarry); (d) from gravel pocket in unit 3c (Bradley Fen Quarry); (e) from sand and
1326 gravel lens at the top of unit 3b of Langford *et al.* (2014b) in West Face Quarry (unit
1327 F2 in Langford *et al.*, 2007); (f) from section SBK at Somersham (West *et al.*, 1994).
1328 The shells in (a)–(c) are from primary contexts in channel B (Langford *et al.*, 2014a),
1329 with those in (b) the oldest. At the right-hand end of (c) the specimen beneath is part
1330 of a conjoined shell. The shells in (b) and (c) have experienced post-depositional
1331 subaerial weathering, but still during MIS 7. Those in (e) were reworked from channel
1332 B some time between MIS 7 and MIS 5b: note that two have Fe staining that occurred
1333 prior to reworking (i.e. during MIS 7), but two do not. Those in (d) were reworked
1334 from channel B in Bradley Fen probably some time in MIS 6 (see text), after
1335 sediments of channel B had been subjected to a temperate weathering phase and
1336 subsequent cold-stage cryogenic processes. In (f) the shells are believed to have been
1337 reworked from pre-existing temperate deposits during the last cold stage
1338 (Devensian/Weichselian).

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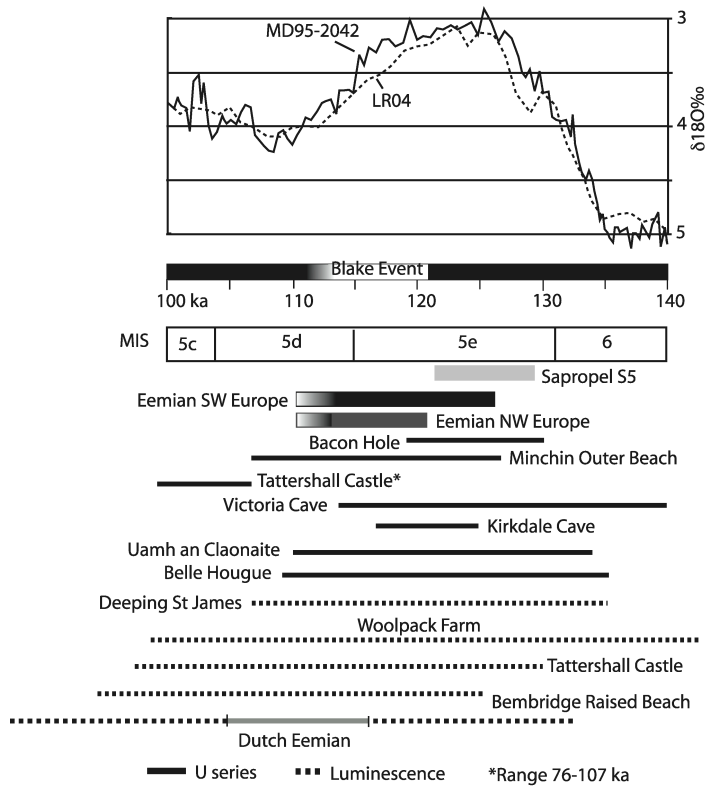
1340 |

1340 **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, 1961)
	Ip IV	Post-temperate substage: <i>Pinus</i> – <i>Betula</i> with <i>Carpinus</i>	E6b E6a
	Ip III	Late temperate substage: <i>Carpinus</i> – <i>Pinus</i> with <i>Betula</i> , <i>Alnus</i> , <i>Quercus</i> and <i>Corylus</i>	E5
<i>f</i> <i>Quercus</i> + <i>Pinus</i> + <i>Corylus</i> , with its base where <i>Corylus</i> starts to increase	Ip IIb	Early temperate substage: <i>Pinus</i> – <i>Quercus</i> – <i>Corylus</i> with <i>Betula</i> – <i>Alnus</i> – <i>Acer</i> – <i>Tilia</i> – <i>Taxus</i>	E4b E4a
<i>e</i> <i>Pinus</i> (dominant) + <i>Betula</i> + <i>Quercus</i> + <i>Ulmus</i> , with its base where <i>Quercus</i> starts to increase	Ip IIa	Early temperate substage: <i>Pinus</i> – <i>Quercus</i> with <i>Betula</i> – <i>Alnus</i> – <i>Fraxinus</i>	E3b E3a
<i>d</i> <i>Betula</i> (dominant) + <i>Pinus</i> + <i>Ulmus</i> , with its base positioned where <i>Pinus</i> and <i>Ulmus</i> start to increase and <i>Betula</i> starts to decline	Ip Ib	Pre-temperate substage: <i>Pinus</i> – <i>Betula</i> with <i>Ulmus</i> – <i>Quercus</i> – <i>Acer</i>	E2b E2a
<i>c</i> <i>Betula</i> (dominant) + <i>Pinus</i>	Ip Ia	Pre-temperate substage: <i>Pinus</i>	E1

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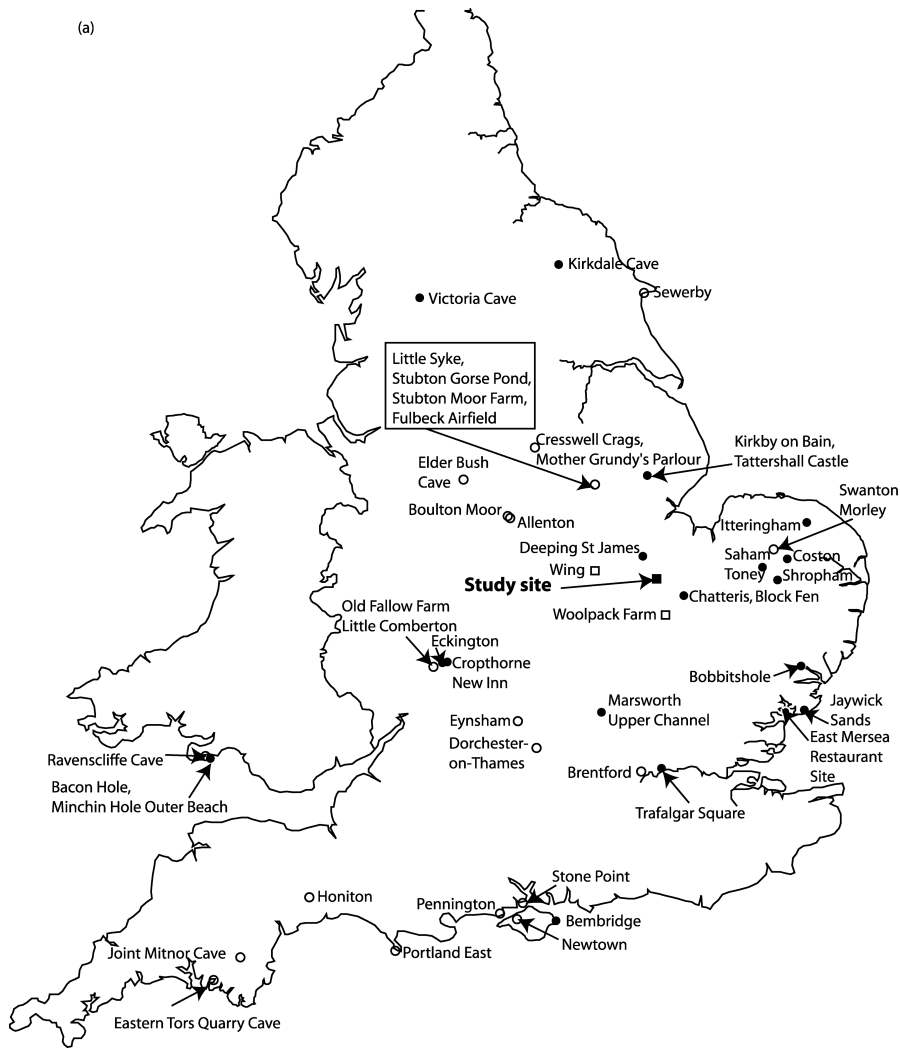


1342

1343 Figure 1

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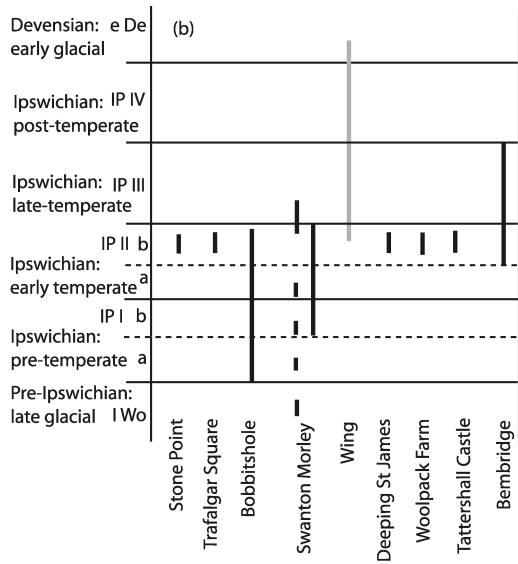
(a)



1344

1345 Figure 2a

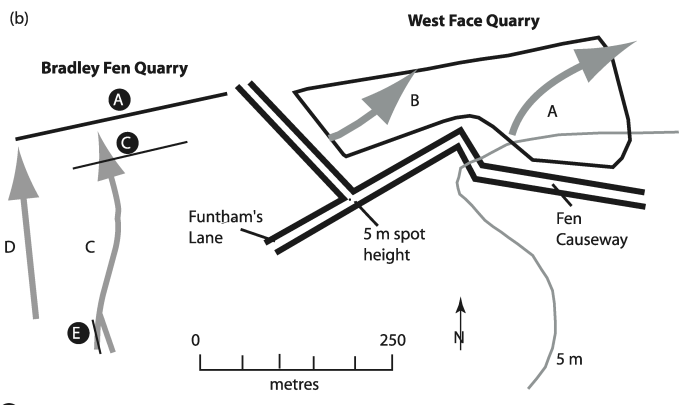
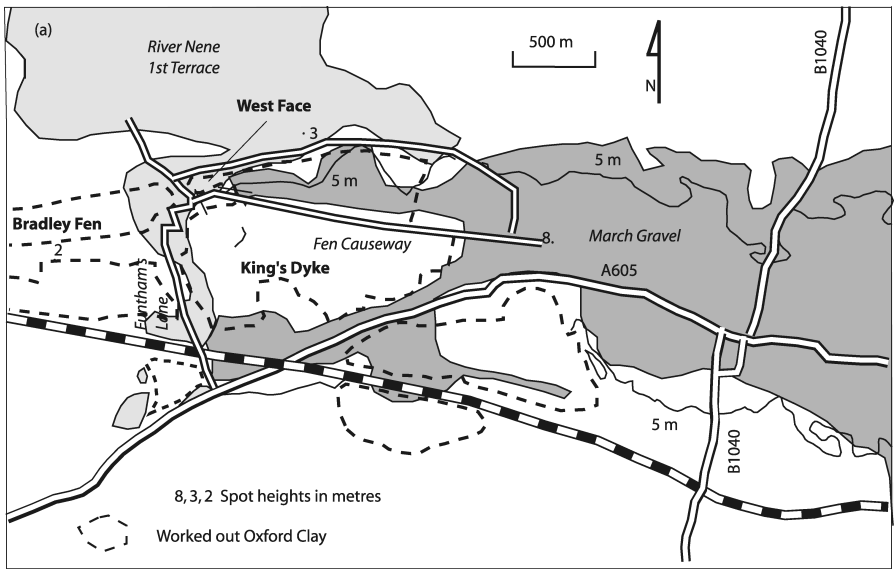
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1347 Figure 2b

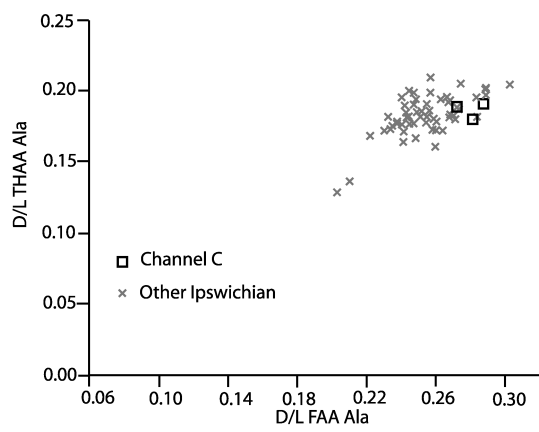
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Ⓐ Section nomenclature follows Langford *et al.* (2004a) except that section J has been included in A
 A = early Devensian channel (Langford *et al.*, 2007) C = Ipswichian channel
 B = MIS 7 channel (Langford *et al.*, 2014a) D = MIS 3 channel (Langford *et al.*, 2014b)

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Figure 3



1350

1351 Figure 4

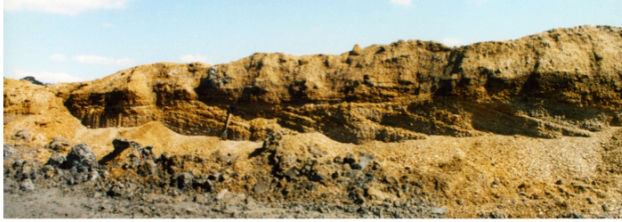
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1355 Figure 6a

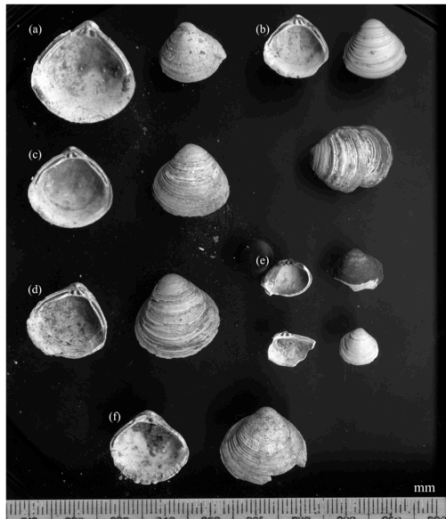
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1357 Figure 6b

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1360

1361 Figure 8

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1362 **Supplementary material**

1363

1364 **Table S1.** *Amino acid data on opercula of Bithynia tentaculata from unit 4a of channel C at Bradley*
 1365 *Fen, Whittlesey determined following standard procedures (Hill, 1965; Sykes et al., 1995; Kaufman &*
 1366 *Manley, 1998; Penkman, 2005; Preece & Penkman, 2005; Langford et al., 2007; Penkman et al.,*
 1367 *2008a, 2008b, 2011, 2013)†*

1368

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

1369 †Error terms represent one standard deviation about the mean for the duplicate analyses for an
 1370 individual sample. Each sample was bleached (b), with the free amino acid fraction signified by 'F' and
 1371 the total hydrolysable fraction by 'H*'.
 1372

1372

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- 1398

1398 **Table S2.** Plant macrofossil analysis for residue from vertebrate sample (10–63 cm from base) of unit
 1399 4a (section A) and residue of mollusc samples from unit 4b (section E) of channel C in Bradley Fen,
 1400 Whittlesey*
 1401

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	<i>Ulmus</i> sp.	Bud	–	3	–	–
Shrubs and terrestrial plants	<i>Cerastium arvense</i>	Seed	–	3	–	–
	<i>Rubus</i> sp.	Seed	–	1	1	3
	<i>Polygonum aviculare</i>	Seed	–	–	–	3
Waterside and damp ground	<i>Eleocharis</i> cf. <i>palustris</i>	Nutlet	–	7	–	–
	<i>Ranunculus</i> sp.	Achene	7	5	2	30
	<i>Scirpus maritimus</i> .	Nutlet	200	58	–	7
	<i>Sparganium erectum</i>	Fruitstone	12	1	–	–
	<i>Sparganium minimum</i>	Fruitstone	3	–	–	–
	<i>Saponaria officinalis</i>	Seed	–	2	–	–
	<i>Carex</i> sp(p).	Biconvex nutlet	1	1	7	1
	<i>Carex</i> sp(p).	Trigonous nutlet	5	24	–	–
	<i>Potentilla</i> sp.	Seed	7	4	–	1
	<i>Hydrocotyle vulgaris</i>	Bract	2	1	–	–
Aquatic	<i>Potamogeton</i> sp.	Fruit	191	200	7	–
	<i>Nymphaea</i> sp.	Seed	4	1	–	–
	<i>Nuphar</i> sp.		1	–	–	–
	<i>Najas minor</i>	Seed	–	29	–	–
	<i>Menyanthes trifoliata</i>	Seed	2	–	–	–

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

1402 *The counts should be treated as abundance/presence/absence data only since volumes of original
1403 sample are not consistent and often not known, because all samples were residues from other fossil
1404 analyses and not all the residue was processed.
1405

<i>Pisidium subtruncatum</i> Malm 1855	1	1			1		1			1
<i>Pisidium supinum</i> A. Schmidt 1851			6	39	2	6	1			
<i>Pisidium henslowanum</i> (Sheppard 1823)		12	17	56	25	29	32	22	31	8
<i>Pisidium nitidum</i> Jenyns 1832*	29	17	26	84	42	30	46	35	25	15
<i>Pisidium moitessierianum</i> Paladilhe 1866		1	8	94	7	2	6	20	36	4
<i>Pisidium</i> spp.	11	8		27	55	107	61	16	10	2
Total	687	666	593	645	576	636	521	328	272	144
Total minus <i>Bithynia</i> opercula counts	613	549	540	563	509	472	439	309	237	110
Terrestrial										
<i>Carychium minimum</i> O. F. Müller 1774*	1	1								
<i>Carychium tridentatum</i> (Risso 1826)		1	1				1	1		
<i>Succinea/Oxyloma</i> sp.	6	3	7	10	2				4	
<i>Cochlicopa</i> cf. <i>lubrica</i> (O. F. Müller 1774)	1					1			5	6
<i>Cochlicopa</i> sp.	2		1		1	1				
<i>Truncatellina cylindrica</i> (A. Férussac 1807)										1
<i>Vertigo antivertigo</i> (Draparnaud 1801)	2	2								
<i>Vertigo pygmaea</i> (Draparnaud 1801)								1	1	
<i>Vertigo</i> sp.						1		1	1	
<i>Pupilla muscorum</i> (Linnaeus 1758)		1	8	7	3	7	4	3	4	13
<i>Vallonia costata</i> (O. F. Müller 1774)					3	6	2			4
<i>Vallonia pulchella</i> (O. F. Müller 1774)	2		1	5					1	13
<i>Vallonia excentrica</i> Sterki 1893	1	1		2						
<i>Vallonia</i> spp.	9	2	18	23	19	21	22	18	13	49
<i>Punctum pygmaeum</i> (Draparnaud 1801)*	2									1
<i>Aegopinella nitidula</i> (Draparnaud 1805)	11	1								
<i>Oxychilus</i> sp.							1			1
<i>Derocerus/Limax</i>	1		2	3						
<i>Euconulus</i> cf. <i>alderi</i> (O. F. Müller 1774)	1									
<i>Helicella itala itala</i> (Linnaeus 1758)					1		1		1	3
<i>Trochulus hispida</i>				3						
<i>Cepaea</i> 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

1408 *Present at Bobbitshole (Sparks, 1957).

1409 †Samples a–d of section A were not available for verifying species identification and so this list differs

1410 from that in Langford *et al.* (2004) as follows: *V. macrostoma* counts have been included in the *V.*

1411 *piscinalis* counts; *A. vortex* counts have been deleted; *S. putris* has been included in *Succinea/Oxyloma*
1412 sp.; *C. nitens* has been included in *Cochlicopa* sp.; *V. enniensis* has been included in *Vallonia* spp.
1413 ‡Juvenile *G. laevis* and *P. planorbis* are difficult to distinguish from each other, with the latter being
1414 consistently present in small numbers in all samples of section E (R. C. Preece, pers. comm., August
1415 2015).
1416 §Includes a small barnacle fragment of indeterminate age.

1417

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1426 **Table S4.** Coleopteran analysis for a bulk sample from 10 to 63 cm from base of unit 4a of channel C
 1427 in Bradley Fen, Whittlesey
 1428

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

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

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

1429 *Species not now living in the British Isles.

1430 †Species used for palaeotemperature reconstruction.

1431

1431 **Table S5.** Ostracod analysis for samples from 10 to 63 cm above base of unit 4a of channel C in
 1432 Bradley Fen, Whittlesey
 1433

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

1434 *From 42 g of dry residue.

1435 †From 54 g of dry residue.

1436 ‡Residue from insect sample (from 30 g of dry residue, half the residue).

1437

1437 **Table S6.** Vertebrate analysis for samples from 10 to 63 cm from base of unit 4a of channel C in
 1438 Bradley Fen, Whittlesey, showing numbers of identified specimens (NISP) and minimum numbers of
 1439 individuals (MNI) for herpetofauna, birds and mammals.

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

1440

1441

1441 **Table S7.** *Thermophile species in channel C and at other Ipswichian sites according to pollen*
 1442 *biozonation*
 1443

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

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