PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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The Hoxnian Interglacial deposits at Woodston, Peterborough

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SUMMARY

Interglacial deposits on the south side of Peterborough have yielded a diverse flora and fauna which lived in an estuarine environment that was affected by marine transgression and regression. Fossils described from six sequences indicate that the deposits accumulated under fully temperate conditions. The Woodston Beds have a diversity of fossils (pollen, plant macrofossils, molluscs, ostracods, insects and mammals) which allows their palaeoecological relationships to be examined, and compared with those of other sites of similar age. The environmental reconstructions based on the individual taxa, although emphasising differing facets of the habitat, are in broad agreement. Some slight discrepancies arise from the assumption that the organisms are characteristic of the sedimentary environment in which they are found. In fact many of the fossils have been transported to the site of deposition from nearby habitats.

Evidence of a closed canopy forest with associated land environments, is provided by the plant remains and the land molluscs, and to a lesser extent by the insects and the mammals. A large, slow-flowing river, with adjacent marsh and meadow areas is also suggested by the taxa of molluscs, ostracods and insects present. Molluscs and ostracods show clearly the presence of marine influences between 11 and 14 m Ordnance Datum.

The climate under which the Woodston Beds were deposited was slightly warmer than the present. An age in the Hoxnian Interglacial of the Middle Pleistocene is proposed.

1. INTRODUCTION

Interglacial sediments have been known in the vicinity of Peterborough for at least 135 years (Horton 1989) and long recognized as a prolific source of fossil Mollusca (Kennard & Woodward, 1922). The term Woodston Beds was first used when these sediments were re-examined during the mapping of the Greater Peterborough area by the British Geological Survey in 1968 (Horton *et al.* 1974). Figures 1 and 2 show their known extent. The Woodston Beds are fluviatile and estuarine in origin and consist largely of silty clays, silts and fine sands overlying beds of gravel. They rest on Jurassic bedrock and are succeeded by, and possibly interdigitate with, gravel deposits which form the Third Terrace of the River Nene.

(*a*) *History of research*

Trimmer (1854, p. 345) reported a section in gravel pits close to Orton Longueville Hall which appears to have been excavated through deposits of the Third Terrace. The sequence described was up to 4.20 m thick and commenced with a basal gravel which contained mammalian bones associated with terrestrial, freshwater and marine shells. This was overlain by a 'seam of sand with grey and brown clay' which yielded freshwater and terrestrial molluscs, and then, at the top, a second bed of gravel. This tripartite sequence was confirmed by Porter (1861, p. 38) who described two pits, one to the west of Orton Longueville Hall [TL 163 964] and one at *circa* TL 169 967 which also yielded molluscan and mammalian remains (figure 2).

Expansion in the brick industry in the late nineteenth century led to the opening of new pits (probably Hicks No 1 [TL 189 960] and Plowmans Pit [TL 193 960]) 'southwards beyond the old series'. These 'encountered an unexpected increase in the depth of the topsoil' which 'proved to be the infill of an old Pleistocene river channel cut into boulder clay and running west to east' (Leeds, 1956, p. 81). Mammalian bones were recorded from the channel sediments. The dimensions of the channel were recorded in 1949 by Dr P. A. Sabine (B.G.S.) (pers. comm.) from measurements taken by Mr G. Wyman Abbot of Stubbington House, Wansford, as '30 yds [27.5 m] wide and 23 ft [6.9 m] deep cutting across the pits west of Fletton'.

Another channel up to 50 ft [15 m] deep was encountered in the London Brick Company No 4 (or Stillwells) Pit. Here, Kendall (1913) noted a 'buried river which traverses the beds of Oxford Clay for some considerable distance in a direction roughly from north-west to south-east'. He recorded a 40–50 ft (12–15 m) section, comprising many feet of rubble and boulders at the base overlain by 25–30 ft (7.5–9 m) of 'sands, marls, clays and gravels'. He collected 53

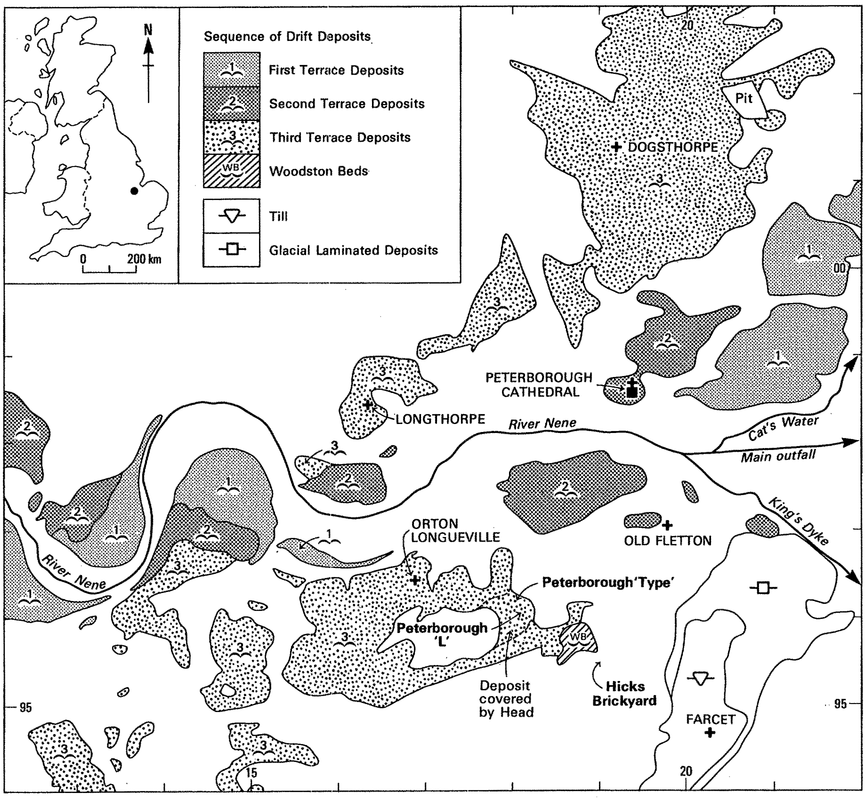

Figure 1. The Peterborough area showing the distribution of Pleistocene deposits and the location of Hicks Brickyard, Peterborough 'Type' and Peterborough 'L' Sections.

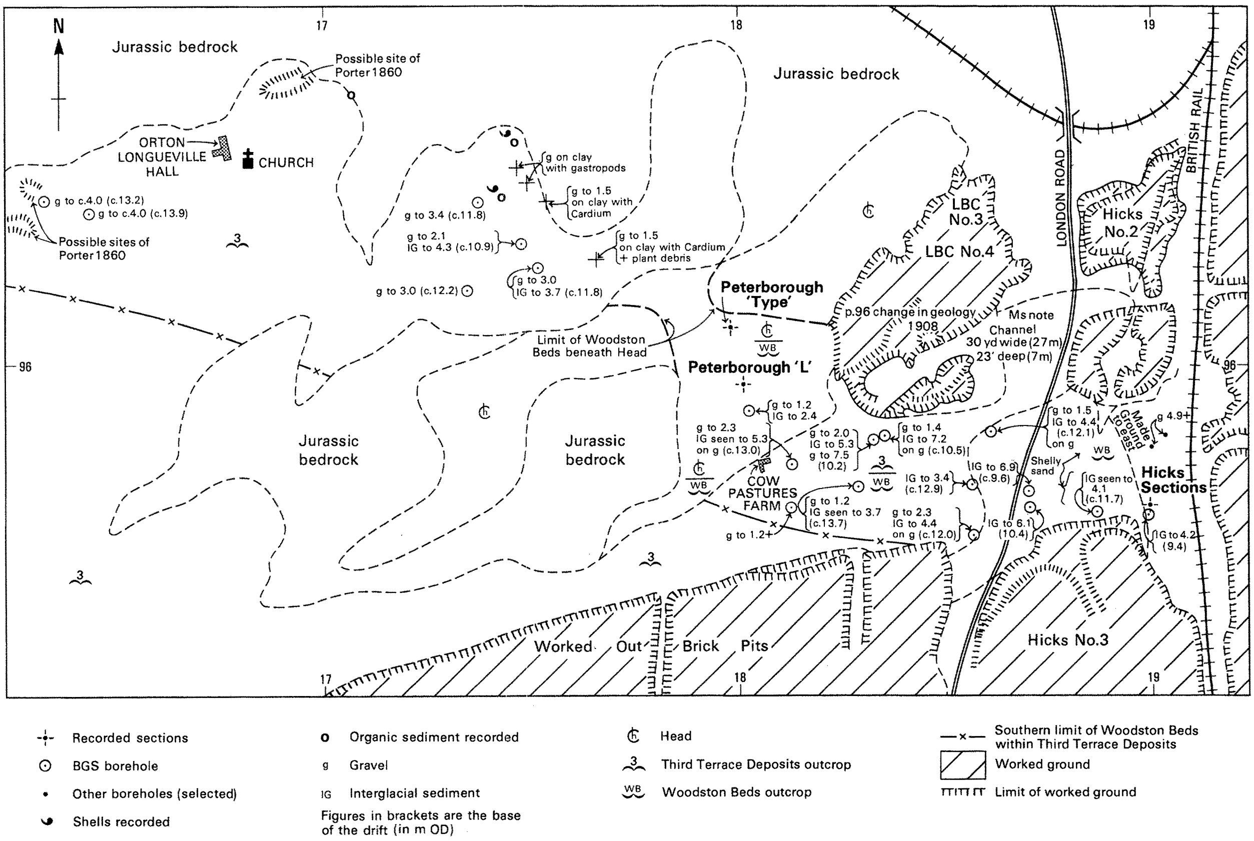

Figure 2. Location of the Hicks 69 and 86 Sections, Peterborough 'Type' and Peterborough 'L' Sections; other sections mentioned in the text, and boreholes to show the thickness of Pleistocene deposits.

species of molluscs of which 28 are terrestrial, and 25 freshwater species. This locality was examined by Kennard & Woodward (1922) who listed 58 molluscan species and correlated the deposits with those at Orton Waterville now mapped as Third Terrace deposits, and with those at Woodston Cemetery [TL 184 935] now thought to underlie the Nene Second Terrace. A further section was recorded by Harrison (1935) in a pit 800 yds (730 m) west of Orton Longueville Hall [*circa* TL 163 963].

2. STRATIGRAPHY

The sections noted above are mostly now lost, but four new sections, recorded during the geological survey of the area in the 1960s, and an excavation undertaken in 1986 for specialist palaeontological investigation, are illustrated in figures 3 and 4 and lithologically described in full in Appendix 1. Their location is indicated in figure 2. Material from two boreholes, Phorpres 1 and 4, was also examined. The terms 'Type' and 'L' were used informally to identify the proximal sections in arable land, but they have become established in the BGS fossil registers. The term 'Type' is retained although it is not a type section in the formal sense.

In general the tripartite succession recorded by earlier investigators is confirmed, although one or other of the three elements may be locally absent. The main impression from the detailed logging of the sections is of a great variety of depositional environments, consistent with the normal variability of depositional conditions on a river floodplain or among the creeks and lagoons of a tidal estuary.

At the base of the tripartite succession a gravel bed is usually present, varying in thickness between sites from a few centimetres to over 2.0 m. The gravel is commonly diversified by lenses and beds of sand and by clay-rich layers. Fossil material is common, both dispersed through the gravel and concentrated as felted plant debris or in shell-rich bands. Large freshwater bivalves may be conspicuous and wood is locally present. Mammalian remains may be present but are nowhere common.

The gravel is succeeded upward by mainly fine-grained sediments of fluvial origin indicative of deposition outside the channel environment. These include silts characteristic of backwater deposition, and sands in lens-shaped bodies and as well as in graded and laminated sheets, both forms suggestive of higher energy flows on the floodplain, with overbank spillage giving rise locally to crevasse splays and to small-scale channelling of the finer floodplain alluvium. Thin seams of gravel are locally present. Fossil material is generally found and often concentrated in very rich horizons.

These fluvial sediments form the lower part of the middle element of the tripartite succession. They pass upward, without any clear break into similar deposits which, on the basis of their contained fauna are

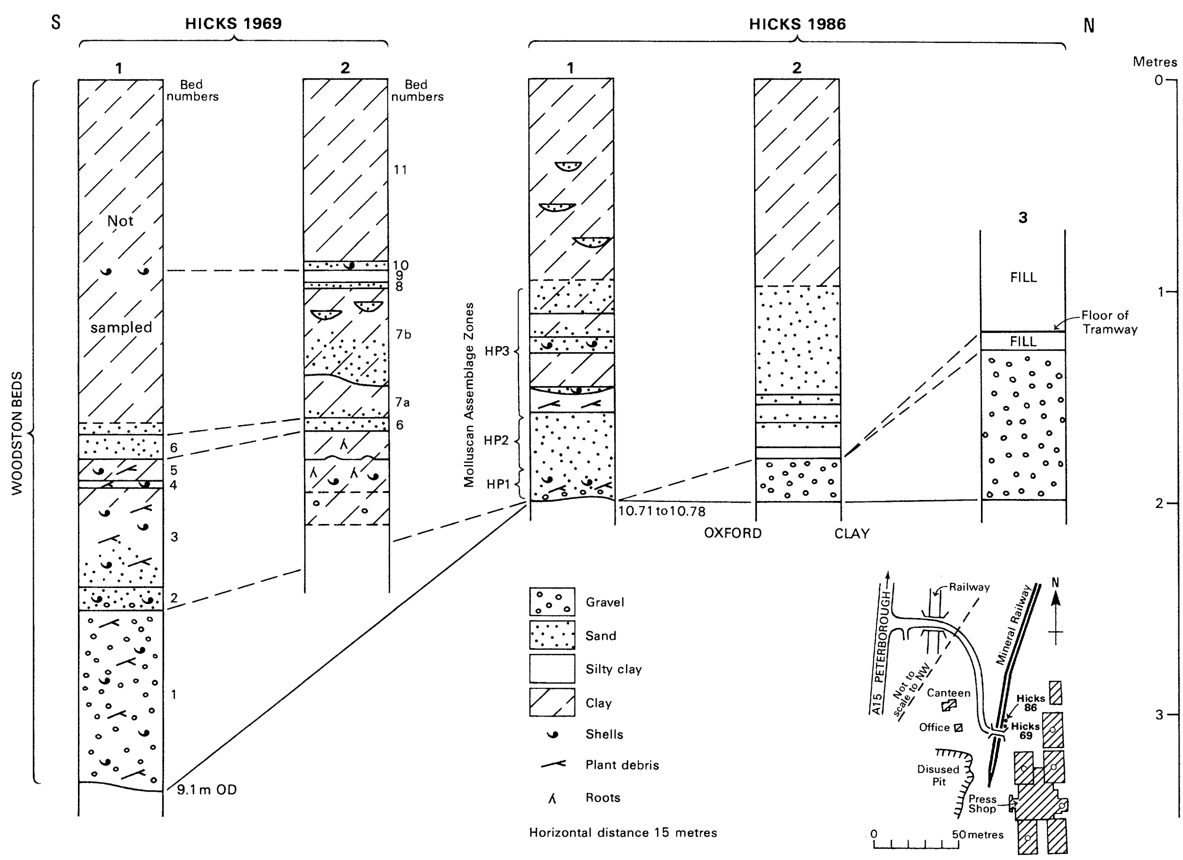

Figure 3. Stratigraphic logs and location plan, Hicks 69 and 86 Sections.

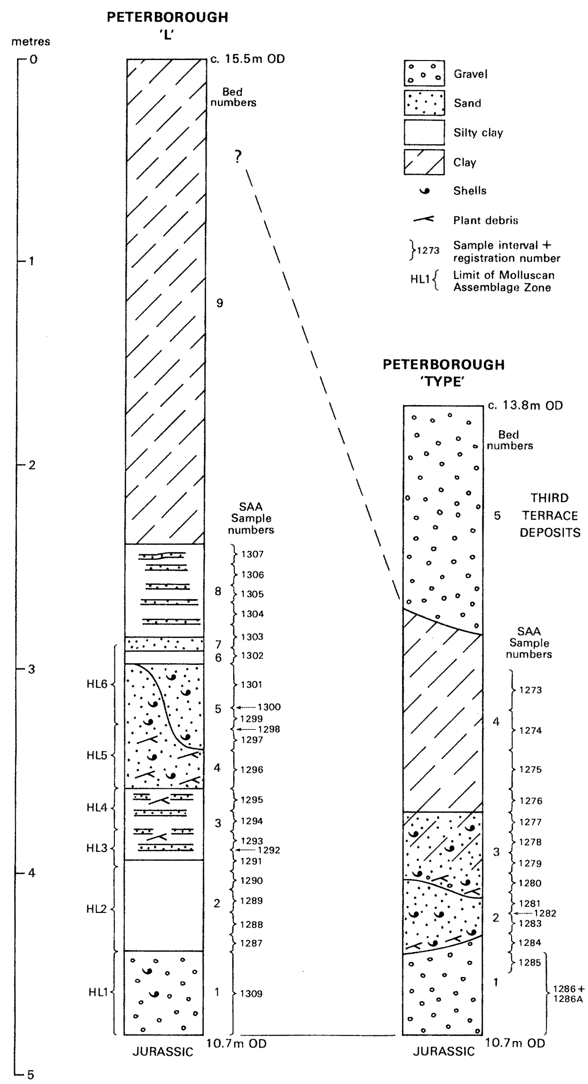

Figure 4. Stratigraphic logs, Peterborough 'Type' and 'L' Sections.

clearly of estuarine origin. Evidence of backwater or lagoonal deposition and of the cutting and filling of minor channels is present. The amount of reworking changes from place to place and suggests varying proximity to the main flow of water in the estuary. Where these fine-grained sediments reach or approach the ground surface, they are commonly oxidized and wholly or partly decalcified. Secondary calcareous concretions (race) may be present.

The uppermost part of the tripartite succession is of gravel. In the few places where details of this bed have been recorded, a thickness of about a metre is indicated.

3. PALAEOBOTANY

(*a*) *Pollen analysis*

Samples taken from the 1969 sections in Hicks Pit were analysed for pollen. The position of the sampled section can be seen in figure 2 and the depth of the samples in figure 5. The results of this analysis can be seen in the pollen diagram (figure 5).

(*b*) *The pollen assemblage*

The pollen spectra are relatively uniform throughout the 2 m of sediment sampled. The assemblage is characterized by a high level of tree pollen, which does not fall below 72% of total land pollen. Type X, an unidentified tricolpate pollen taxon, occurs and has previously been found in Hoxnian deposits at Hoxne, Marks Tey, the Nar Valley, Barford and Clacton in East Anglia, at Kilbeg and Gort in Ireland, and in south-west France. Its incidence in the temperate part of an interglacial suggests a shrub origin (Turner 1970).

The vegetation indicated by the pollen analyses is a mixed oak forest dominated by *Ulmus*, *Quercus*, and *Alnus*, and rich in tree species with pollen of *Betula*, *Pinus*, *Tilia*, *Fraxinus* and *Picea* occurring throughout the sequence. The only evidence for change in vegetation is a slight upward increase in *Pinus* and some decline in *Ulmus* and *Quercus* percentages. Among the shrubs, *Corylus* and Type X are of equal importance and appear to have complementary curves suggesting that they may occupy contrasting ecological niches in the forest. There is one record of '*Erica* cf. *terminalis*', now re-identified as *Bruckenthalia* sp. This taxon is also found in the Hoxnian deposits at Marks Tey, principally in zone Ho IV but also sporadically in zones Ho II and Ho III (Turner, 1970). Low herbaceous pollen values indicate an almost complete forest cover. Small areas of open ground are suggested by the presence of grasses and by infrequent occurrences of plants of open habitats such as *Armeria*, *Artemisia*, *Scleranthus annuus* Linné, *Plantago major/media* and *Helianthemum*. The other herbaceous plants can probably be assigned to the field layer of the forest. Aquatic plant pollen is surprisingly sparse, but there is a record of a barb of the water fern *Azolla filiculoides* Lamarck, a plant characteristic of Hoxnian and earlier interglacial periods. This species is not known from younger sites and appears to have become extinct in western Europe until reintroduced from America in recent times.

Pollen was also examined in samples from the 'Type' and 'L' sections and from borehole Phorpres 1 [TL 1833 9582]. The pollen from these sites was poorly preserved and in low concentration. In the 'Type' section it was too degraded to count. The pollen analyses from the three samples from the 'L' and Phorpres 1 sequences (table 1) resemble one another, with high values for *Ulmus*, *Alnus*, *Corylus* and Type X and also conform closely with the more complete sequence from Hicks 69.

(*c*) *Plant macrofossils*

Serial samples each representing approximately 0.15 m of sediment were taken from the lowest 1.05 m of the Woodston Beds in the Hicks 86 section. Although the Hicks 69 and 86 sites are about 10 m apart, their similar stratigraphy (see above) indicates that the pollen and plant macrofossils are from the same horizons and thus complement each other.

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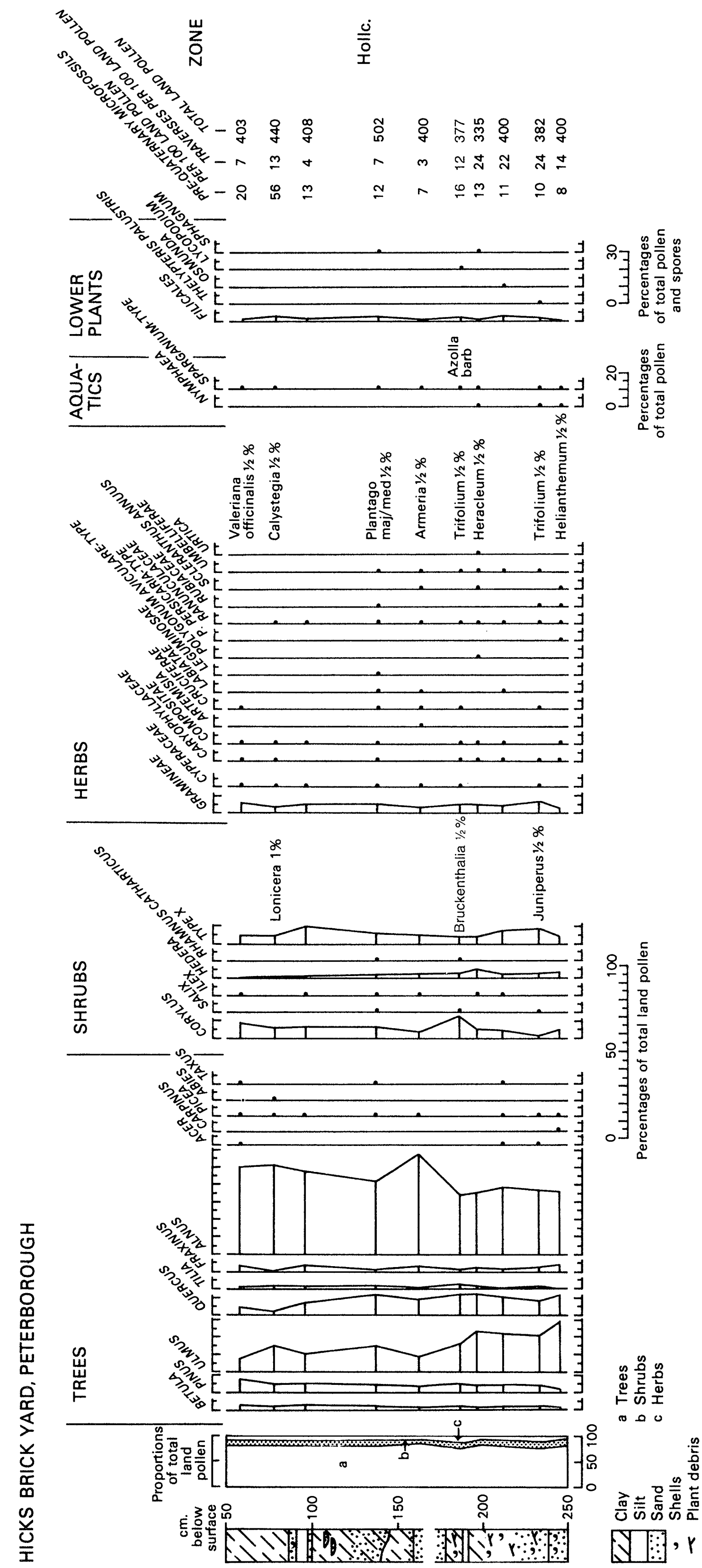

Figure 5. Pollen diagram, Hicks 69 section.

Table 1. *Pollen analyses from the Peterborough 'L' Section and from the borehole Ph 1*

(All figures are percentages of total land pollen.)

	'L' 0.10 m	'L' 1.60 m	Ph 1 12 ft (3.65 m)
Betula		1	1
Pinus	6	8	2
Ulmus	21	19	10
Quercus	6	5	5
Tilia		2	1
Alnus	38	45	42
Fraxinus			4
Abies			0.5
Picea	1		0.5
Taxus	1	1	
Corylus	9	10	13
Hedera	2	3	7
Ilex	1	1	
Type X	7	2	4
Gramineae	6	1	5
Cyperaceae			1
Compositae	2		
Chenopodiaceae			0.5
Cruciferae			1.5
Umbelliferae	2	2	

(*d*) *The plant macrofossil assemblage*

Macrofossils from the topmost 0.30 m of the profile showed deterioration due to weathering. The remaining samples yielded a well preserved and diverse assemblage (table 2). The most abundant tree species was *Alnus glutinosa* (Linné), but *Taxus baccata* Linné and *Betula* sp. also occur. The predominance of alder probably reflects its preference for waterside habitats and its high productivity of fruits. Two shrub species were identified, *Cornus sanguinea* Linné and *Sambucus nigra/racemosa* type.

Herbs from several habitats are present. *Lapsana communis* Linné and *Silene dioica* (Linné) indicate woodland margin habitats. Ruderals and plants of disturbed ground are represented by eight taxa [*Aethusa cynapium* Linné, *Aphanes arvensis* Linné, *Atriplex* spp., *Chenopodium album* Linné, *Chenopodium polyspermum* Linné, *Chenopodium* spp., *Lamium* sp., *Sonchus asper* (Linné) and *Stellaria media* (Linné)], and are the largest group in the assemblage. They probably grew on drier bare areas on the flood plain or on areas exposed by bank collapse.

The record of *Ranunculus* subgenus *Ranunculus* and the presence of *Torilis japonica* (Houtt) and *Plantago media* Linné suggests the occurrence of grassland areas on the floodplain.

Fragments of *Lycopus europaeus* Linné, *Bidens tripartita* Linné and *Eupatorium cannabinum* Linné provide evidence of waterside and fen habitats close to the site of deposition. Plants of shallow water include *Ranunculus* subgenus *Batrachium* and *Sagittaria sagittifolia* Linné. These probably grew at the stream margin or in pools on the flood plain.

Seven taxa (table 2) are plants of strictly aquatic conditions and all are characteristic of slowly moving water.

(*e*) *Wood fragments from the Hicks 86 section*

Eighteen pieces of wood from the lowest metre of the Hicks 86 excavation were submitted to the Royal Botanic Garden, Kew, for identification. Most numerous (seven samples) was the wood of *Quercus*. Three fragments each were of *T. baccata* and Rosaceae subfamily Pomoideae. Two samples were of *Fraxinus* sp., and one each of *Carpinus betulus* Linné, *Ulmus* and indeterminate gymnosperm bark. The fragments of *Quercus* exhibited narrow growth rings suggesting slow growth.

The wood remains confirm the presence in the forest of tree taxa indicated by pollen, fruits and seeds. Although the seeds of *T. baccata* are the most numerous it is outnumbered in the wood remains by *Quercus* suggesting that the regional forest had considerable stands of oak. The absence of wood of *Alnus* is surprising in view of the occurrence of this taxon in waterside habitats, the abundance of its cones in the Hicks 86 samples, and its pollen in the Hicks 69 samples.

(*f*) *Environmental indications from the floral remains*

The pollen and macrofossil assemblages suggest that the vegetation during the deposition of the Woodston Beds was that of a closed canopy forest. It is interesting to note that the pollen, plant macrofossils and wood data give different indications of forest composition. The pollen evidence indicates an abundance of alder with subsidiary elm and oak, the macrofossils are dominated by alder, but the most common seeds are those of yew, whilst oak is the most numerous wood fragment. They are, however, in broad agreement and the differences probably arise from local vagaries of transportation and preservation and to the site proximity to specimens of particular taxa.

Both pollen and macrofossil evidence confirm the existence of grassland and disturbed ground during the deposition of the Woodston Beds. However, there is little pollen from aquatic plants, despite the macrofossil evidence of a varied water plant flora close to the site of deposition. The reason for this discrepancy is not clear.

The palaeobotanical evidence suggests fully interglacial conditions during the deposition of the Woodston Beds. The occurrence of *Najas minor* Allioni, which has a current distribution in southern and eastern Europe (Fitter, 1978), suggests a climate warmer than at present. The occurrence of *Hedera* in some quantity, and of *Ilex* indicates a climate with winters not significantly colder than now (Iversen, 1944).

(*g*) *Indication of age of the flora*

Comparison of the pollen diagram from the Hicks 69 site (figure 5) with those from other Hoxnian sites (West, 1956; Kelly, 1964; Turner, 1970; Phillips, 1976) suggests a Hoxnian age for the Woodston Beds. The major indicators are: (i) High values for *Ulmus* in

Table 2. *Plant macro fossil assemblages from the Hicks 86 section*

(a – achene, c – capsule, f – fruit, fa – achene fragment, fc – female catkin, ff – fruit fragment, fs – seed fragment, l – leaf, li – lid, n – nutlet, n + p – nutlet and perianth, ps – place of stem, s – seed, sa – scale, sc – scale from cone, spo – sporangia, st – stone, th – thorn, tn – trigonal nutlet, tu – tubercle.)

		1.05–1.20 m	1.20–1.35 m	1.35–1.50 m	1.50–1.65 m	1.65–1.80 m	1.80–2.00 m
TREES							
Alnus glutinosa (Linné) Gaertn.	f	—	—	1	38	214	61
	fc	—	—	—	—	2	—
Alnus sp. (p.)	f	—	—	—	12	87	69
	sc	—	—	—	—	2	3
Betula sp.	sa	—	—	—	1	—	—
Taxus baccata Linné	s	—	—	10	8	3	13
	fs	—	—	32	6	2	25
WOODS, WOOD MARGINS & SCRUB							
cf. *Dryopteris* sp.	spo	—	—	—	—	—	1
Cornus sanguinea Linné	st	—	1	—	—	3	—
Lapsana communis Linné	a	—	—	—	2	9	5
	fa	—	—	—	—	3	4
Sambucus nigra Linné/*racemosa* Linné type	a	1	12	1	5	27	8
	fs	1	1	1	6	21	2
Silene dioica (Linné) Clairv.	s	—	—	—	1	4	2
Viola odorata Linné/*hirta* Linné type	fs	—	—	—	—	6	1
BARE GROUND/RUDERALS							
Aethusa cynapium Linné	f	—	—	—	—	1	—
	ff	—	—	—	—	2	—
Aphanes arvensis Linné	f	—	—	—	—	1	1
Atriplex sp. (p.)	a	—	—	—	—	2	—
Chenopodium album Linné	a	—	—	—	2	8	4
Chenopodium polyspermum Linné	s	—	—	—	6	32	4
Chenopodium sp. (p.)	s	—	—	—	1	17	2
Lamium sp.	n	—	—	—	—	—	1
Sonchus asper (Linné) Hill	a	—	—	—	1	—	1
Stellaria media (Linné) Vill.	s	—	—	—	6	75	9
	fs	—	—	—	—	11	—
GRASSLAND							
Plantago media Linné	c	—	—	—	—	1	—
Ranunculus subg. *Ranunculus*	a	—	—	1	3	14	4
	fa	—	—	—	—	2	1
Rumex conglomeratus Murr./*sanguinus* Linné type	n	—	—	—	2	10	—
	n + p	—	—	—	—	4	—
Torilis japonica (Houtt.) DC.	f	—	—	—	—	9	2
	ff	—	—	—	—	—	1
FENS & WATERSIDE							
Bidens tripartita Linné	a	—	—	—	—	2	2
Bidens sp.	a	—	—	—	—	1	—
Eupatorium cannabinum Linné	a	—	1	—	—	—	1
Lycopus europaeus Linné	n	—	—	—	1	1	3
Stachys palustris Linné	n	—	—	—	—	3	—
Thalictrum sp.	a	—	—	1	—	—	—
WET MUDDY PLACES & SHALLOW WATER							
Callitriche sp. (p.)	s	—	—	1	—	6	5
Polygonum hydropiper Linné	f	—	—	—	—	4	1
Ranunculus subg. *Batrachium*	a	—	—	1	—	16	4
Sagittaria saggittifolia Linné	f	—	—	—	—	—	1

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Table 2 (*contd*)

		1.05–1.20 m	1.20–1.35 m	1.35–1.50 m	1.50–1.65 m	1.65–1.80 m	1.80–2.00 m
AQUATIC							
Hippuris vulgaris Linné	f	—	—	—	—	1	—
Najas minor All.	s	—	—	—	6	44	15
	fs	—	—	—	—	3	—
Potamogeton cf. *perfoliatus* Linné	f	—	—	—	—	2	—
Potamogeton cf. *pusillus* Linné	f	—	—	—	—	6	—
Potamogeton cf. *natans* Linné	f	—	—	—	—	7	—
Potamogeton sp.(p.)	f	—	—	—	1	2	—
	li	—	—	—	—	2	3
Zannichellia palustris Linné	f	—	—	—	—	2	1
UNCLASSIFIED							
Carduus/Cirsium sp.(p.)	a	—	—	—	—	1	1
Carex sp.(p.)	tn	—	—	—	—	3	—
Musci sp.(p.)	ps	—	—	5	47	58	204
	l	—	—	—	2	9	34
Rosa/Rubus sp.(p.)	th	—	—	—	1	7	—
Rumex subg. *Rumex* sp.(p.)	n	—	—	—	1	—	—
	n+p	—	—	—	—	—	1
	tu	—	—	—	1	—	—
Solanum dulcamara Linné	s	—	—	—	—	2	—
Urtica dioica Linné	a	—	—	3	21	95	45
Viola sp.(p.)	fs	—	—	—	—	5	2
Buds		—	—	—	—	3	4
Bud scales		—	—	—	10	78	297

the mixed oak forest; (ii) The consistent occurrence of *Tilia*; (iii) The low curve for *Picea* before the rise of *Carpinus*; (iv) The consistent occurrence of *Ilex*; (v) The occurrence of Type X; (vi) The presence of *A. filiculoides*.

These features distinguish the Woodston pollen diagram from those of any other interglacial recognized in eastern England. Details of the Hicks 69 assemblage place it in pollen assemblage zone Ho II of the interglacial. The progressive upward decline of *Ulmus*, the high *Alnus* content and increase in *Corylus*, all suggest subzone Ho IIc, but the high non-arboreal pollen phase present in Ho IIc at Hoxne and Marks Tey is not represented at Woodston so this correlation must remain tentative. Two other peculiarities of the Woodston pollen assemblage deserve attention. Firstly, levels of *Taxus* at Woodston are low relative to other Hoxnian sites. However, scarcity of *Taxus* pollen is accompanied by abundance of plant macrofossils of this taxon, and the presence of its wood clearly indicates its occurrence in the forest. Secondly, Type X values at Woodston are higher than at other sites, although this pollen does reach 9% of tree pollen in zone Ho II at Hoxne, and 8% of the total land pollen in zone Ho III at Barford (Phillips, 1976). These differences are likely to be of only local significance.

4. MOLLUSCA

Molluscs were first recorded from the Woodston Beds in 1854 and were the only fossils to receive detailed examination prior to the present study (Kennard and Woodward, 1922). Samples from the 'Type', 'L' and Hicks 69 sections were collected by the B.G.S. during site investigation studies following the geological survey of Peterborough. Molluscs from these samples were examined by D. K. Graham. The lower part of the Hicks section was reopened in 1986 (Hicks 86 section) and sampled at approximately 0.15 m intervals.

All this molluscan material has been examined or re-examined by D. H. Keen during the present investigation to ensure consistent identification. The nomenclature of the Mollusca follows Kerney (1976*a*) for aquatic species and Kerney & Cameron (1979) for land species.

(*a*) *The Hicks 86 section fauna*

From the serial samples, 3993 individuals of 79 taxa were counted. A further 12 taxa were recorded from the bulk samples which provided a further 4673 individuals (table 3, figure 6).

The fauna is dominated by species which inhabit large rivers with *Valvata piscinalis* (Müller) and *Bithynia tentaculata* (Linné) always prominent. *Ancylus fluviatilis* (Müller), *Pisidium henslowanum* (Sheppard) and *Pisidium moitessierianum* Paladilhe, also occur throughout the sequence and confirm the presence of flowing water. The large numbers of unionid bivalves are also

Table 3. *The Mollusca of the Hicks 86 Section*

	Bulk B	JCB	Al	0–0.15	0.15–0.30	0.30–0.45	0.45–0.60	0.60–0.75	0.75–0.90	0.90–1.00	1.00–1.20	1.20–1.40	1.40–1.60	1.60–1.80	1.80–2.00	2.00–2.20
Valvata cristata Müller	45	3	4				1	1		1	3		5	12	9	
Valvata piscinalis (Müller)	457	65	81			3	1		4	52	67	21	77	163	240	
Bithynia tentaculata (Linné)	738	32	31	1			1	1	1	50	49	5	41	183	239	
Bithynia troscheli (Paasch)	1															
Bithynia opercula	282	41	57	7		36	18	43	32	339	185	66	42	61	89	
Lymnaea truncatula (Müller)	7	1				2			1	1	2		1	1	10	
Lymnaea palustris (Müller)	1														1	
Lymnaea stagnalis (Linné)	5		1													
Lymnaea peregra (Müller)	93	15	10							1	3	1	4	30	25	
Myxas glutinosa (Müller)														1		
Planorbis planorbis (Linné)	13	1	1							2	5		1	12	16	
Anisus leucostoma (Millet)	2													2	1	
Anisus vorticulus (Troschel)	5	1												2	1	
Bathyomphalus contortus (Linné)	32	2	1									1			1	
Gyraulus laevis (Alder)	5									3	1	2	4	8	24	
Gyraulus albus (Müller)											1	1	1	2	2	
Gyraulus acronicus Férussac															1	
Armiger crista (Linné)	119	12	10			2				2	15	3	58	81	69	
Hippeutis complanatus (Linné)	2		1											4	6	
Segmentina nitida (Müller)	8															
Planorbarius corneus (Linné)	18	4	1													
Planorbidae species undet.							1					1				
Ancylus fluviatilis (Müller)	62	3	11							1	8	1	9	7	28	
Acroloxus lacustris (Linné)	8		1										8	2		
Unio pictorum (Linné)	1													1		
Anodonta cygnaea (Linné)	1									3		1			2	
Unionidae species undet.	1		1							1	1	2	1		2	
Sphaerium corneum (Linné)	8	1	3				1			3	2	1	13	5	6	
Sphaerium lacustre (Müller)	1												1			
Pisidium amnicum (Müller)	38	4	17							10	7	4	6	5	5	
Pisidium clessini Neumayr											1					
Pisidium casertanum (Poli)	70	6	10							2	6	2	10	18	21	
Pisidium personatum Malm	26	3	2							1	5	2	2	15	12	
Pisidium obtusale (Lamarck)	1															
Pisidium milium Held	4	1	1													
Pisidium subtruncatum Malm	25		3					1		1	4	1	4	13	9	
Pisidium henslowanum (Sheppard)	45	3	12					1		2	2	3	5	14	11	
Pisidium hibernicum Westerlund	1										1		11			
Pisidium nitidum Jenyns	72	6	4			1	1	1		1	3	1	9	18	17	

Table 3 (*contd*)

	Bulk B	JCB	Al	0–0.15	0.15–0.30	0.30–0.45	0.45–0.60	0.60–0.75	0.75–0.90	0.90–1.00	1.00–1.20	1.20–1.40	1.40–1.60	1.60–1.80	1.80–2.00	2.00–2.20
Pisidium moitessierianum Paladilhe	55	17	21							3	7	5	22	14	21	
Pisidium sp.	3		3					1			5	2	5	1	3	
Carychium minimum Müller	75	16	5				1			8	5	1	4	62	33	
Carychium tridentatum (Risso)	40	25	6							14	2		5	31	14	
Carychium sp.	57	35	16			4				10	7	1	8	30	21	
Succinea oblonga Draparnaud															1	
Succinea putris (Linné)	11	2	4													
Oxyloma pfeiffer (Rossmässler)														4	1	
Azeca goodalli (Férussac)	77	63	60	1		4	1	8	6	74	27	3	8	20	22	
Cochlicopa lubrica (Müller)	24	4	3											19	9	
Cochlicopa lubricella (Porro)	4															
Cochlicopa sp.	4	22						1	1		6	1	1			
Columella sp.	1														2	
Truncatellina cylindrica (Férussac)	11	3	2											7	2	
Truncatellina callicratis (Scacchi)	1									1				1		
Truncatellina sp.											1		1			
Vertigo antivertigo (Draparnaud)	1															
Vertigo substriata (Jeffreys)	1															
Vertigo pygmaea (Draparnaud)	2									1	1			1		
Vertigo moulinsiana (Dupuy)	2	1														
Vertigo alpestris Alder	2	1												2		
Vertigo angustior Jeffreys	4		8							1				1	1	
Vertigo pusilla/angustior	2	16	6							2	2	1	1	7	2	
Vertigo sp.	1					1				1	1					
Pupilla muscorum (Linné)	36	2	5							1	2		1	21	9	
Vallonia costata (Müller)	58	120	17			6		2	2	28	9	4	14	85	44	
Vallonia pulchella (Müller)	117	79	53			1		1		5	2	1	7	95	41	
Vallonia enniensis (Gredler)	115	57	43					1	1	4	1			21	14	
Vallonia excentrica Sterki	20										1			13	6	
Vallonia sp.	130		10			2		1		9	9	5	9	97	56	
Acanthinula aculeata (Müller)	6	3								1				1		
Ena montana (Draparnaud)		1								5		1		1	2	
Punctum pygmaeum (Draparnaud)	25	51	13							1	6		2	24	15	
Discus ruderatus (Férussac)	29	5	2	1			1	1		7	2		2	11	12	
Discus rotundatus (Müller)	2	1														
cf. *Vitrinobrachium breve* (Férussac)	10	9	5							2	2		1	3		
Vitrea crystallina (Müller)	20	5												10	2	
Vitrea contracta (Westerlund)	7	8	3							1	1		3		4	

Table 3 (*contd*)

	Bulk B	JCB	Al	0–0.15	0.15–0.30	0.30–0.45	0.45–0.60	0.60–0.75	0.75–0.90	0.90–1.00	1.00–1.20	1.20–1.40	1.40–1.60	1.60–1.80	1.80–2.00	2.00–2.20
Vitrea sp.	10	6	1							1	1	1	3	5	4	
Nesovitrea hammonis (Ström)	22									1				11		
Aegopinella nitidula (Draparnaud)	29	24	8						1	4	1	1	3	13	2	
Aegopinella sp.													1			
Oxychilus cellarius (Müller)			2													
Oxychilus sp.	2	6	7													
Zonitoides nitidus (Müller)	2										1			1	3	
Milax sp.	13	6	7							14	1			5	4	
Limax sp.	1	5	2	1		1		2	3	23	8	1			4	
Deroceras sp.		2	4						5					3		
Euconulus fulvus (Müller)	1		1													
Cochlodina laminata (Montagu)	1	1												1		
Clausilia bidentata (Ström)	25	10	6												3	
Clausilia pumila Pfeifferi	13		14													
Clausilia sp.	46	45	36			6	3	5	4	111	17	2	7	17	12	
Candidula crayfordensis Jackson	24		2							5	1			2	3	
Trichia hispida (Linné)	208	43	28			1		4	1	40	22	4	4	92	50	
Cepaea nemoralis (Linné)	4															
Cepaea sp.	5	6	1	1	1		1	1	10							
Arianta arbustorum (Linné)	1															
Hydrobia ventrosa Montagu										3						
total	3203	874	596	12	1	34	14	44	33	537	331	87	375	1338	1193	

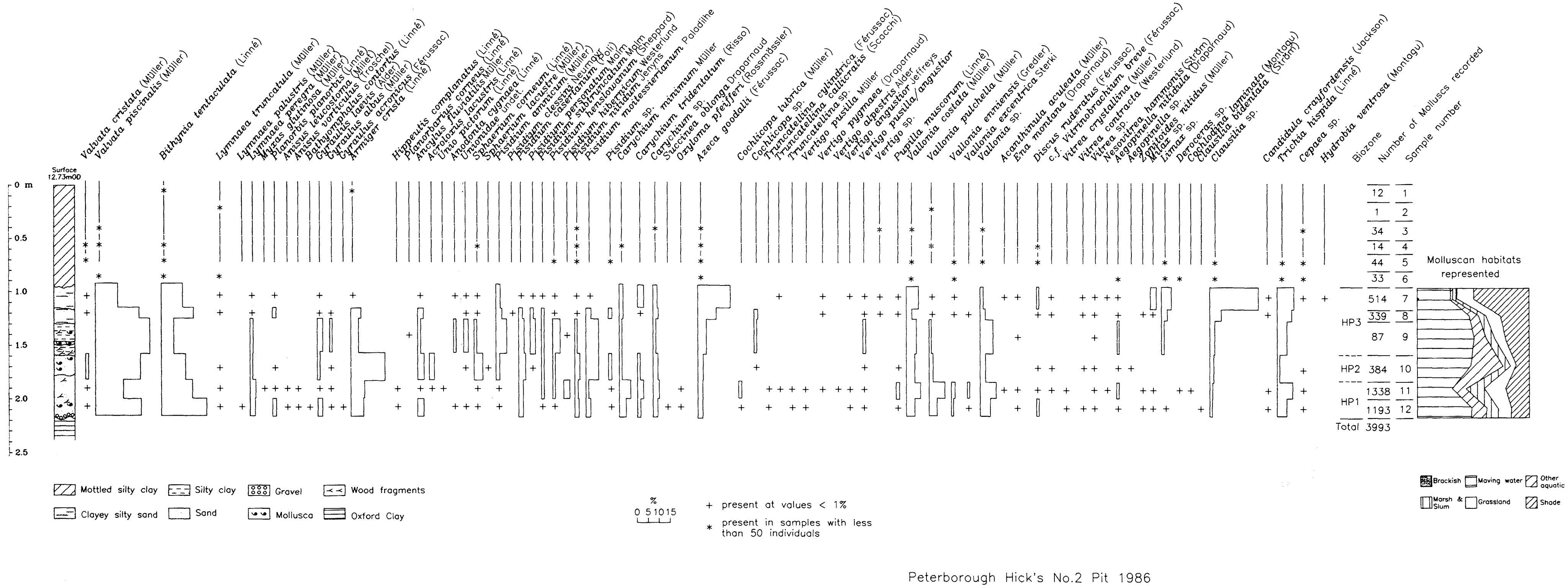

Figure 6. Percentage mollusc diagram, Hicks 86 section.

indicative of well-oxygenated river habitats. At certain horizons in the Hicks 86 succession individual bedding surfaces were completely covered by fragmentary shells which from their size, 15 cm along their anterior-posterior axis, could only be *Anodonta cygnaea* (Linné). Specimens of *Unio pictorum* (Linné) were also present. Kennard and Woodward (1922) noted '*Potomida*' *(Psilunio) littoralis* (Lamarck) among the bivalves of the Woodston Beds, but no specimens of this species were found in the current investigation.

Figure 6 shows the stratigraphic distribution of the molluscs by habitats. The faunal sequence is divided into local molluscan assemblage biozones characterized using the ecological groups of Sparks (1961) and thus reflecting the changing environment. These zones have no wider significance for correlation or age. Zone HP1 (Hicks Pit, molluscan assemblage zone 1) contains a moving water assemblage dominated by the species noted above. Zone HP2 by contrast has higher levels of still-water and weed-dwelling species such as *Valvata cristata* Müller, *Armiger crista* (Linné) and *Acroloxus lacustris* (Linné). Zone HP3 is again a predominantly moving water zone with lower levels of *V. cristata*, *A. crista* and *A. lacustris* and a return to prominance of the *V. piscinalis*/*B. tentaculata* fauna.

This zonation based on species abundance is confirmed by the *Bithynia* ratio (Gilbertson & Hawkins, 1978) in which high numbers of opercula to shells indicates a greater degree of current activity. In the Hicks 86 sequence the *Bithynia* ratio is 3:1 in zone HP1, 1:1 in HP2 and up to 1:13 in zone HP3. Clearly in zone HP2 *post mortem* disturbance of the molluscs is at a minimum, which accords with the species composition. By contrast in zone HP3 considerable reworking of the shells is indicated. Zone HP1 is more difficult to interpret with its preponderance of shells over opercula, but possibly the river was slow-flowing, but still moving fast enough to supplement the local population of *Bithynia* (shells and opercula) with shells from elsewhere.

The land-snail fauna consists of numerous species, but with each represented by only a few individuals. The shade-demanding species *Aegopinella nitidula* (Draparnaud), *Clausilia bidentata* (Ström), *Clausilia pumila* Pfeiffer, *Discus ruderatus* (Férussac) and *Discus rotundatus* (Müller) dominate the fauna. Other habitats represented are dry, predominantly calcareous grassland [*Vallonia costata* (Müller), *Pupilla muscorum* (Linné), *Truncatellina callicratis* (Scacchi), *Vertigo pygmaea* (Draparnaud) and *Vertigo alpestris* Alder], and marsh or damp habitats [*Vertigo angustior* Jeffreys, *Vallonia pulchella* (Müller), *Carychium minimum* Müller]. The extinct helicellid species *Candidula crayfordensis* Jackson, is presumed to have inhabitated open grassy

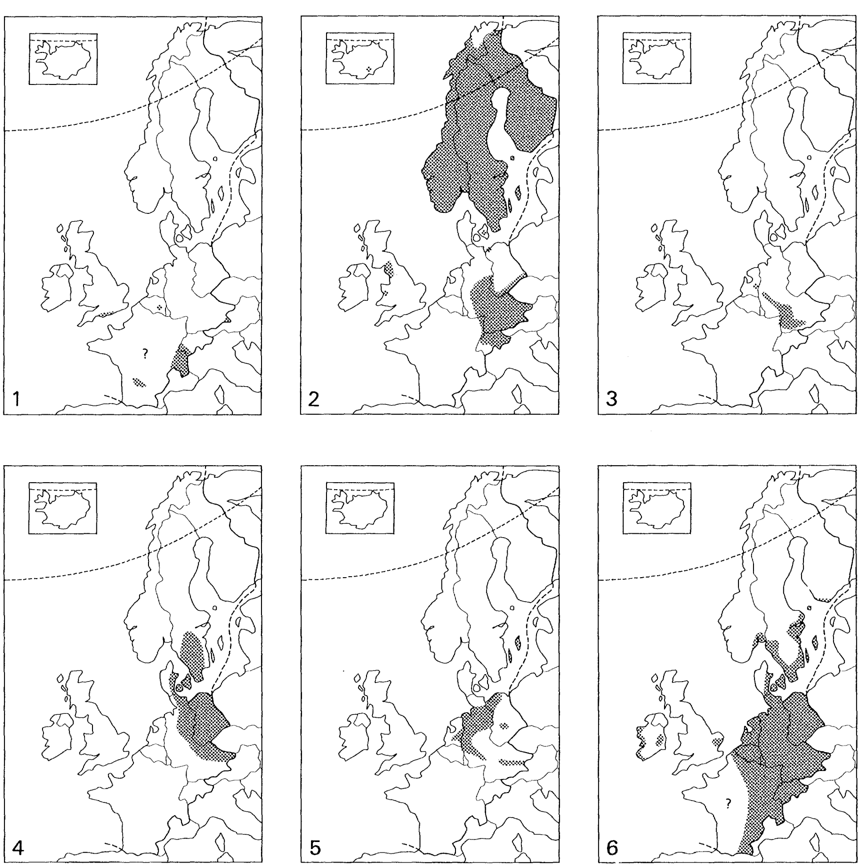

Figure 7. Recent distribution maps for species of land molluscs from the Woodston Beds: 1. *Truncatellina callicratis* (Scacchi); 2. *Vertigo alpestris* Alder; 3. *Vitrinobrachium breve* (Férussac); 4. *Clausilia pumila* (Pfeiffer); 5. *Perforatella rubiginosa* (Schmidt); 6. *Vertigo angustior* Jeffreys. Maps reproduced from Kerney and Cameron (1979) by permisson of Harper Collins Ltd.

conditions similar to extant species of *Candidula*. Kennard and Woodward (1922) record '*Clausilia ventricosa*' [*Macrogastra ventricosa* (Draparnaud)], which is also a shade demanding species, but no specimens were found during the present study.

Taxa among the land snail elements which are not now found in Midland England (figure 7) include *V. alpestris* (known only in Cumbria and North Wales in Britain and otherwise in central Europe and Scandanavia), *C. pumila* (southern Sweden, Denmark and eastern Germany), *Perforatella rubiginosa* (Schmidt) (western Germany and The Netherlands), and *T. callicratis* (restricted to a few localities on the south coast of England and south-east France). These present-day distributions represent either a change of range for these species, or evidence of formerly more continental or south European climatic conditions.

In the lower levels of the succession the land fauna is well preserved with the micro-sculpture of shells and the colour bands of *Cepaea nemoralis* (Linné) still intact. These details suggests that the shells suffered virtually no transport before being incorporated in the sediment. This, coupled with the presence of wood of tree trunk size, suggests that many of the land shells were incorporated in the sediments as 'passengers' on trees and other debris which was caught up in floodwater or fell into the river due to bank collapse. The undulating nature of the top of the basal gravel suggests that deposition was on the surface of a gravel bar, perhaps on the outside of a meander bend where floating debris, including shells, became stranded during floods.

The well-preserved colour banding on the shells of *C. nemoralis* was described following the formula of Ellis (1969). Six complete shells were recovered, all from zone HP 1. Iron oxide obscured the banding of one specimen; three were of the five banded variety, 12345, and one each of the formula 1(23)45, with two fused bands, and 00345, with the upper two bands absent. Modern studies on this banding (Cain *et al.* 1968; Cain & Currey 1968; Cain 1971) has developed a considerable body of data on the genetic and ecological controls of this polymorphism. In particular, unbanded forms seem related to periods of warmer and drier climate than that occuring at present in Britain such as that of the Flandrian climatic optimum. Banded patterns in fossil *Cepaea* have previously been described only from the Ipswichian deposits of Tattershall, Lincolnshire (Holyoak & Preece 1985) dated to *circa* 125000 year b.p. The age of the Woodston deposits exceeds the latter date by a considerable amount, hence these examples of *C. nemoralis* represent the earliest record of polymorphic banding so far noted.

Only land and freshwater molluscs occur in the most fossiliferous part of the Hicks 86 section, but in the upper part of zone HP 3 three specimens of *Hydrobia ventrosa* Montagu were found. This species occurs in brackish water in the upstream limit of estuaries and in coastal lagoons (Fretter & Graham 1962). Its presence suggests an increase in salinity in the Woodston Beds river, and is a precursor of the full marine transgression indicated in the Hicks 69 section.

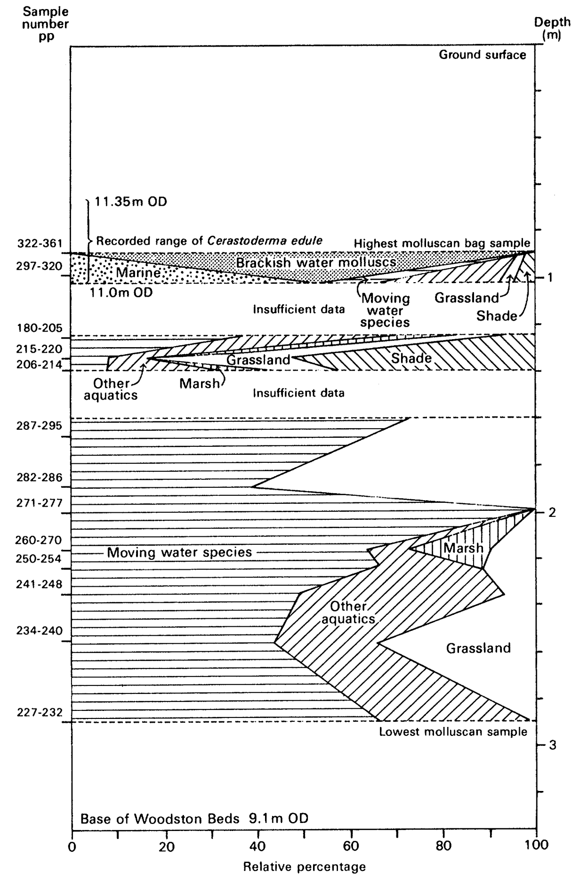

Figure 8. Summary diagram of molluscan habitats, Hicks 69 Section.

(*b*) *The Hicks 69 section fauna*

This fauna was much less abundant than that collected from the Hicks 86 section. Although less reliable for this reason, the stratigraphic distribution of the molluscs grouped by habitat is summarized in figure 8. The fauna of the lowest 1.7 m closely resembles the assemblages described from the Hicks 86 section. Samples from 1.7 to 2.43 m within the oxidized zone, contained shell debris but no intact land or freshwater shells. The data plotted within this height range on figure 8 is derived from samples collected at this stratigraphic level from temporary exposures just outside the trench. Two 'cockle beds' were recorded at 2.31–2.33 and 2.39–2.43 m above the base respectively. These contained the robust shells of the marine species *Ostrea edulis* Linné, *Cerastoderma edule* (Linné), *Scrobicularia plana* (da Costa), *Spisula elliptica* (Brown) and the brackish species *H. ventrosa*. The occurrence of these brackish and marine species suggests strong saline influences in the Hicks locality above 2.31 m from the base.

(*c*) *The Peterborough 'Type' section fauna*

Owing to decalcification in its upper levels, only the basal one metre of sediment yielded numerous molluscs (table 4, figure 9), with 2290 individuals of 42 taxa recovered.

The taxa in the 'Type' section resemble those from the Hicks Pit sections. The palaeoecological summary diagram (figure 9) shows that the moving water assemblage comprises 60–70% of the total fauna, and the fauna is dominated by *V. piscinalis*, *B. tentaculata* and *A. fluviatilis*. Unlike the fauna in the Hicks sections, these moving water molluscs are accompanied by *Lymnaea peregra* (Müller) which constitutes 20% of the fauna at several levels in the succession. *L. peregra* is included in Sparks' (1961) catholic group and prefers standing water, although it is not intolerant of rivers, living in quiet water out of the main channel. The presence of still-water habitats is further supported by the *Bithynia* ratio which at most levels is close to 1:1 indicating a minimum of disturbance of the fossil assemblage after death.

The land fauna in the 'Type' section is limited (table 4), but shows the same ecological groups as the fauna in the Hicks sections. Small numbers of *H. ventrosa* occur, at two separate horizons (figure 9) and suggest the early brackish stages of a marine transgression interrupted by a slight regression.

(*d*) *The Peterborough 'L' section fauna*

The 'L' section was also decalcified and the majority of the molluscs occur in the silts and sands between 2.8 and 4.00 m from the surface. The clays between 4.00 and 4.40 m depth are virtually devoid of molluscan material and only one bulk sample was taken from the basal gravel (table 5; figure 10). The total number of individual molluscs recovered was 8671 of 64 taxa. A sequence of molluscan assemblage zones (HL1-HL6) comparable to the Hicks 86 series was established.

The fauna of the basal gravel unit (zone HL1) is closely similar in ecological character to that from the basal gravels of the Hicks 69 and 'Type' sections and the basal silt of the Hicks 86 sections. *V. piscinalis*, *B. tentaculata* and *A. fluviatilis* are all represented, while the occurrence of *Armiger crista* (Linné) suggests still water with weed growth. The virtual absence of the opercula of *Bithynia* sp. may indicate deposition of this bed away from the main channel in quiet water, into which the buoyant shells of *Bithynia* could float. Land species are scarce, but consist of the same taxa and ecological groups that make up the land elements in the 'Type' and Hicks sections. A very few specimens of *H. ventrosa* indicate the existence of slightly brackish conditions in the river.

Zone HL2 is almost devoid of molluscs and when fossils become abundant again above 4.00 m, a complete change has occurred in the fauna. Although the same land and freshwater faunas are still present, brackish species are the dominant group in this assemblage. *H. ventrosa* forms up to 80% of the total fauna in zone HL3 and is accompanied by the other brackish species *Hydrobia ulvae* (Pennant) and *Pseudamnicola confusa* Frauenfeld. The occurrence of '*Paludestrina deani*' (*Semisalsa stagnorum* Gmelin) first described by Kendall (1913) and Kennard & Woodward (1922) is confirmed in the 'L' section, but because of its very close similarity to *H. ventrosa* it was impossible to separate all but two most perfectly preserved specimens, so the counts for *H. ventrosa* in Table 5 and figure 10 probably contains examples of *S. stagnorum*.

The hydrobiid species are tolerant of different salinities. *S. stagnorum* and *P. confusa* being indicative of the lowest levels, *H. ventrosa* intermediate in tolerance, and *H. ulvae* being most tolerant of saline conditions.

The predominance of *H. ventrosa* over the other halophile species at the base of zone HL3 suggests only a moderate degree of salinity at this stage. *P. confusa* which is often abundant in the early stages of a transgression (e.g. Tattershall, Lincolnshire (Holyoak & Preece 1985)) is rare. This may reflect unsuitable conditions of either deposition or preservation in the poorly fossiliferous zone HL2 which precedes the first *H. ventrosa* peak.

The subsequent history of the 'L' section was complex with three peaks of marine influence (table 6; figure 10). After the first expansion of brackish taxa in HL3 a resurgence of the freshwater fauna occurs with the hydrobiids reduced in zone HL4 to 40 per cent of the fauna. This freshwater peak and a second near the top of the sequence (in HL6) may be due either to a short-lived event like an individual flood, or to a longer phase of marine regression. The second marine incursion (zone HL5) has higher values for *H. ulvae* than the first and so was probably more saline. After the second resurgence of the land and freshwater fauna, the beginnings of a third and yet more saline phase (HL6) are seen up to the level of major decalcification. In this final saline phase, true marine species [*Littorina littorea* (Linné), *Mytilus edulis* Linné, *O. edulis*, *C. edule*, and *S. elliptica*] occur for the first time and suggest a degree of salinity comparable to that indicated at the top of the Hicks 69 section. These marine species are all tolerant of reduced salinities, thus fully marine conditions are not necessarily indicated.

Pockets of marine molluscs occur in the largely decalcified sediment at the top of the 'L' section up to a height of 14.10 m ordnance datum (O.D.) thus marine influences occur to at least this level in the Woodston succession.

(*e*) *Environmental summary: Mollusca*

(*i*) *Local environment*

The freshwater fauna from the Woodston Beds suggests a slow flowing, well-oxygenated river habitat. In places current velocities were slow enough to allow macrophytic plant growth in almost still water. The river flowed through marsh, probably close to the channel, which gave way to dry, calcareous grassland further away. Shade-dwelling molluscs indicate woodland which may have come close to the river bank and allowed snails to fall into the river from the trees themselves or as a result of bank collapse.

All three sequences show evidence of marine transgression appearing at approximately the same level throughout the area at 11.0–11.6 m O.D. In the Hicks and 'Type' sections decalcification obscures the record of transgression, but in the 'L' section there is a gradual increase in brackish indicators with truly marine species present at 12.2 m O.D.

(ii) Regional environment

Eighty-three land and freshwater molluscan taxa, plus eleven brackish and marine taxa have been recorded in the Woodston Beds. Such an abundance can only have occurred during an interglacial period. The land fauna shows several species which have current ranges in central Europe (figure 7). Assuming that none of these species has changed its climatic preferences since the Middle Pleistocene, a more continental climate than that of the present is indicated.

(*f*) *The age of the mollusc fauna*

There are very few Middle Pleistocene interglacial sites for which the age is well established on pollen, or other grounds, which also contain molluscs. From the paucity of evidence for comparison the most that can be said about the age of the Woodston Beds from the molluscan evidence alone, is that they date from an interglacial in the Middle Pleistocene. Most of the sites which have been described represent different depositional environments from the fluviatile habitat of the Woodston Beds. They include lake basins such as Hoxne (West 1956) or Hatfield (Sparks *et al.* 1969) or fluvial sites with a poor fauna such as Clacton (Kerney 1971) or the Nar Valley (Ventris 1985). The only species-rich large river fauna generally regarded as Hoxnian is from Swanscombe in Kent (Kerney 1971), unfortunately the apparent absence of both pollen and insect remains at Swanscombe prevents comparison, and there are numerous differences between the molluscan faunas. At Swanscombe the freshwater element includes such species as '*Theodoxus serratiliniformis*' [*Theodoxus danubialis* (Pfeiffer)], *Corbicula fluminalis* (Müller) and *Valvata naticina* Menke. None of these exotic species (Kennard's 'Rhenish fauna'; Kennard 1942) occurs at Woodston. There are at least two possible explanations for their absence. First, the Woodston fauna, belonging to Hoxnian pollen zone II may be older than the Swanscombe fauna which may have migrated into Britain later in same the interglacial. Alternatively, the two faunas may have been geographically isolated from one another by the watersheds separating the Thames, Wash and North Sea rivers. However, some freshwater molluscs are very mobile as is shown by the migration of *Dreissena polymorpha* (Pallas) from eastern Europe in the last 150 years (Kerney 1976*b*); and in general by the close similarity of the present-day mollusc faunas of the large rivers of lowland Britain, showing that there are no significant ecological barriers between catchments under the prevailing temperate conditions. Thus the differences in the molluscan faunas at Woodston and Swanscombe perhaps allow a third possibility that the sites are not of the same age.

5. OSTRACODS

The ostracod fauna has been determined from washed residues prepared by the British Geological Survey from the Peterborough 'Type' (B.G.S. catalogue numbers SAA 1273–1286 base) and 'L' (SAA 1309–1287) sections, from the Hicks 86 excavation, and the Phorpres 4 borehole. Samples were sieved to 125 m to provide the usual range of valves for study, but in the case of the 'L' section the numbers were augmented from samples sorted for other fossils. Specimens from the Hicks 86 excavation were picked from samples processed for molluscs by D. H. Keen. The ostracod fauna is listed table 7, and the relative proportions of brackish and freshwater species in the Hicks 69 and Peterborough 'L' section is shown in figure 11.

Although the 'Type' (table 9) and 'L' (table 10) sections are situated close to each other the ostracod faunas have contrasting characters. All the samples contained reworked Jurassic and Cretaceous foraminifers and ostracods. At some levels these outnumber the Pleistocene forms.

(*a*) *The Hicks 86 section fauna*

Ostracods were recovered only from the basal 1.50 m of the section, from the samples sorted for molluscs (table 8). The basal 15 cm (2.05–2.2 m from the surface) provided a single valve of *Prionocypris serrata* (Norman). This is a large, robust-valved species which occurs in shallow streamlets or marshy ground associated with springs. The same species also occurred in the following sample (1.65–1.80 m depth) associated with broken fragments of *Herpetocypris reptans* (Baird), a large non-swimming ostracod. The same species, together with *Candona* spp., made up a sparse fauna to sample depth 1.20 m. Between 1.00 and 1.20 m, this assemblage is augmented by the brackish species *Cyprideis torosa* (Jones) and valves of the spatulate *Ilyocypris* cf. *decipiens* Masi. The latter species is known from present-day habitats such as brackish marshes flanking the Humber estuary (Faxfleet, near Goole) and from interglacial sands and gravels at Tattershall, Lincolnshire (Holyoak & Preece 1985). Above 1.00 m the fauna is dominated by *C. torosa* indicating saline influence.

(*b*) *The Peterborough 'Type' section fauna*

This section (table 9) was generally poor in ostracods, but those present were largely freshwater in character. The basal gravel between 3.10 and 2.60 m from the surface contained a sparse fauna of *Candona compressa* (Koch), *Candona* cf. *lozeki* Absolon, *Ilyocypris gibba* Ramdohr, and *Ilyocypris inermis* Kaufmann. These are freshwater species, with *C. compressa* characterising the sandy margins of water bodies (Klie 1938; Nüchterlein 1969) and *C. lozeki* presumably occupying the shallow lakes preferred by its modern relative *Candona neglecta* Sars. *I. inermis* and *C. lozeki* have both been described as stenothermal-cold temperate, although in the case of the first species, this may relate to an association with springs (Absolon 1971).

In upward succession, the presence of the delicate valves of *H. reptans* at depths between 2.40 to 2.60 m indicates quiet or still water conditions. Small amounts of *post mortem* transport are sufficient to break

Table 4. *The Mollusca of the Peterborough 'Type' section*

	sample depths below surface											
	1.0–1.70	1.70–1.90	1.90–2.00	2.00–2.10	2.10–2.20	2.20–2.30	2.30–2.40	2.40–2.50	2.50–2.60	2.60–2.70	2.70–2.80	2.80–3.10
Valvata cristata Müller									1			
Valvata piscinalis (Müller)	4	13	7	1	5	123	124	194	82	28	30	388
Bithynia tentaculata (Linné)		2				31	50	63	67	3	31	185
Bithynia opercula		7			1	33	14	47	26	7	29	225
Lymnaea truncatula (Müller)						1						13
Lymnaea auricularia (Linné)									1			
Lymnaea peregra (Müller)		2			1	66	47	87	43	10	20	102
Planorbis planorbis (Linné)							2	2		1		13
Anisus leucostoma (Millet)							1					
Anisus vortex (Linné)							1					
Anisus vorticulus (Troschel)						1						
Gyraulus laevis (Adler)											1	
Armiger crista (Linné)						1	2				1	3
Planorbidae species undet.						1		1				4
Ancylus fluviatilis (Müller)						29	29	31	12	2	6	21
Sphaerium corneum (Linné)							1					
Sphaerium lacustre (Müller)								1				
Pisidium amnicum (Müller)						3	4	3	2	2		1
Pisidium casertanum (Poli)		1				13		10	1	2	3	14
Pisidium personatum Malm						1		4			3	2
Pisidium milium Held												1
Pisidium subtruncatum Malm						7	8	5		1		4
Pisidium henslowanum (Sheppard)						3	1	2	2		1	7
Pisidium nitidum Jenyns						3		5				2
Pisidium moitessierianum Paladilhe						3		1				1
Pisidium sp.		1			1	1		2	1	1	3	1
Succinea putris (Linné)									1			
Azeca goodalli (Férussac)							3		1			
Cochlicopa lubrica (Müller)	1					1				1		
Cochlicopa sp.						1			1			
Truncatellina cylindrica (Férussac)												1
Truncatellina callicratis (Scacchi)						1						
Truncatellina sp.						1		1				
Vertigo pusilla Müller							1					
Vertigo angustior Jeffreys						1						
Vertigo pusilla/angustior	1						1	1				
Vertigo sp.						1						
Pupilla muscorum (Linné)							1					
Vallonia costata (Müller)						8	4	4				4
Vallonia pulchella (Müller)		1				1		2				

Table 4 (*contd*)

	sample depths below surface											
	1.0–1.70	1.70–1.90	1.90–2.00	2.00–2.10	2.10–2.20	2.20–2.30	2.30–2.40	2.40–2.50	2.50–2.60	2.60–2.70	2.70–2.80	2.80–3.10
Vallonia sp.									3			10
Punctum pygmaeum (Draparnaud)	1			1		2	2					5
Discus ruderatus (Férussac)												1
cf. *Vitrinobrachium breve* (Férussac)												1
Vitrea contracta (Westerlund)									1			
Nesovitrea hammonis (Ström)						1						1
Aegopinella sp.						1			1		1	
Oxychilus sp.						1	1		1			
Zonitoides nitidus (Müller)						2	1					3
Clausilia bidentata (Ström)									1			
Clausilia sp.						1		10	4	1		2
Candidula crayfordensis Jackson								4				
Trichia hispida (Linné)						1	1	8	1	2		4
Cepaea sp.												2
Hydrobia ventrosa Montagu					1			2			2	
total	7	20	7	2	7	309	304	444	225	53	123	789

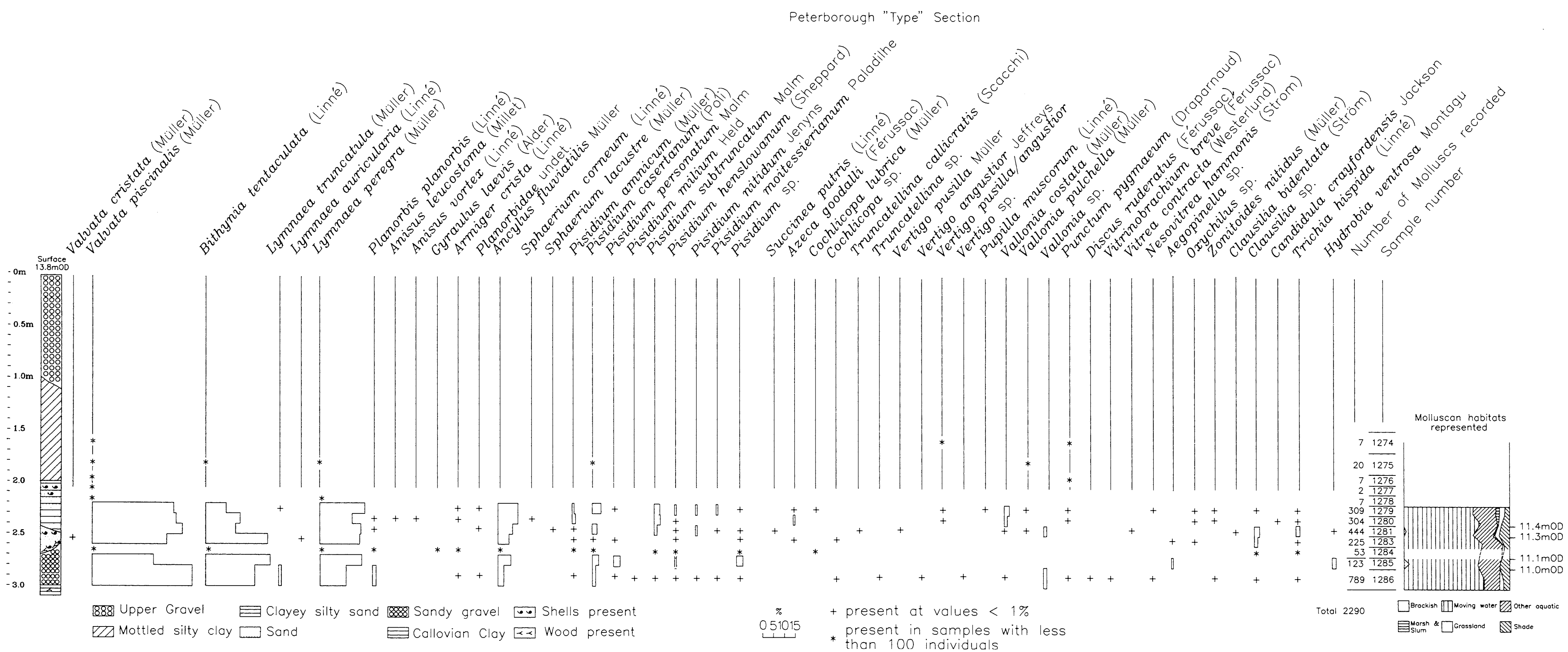

Figure 9. Percentage molluscan diagram, Peterborough 'Type' Section.

the valves, so their preservation reflects the energy level of the environment. Here the valves are broken but not fragmented beyond recognition. The fauna between 2.40 and 2.60 m generally represents an environment of ponded drainage in a broad, slow flowing river. The samples from these levels also contain the spring-dwelling ostracod *Potamocypris foxi* Sywula, which may have been transported into the assemblge, and a sample from 2.10 to 2.20 m included a small number of *Heterocypris salina* (Brady), a species inhabiting saline springs or the landward fringe of an estuary. Above this level, higher than 2 m in the section, the ostracod fauna was poor, but was similar to that in the basal 50 cm.

(*c*) *The Peterborough 'L' section fauna*

The basal gravel of this sequence (table 10) below 4.00 m from the surface produced a fauna dominated by *Cypridopsis vidua* (O. F. Müller) and *H. reptans*, supported by smaller numbers of *H. salina*, *P. serrata* and *I. gibba*. These species together indicate the diversity of ecological niches typical of a river channel system.

The overlying grey silty clays between 4.20 and 4.40 m depth yielded a sparse freshwater fauna of juvenile valves of *Candona*, *Ilyocypris* and *Herpetocypris* spp. At 4.30 m the meagre freshwater association is accompanied by numerous valves of *C. torosa* indicating a saline influence, although the degree of salinity is uncertain as this species tolerates a range of salinities from 0.5% to fully marine (Klie 1938; Neale 1965; Vesper 1972; Van Harten 1975). Also present were three specimens of the brackish indicator *Cytheromorpha fuscata* (Brady)(Neale and Delorme 1985). This is a rare species, recorded in Britain only from the Suffolk Stour estuary and localities in the Norfolk Broads. It always occurs marginal to the tidal influx and this habitat preference has been used in palaeoecological interpretations in The Netherlands, north Germany and the Baltic (Klie 1938; Elofson 1941; Wagner 1957).

Only 10 cm higher in the succession, the fauna indicates brackish to marine conditions with salinities between 18 and 25%, since the freshwater species are reduced to a few immature *Candona* and one valve of *C. vidua*. By contrast *C. torosa* is present as male and female dimorphs, many with valves articulated. These full-grown adults are found with no fewer than five moult stages. This association of ages is evidence of the species living and breeding where it was fossilised. *C. fuscata* and a test of the inshore foraminifer *Elphidium* sp. are also present at this horizon.

The same association occurs at 4.00 m in the section and the grey silty clay, crowded with plant debris, resembles the muds accumulating today on the fringes of tidal creeks and salt marshes. Above this level the ostracods become those of a tidal estuary with increasing numbers of *C. torosa* which remain dominant at levels up to 2.90 m. Another marine marginal species, *Loxoconcha elliptica* (Brady), is also present, and 'freshwater' species tolerant of low salinities such as *Candona angulata* G. W. Müller and *H. salina* occur. This sequence of silty clays is interrupted by a bed of sand between 3.10 and 3.80 m down the section containing little fossil material, and suggesting rapid flow in a tidal channel. Above, at a depth of 2.80 m freshwater species reappear in significant numbers and at levels above this become increasingly common, although *C. torosa* is present in the assemblage to the higher level. The species which are present, *C. angulata*, *C. compressa*, *C. vidua*, *H. reptans*, *Cyclocypris laevis* (O. F. Müller) and *Ilyocypris* spp. indicate quiet, open-water conditions of low salinity.

(*d*) *Environmental summary: Ostracoda*

The ostracod faunas from the Hicks 86 and 'Type' sections are essentially freshwater in character although the Hicks assemblage has a small brackish element. Although the 'Type' and 'L' sections are close to each other they have contrasting characters. The ostracod fauna from the 'L' section changes rapidly upwards and records a marine transgression starting at 4.40 m (11.10 m O.D.: see figure 11) below the surface and reaching a peak at 4.00 m (11.50 m O.D.). After a slight regression between 4.00 and 3.80 m (11.70 m O.D.) a renewed transgression was sustained through a sequence of 0.50 m of sediment up to a break in succession at 3.30 m (12.20 m O.D.). Following a sand-filled channel with only fragmentary ostracods, a strong marine influx was followed by a steady increase in freshwater elements up to the final sample 1.4–1.65 m (14.10–13.85 m O.D.) from the surface which had no trace of saline species.

(*e*) *The age of the ostracod fauna*

The ostracods give rather contradictory evidence of the age of the Woodston Beds. *Candona levanderi* Hirschmann and *C. cf. lozeki* have previously been recorded from Middle Pleistocene interglacials in southern England including the pre-Hoxnian site at Waverley Wood Farm south of Coventry (the late F. W. Shotton, pers. comm.). The delicate spined form of *I. gibba* is also found in the interglacial deposits at Stoke Goldington in the Great Ouse valley in Bedfordshire (G.R.C., C.P.G., D.H.K. and J.E.R., unpublished data), and in deposits thought to be of similar age at Stanton Harcourt in the Thames Valley south of Oxford (Briggs, Coope & Gilbertson 1984). Both deposits have been attributed to an interglacial in the late Middle Pleistocene somewhere between the conventional Hoxnian and Ipswichian.

C. fuscata occurs in abundance in the *Balanus* Bed of the March Gravels at Somersham (J.E.R. unpublished data) and at Eye (Keen *et al.* 1990), both in Cambridgeshire and of supposed Ipswichian age. The species is now rare in Britain so there may be a stratigraphic association in the Middle and Late Pleistocene with the area around the Wash.

6. COLEOPTERA

Six samples, each of about 5 kg mass, from the Hicks 86 section were examined for insect remains. These

Table 5. *The Mollusca of the Peterborough 'L' Section*

	Sample depths below surface																		
	1.4–1.7	2.40–2.50	2.50–2.60	2.60–2.70	2.70–2.80	2.90–3.00	3.00–3.20	3.20–3.30	3.30–3.40	3.40–3.60	3.60–3.70	3.70–3.80	3.80–3.90	3.90–4.00	4.00–4.10	4.10–4.20	4.20–4.30	4.30–4.40	basal sample
Valvata cristata Müller						8	30	16		2	7			5					7
Valvata piscinalis (Müller)	28					131	208	161		22	22	53	5	40	2		1	13	103
Bithynia tentaculata (Linné)	7					131	354	177	5	80	53	67	7	33				2	122
Bithynia troscheli (Paasch)							1												
Bithynia opercula	20		1			2	1			1				1	1			3	17
Lymnaea truncatula (Müller)	1					5				2	1	2		2				1	7
Lymnaea palustris (Müller)																			
Lymnaea peregra (Müller)	4					26	89	67	1	29	5	40	2	28					33
Planorbis planorbis (Linné)						2	10	6		4			1				1	1	1
Anisus leucostoma (Millet)							1	1				1							
Anisus vortex (Linné)								1				2	1						
Gyraulus laevis (Alder)						29	55	38		2	9	23		14					108
Armiger crista (Linné)	2					53	33	7		20	58	60	2	23				4	8
Hippeutis complanatus (Linné)						7	1			2	2	7							
Planorbidae species undet.								1	1	9	4	13							5
Ancylus fluviatilis (Müller)						102	30	42	3	112	58	59	8	16					21
Acroloxus lacustris (Linné)						1				2									1
Anodonta cygnaea (Linné)																			
Unionidae species undet.																		1	
Sphaerium corneum (Linné)							2			1	1			1				1	4
Sphaerium lacustre (Müller)												1							2
Pisidium amnicum (Müller)							2	1			1	1						1	8
Pisidium casertanum (Poli)						13	20	24			9	5	1	15					16
Pisidium personatum Malm						8	13	3			3	1		5					
Pisidium milium Held							2	2			1	1		1					3
Pisidium subtruncatum Malm						18	14	21		2	9	12	2	9			1	1	26
Pisidium supinum Schmidt							1												
Pisidium henslowanum (Sheppard)						18	12	5	1	8	16	12	1	8				1	36
Pisidium nitidum Jenyns	1		1			26	13	6		4	1	13	3	5	1			2	19
Pisidium moitessierianum Paladilhe						19	2	1		2	5	6	1	12					17
Pisidium sp.			1			45	4		1	25	33	35	6	29				1	
Carychium minimum Müller						10							1	1					9
Carychium tridentatum (Risso)						3	4	1	1	19	8	15	1	3					4
Carychium sp.	1					4	3			18	2	6		1					10
Succinea oblonga Draparnaud										10									1
Succinea putris (Linné)							1												
Oxyloma pfeifferi (Rossmässler)						2													
Azeca goodalli (Férussac)										5									5
Cochlicopa lubrica (Müller)							2	2						2					2
Cochlicopa sp.						2	1												2

Table 5 (*contd*)

	Sample depths below surface																		
	1.4–1.7	2.40–2.50	2.50–2.60	2.60–2.70	2.70–2.80	2.90–3.00	3.00–3.20	3.20–3.30	3.30–3.40	3.40–3.60	3.60–3.70	3.70–3.80	3.80–3.90	3.90–4.00	4.00–4.10	4.10–4.20	4.20–4.30	4.30–4.40	basal sample
Truncatellina sp.						1				1				1				1	1
Vertigo pusilla Müller												1							
Vertigo moulinsiana (Dupuy)								1											
Vertigo angustior Jeffreys														1					
Vertigo pusilla/angustior						1				1		1							
Vertigo sp.						3						1		1					
Pupilla muscorum (Linné)							1	5											1
Lauria cylindracea (da Costa)							1												1
Vallonia costata (Müller)						10	9	21		7	2	8		8					6
Vallonia pulchella (Müller)						2	19	2		3	3			3					6
Vallonia enniensis (Gredler)							1	1											
Vallonia excentrica Sterki								1			1			1					2
Vallonia sp.	1					18	3	3		11	4	14		6					19
Acanthinula aculeata (Müller)											1								
Punctum pygmaeum (Draparnaud)						2	2			3	2								
Discus ruderatus (Férussac)							2	5				1		2					
Discus rotundatus (Müller)							1												
Vitrea crystallina (Müller)							1	1											
Vitrea contracta (Westerlund)						2		2		3	1	1							
Vitrea sp.						11													2
Nesovitrea hammonis (Ström)							1	1				1							1
Aegopinella pura (Alder)							1	6											
Aegopinella nitidula (Draparnaud)								1											
Zonitoides nitidus (Müller)							10	9		2								1	1
Euconulus fulvus (Müller)																			1
Cochlodina laminata (Montagu)							4												1
Clausilia sp.							1	2											2
Candidula crayfordensis Jackson							3												1
Trichia hispida (Linné)							6	6											8
Cepaea sp.																			1
Semisalsa stagnorum Gmelin														2					
Hydrobia ventrosa Montagu	1	1	3	17	6	767	437	203	89	483	205	515	276	807	20	21	1		2
Hydrobia ulvae (Pennant)						8	49	39	3	3	1	1	3	10					
Hydrobia sp.		9	5				20		1		1				11				
Pseudamnicola confusa Frauenfeld						1	3		2	4					1				
Littorina littorea (Linné)							1												
Mytilus edulis Linné									1										
Ostrea edulis Linné							10	2	1										
Cerastoderma edule (Linné)						1	5	1	1										
Spisula elliptica (Brown)							3					1							
Scrobicularia plana (da Costa)							3	1							1				
total	46	10	11	17	6	1492	1506	896	112	897	527	979	322	1095	36	21	4	34	662

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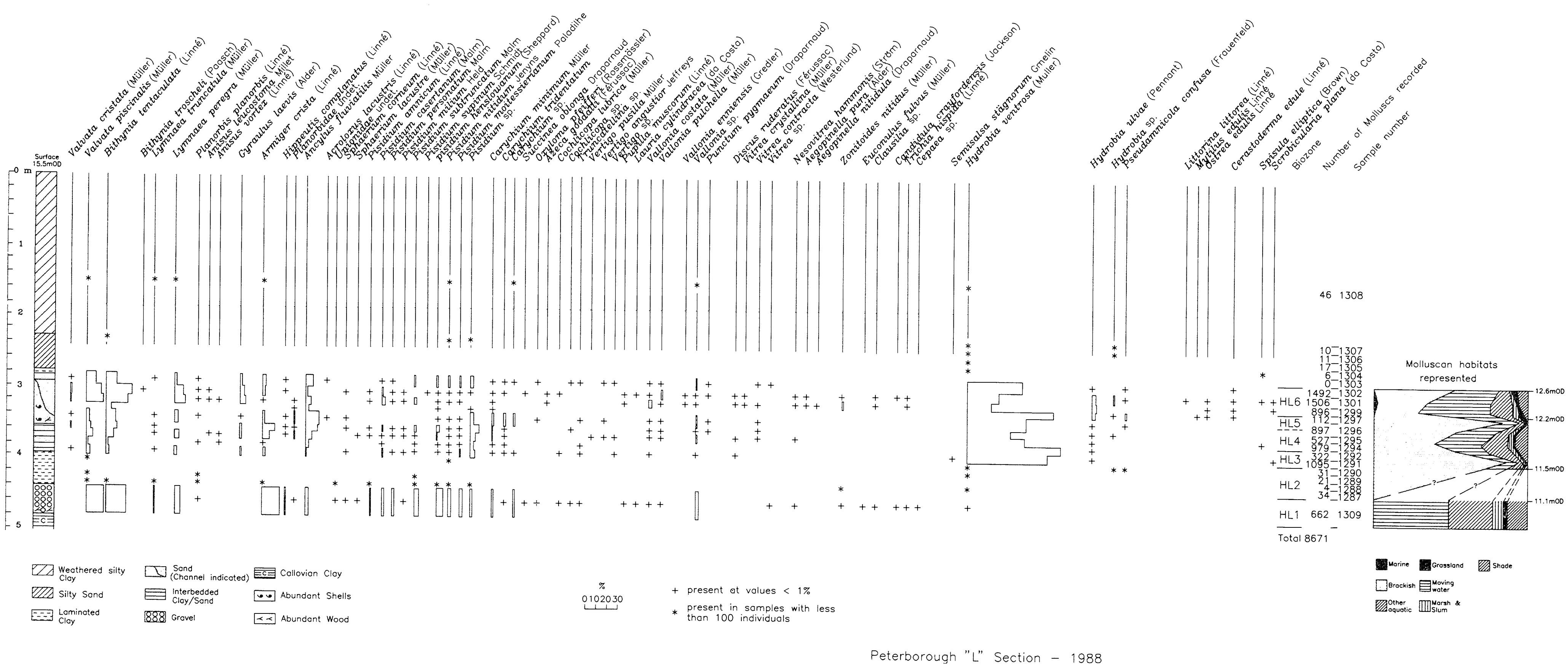

Figure 10. Percentage molluscan diagram, Peterborough 'L' Section.

Table 6. *Altitudes at which marine and brackish faunas were first recorded*

(All heights in metres above Ordnance Datum.)

	Molluscan species		Ostracod species
section	brackish water	marine	brackish water
Hicks 86	11.6	—	11.5
Hicks 69	11.0	11.0	—
Peterborough 'Type'	11.0	—	?11.6
Peterborough 'L'	below 11.5	12.2	11.1

samples were taken in 15 cm slices from the lowest metre of the sequence. Fossil insects were common in the basal 0.30 m, but above this were corroded. The upward impoverishment of the fauna is thus almost certainly due to weathering of the deposit.

Most of the identifiable insect fossils were of Coleoptera. Of other insects present, only the larval Trichoptera and Megaloptera are named. The beetles recovered are listed in table 11 and presented here in the nomenclatural and taxonomic order adopted of Lucht 1987. The numbers recorded are the minimum individuals of each species present in each sample.

(*a*) *Environmental interpretation*

The insect assemblage reflects a variety of habitat preferences, probably brought together passively by fluvial action into the deposit. Proximal fluvial habitats are described first followed by those of the marginal riparian environment and finally more distal

Table 7. *Ostracod faunal list*

species	section			
Candona angulata (Müller)			Hicks 86	
Candona compressa (Koch)	Type	'L'		
Candona levanderi Hirschmann	Type			BH4
Candona cf. *lozeki* Absolon	Type	'L'		
Candona neglecta Sars		'L'		
Cyclocypris laevis (O. F. Müller)	Type	'L'		
Cyprideis torosa (Jones)	Type	'L'	Hicks 86	
Cypridopsis vidua (O. F. Müller)	Type	'L'		BH4
Cytheromorpha fuscata (Brady)		'L'		
Darwinula stevensoni (Brady, Crosskey & Robertson)		'L'		
Herpetocypris reptans (Baird)	Type	'L'	Hicks 86	BH4
Heterocypris salina (Brady)	Type	'L'		
Ilyocypris bradyi Sars		'L'		BH4
Ilyocypris cf. *decipiens* Masi		'L'	Hicks 86	
Ilyocypris papillata Robinson			Hicks 86	
Ilyocypris gibba (Ramdohr)	Type	'L'		
Ilyocypris inermis Kaufmann	Type	'L'		
Potamocypris foxi Sywula	Type	'L'		
Prionocypris serrata (Norman)	Type	'L'	Hicks 86	

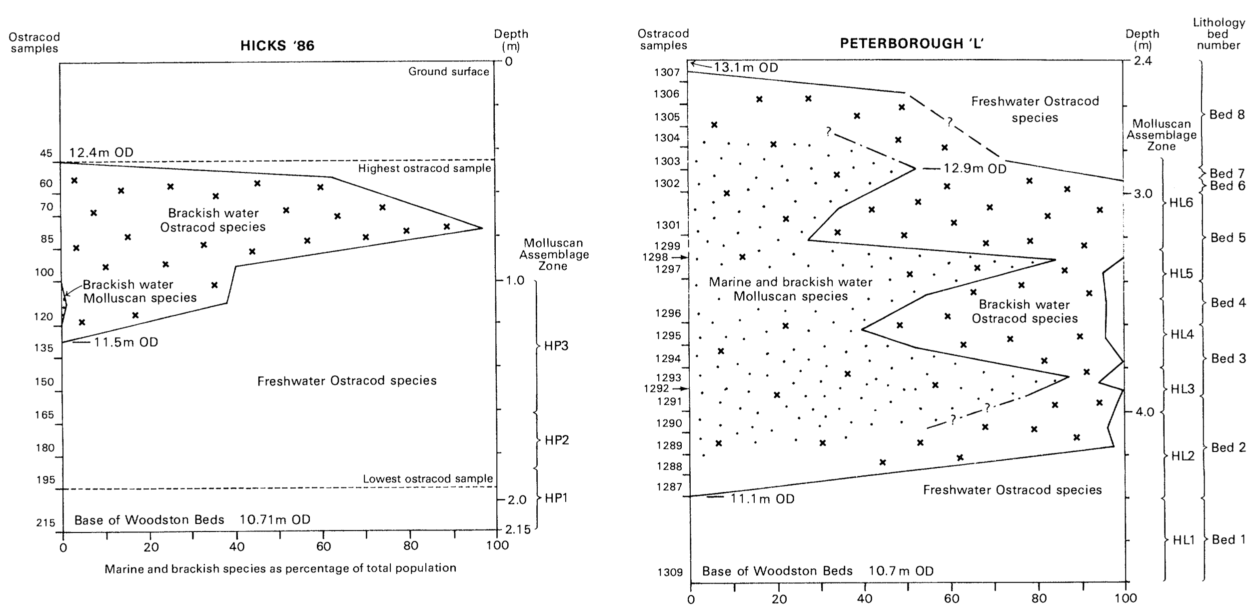

Figure 11. Environment and salinity, Hicks 86 and Peterborough 'L' Sections as indicated by molluscs and ostracods.

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Table 8. *The ostracod population of the Woodston Beds in the Hicks Pit 86 section*

(Abundance recorded as percentage of total number of valves collected from each sample; tr represents fragments present.)

	sample depth from datum 195 cm above base of Woodston Beds								
species	45–60	70–85	85–100	100–120	120–135	135–150	150–165	165–180	180–195
Candona cf. *lozeki* Absolon	3.4	—	25.0	—	—	11.1	—	—	—
Candona neglecta Sars	17.2	—	—	18.8	63.6	44.4	80.0	—	—
Cyprideis torosa (Jones)	62.0	95.5	66.7	62.5	—	—	—	—	—
Herpetocypris reptans (Baird)	tr	tr	tr	—	—	22.2	tr	tr	?tr
Herpetocypris salina (Brady)	—	—	—	—	18.2	—	20.0	—	—
Ilyocypris cf. *decipiens* Masi	10.3	—	8.3	6.2	9.1	—	—	—	—
Ilyocypris papillata Robinson	—	—	—	6.2	—	—	—	—	—
Proniocypris serrata (Norman)	—	4.5	—	6.2	9.1	22.2	—	100	100
Total number of valves counted	29	22	12	16	11	9	5	1	—

drier areas. The aquatic habitats can be divided into two main types; stationary and flowing water. The first is represented by few species of low abundance. *Ilybius* sp. is a free-swimming carnivore both as a larva and imago. *Gyrinus* sp. hunts over the water surface for stranded insects. Both are most frequently found in still or slowly flowing water. The hydrophilids *Coelostoma orbiculare* (Fabricius), *Hydrobius fuscipes* (Linné) and *Limnoxenus niger* (Zachach) live in stagnant water choked with decomposing vegetation.

In contrast, running-water species are well represented. Particularly important are the dryopids *Esolus parallelepipedus* (Mueller), *Oulimnius tuberculatus* (Mueller) and *Normandia nitens* (Mueller), all of which require well-aerated water running over a stony substrate. Similar habitats are necessary for all the listed Trichoptera. The hydropsychids have larvae that construct elaborate capture nets set across the current and anchored to a firm bottom. *Hydropsyche contubernalis* McLachlan is most frequent in relatively large slow flowing rivers and *Cheumatopsyche lepida* Pictet lives in small or large rivers with a stony bottom, but avoids large calm rivers (Lepneva 1970). The mode of life of the larvae of *Anabolia nervosa* Curtis is given by Lepneva (1971) as follows: 'feeding on diatoms, filamentous algae in vegetation on stones and tree remnants, some detritus may be present in the food; the species occurs in slow, clear water with a current speed of 0.05–0.2 m per sec, rarely 0.5 m per sec, often in spring fed brooks or in more sunlit streams with a summer temperature of 18–20°C; usually on a bottom of stone or sand with detritus'. This description illustrates the precision (perhaps over precision) of the environmental data that these insects can contribute to palaeoecological reconstructions.

Finally, the larvae of *Notidobia ciliaris* (Linné) are phytophagous, living in shallow water in clear rivulets or brooks, while those of *Sialis fuliginosum* Pictet are voracious predators living amongst stones in running water.

In summary the aquatic insects show that the basal 1 m of the Hicks 86 sequence was laid down by a substantial river in which the water was energetic enough in places to produce shallow rapids over a

Table 9. *The ostracod population of the Woodston Beds in the Peterborough 'Type' Section*

(Abundance recorded as percentage of total number of valves collected from each sample.)

	SAA sample number										
species	1286	1285	1284	1283	1281	1280	1279	1279(ii)	1278	1277	1276
Candona compressa (Koch)	13.0	—	39.3	83.3	28.2	38.2	—	41.9	30.9	60.0	—
Candona levanderi Hirschmann	26.0	—	26.2	—	—	—	—	—	—	—	—
Candona cf. *lozeki* Absolon	17.4	—	—	8.3	15.4	10.9	—	23.3	13.4	—	—
Cyclocypris laevis (O. F. Müller)	13.0	—	3.3	—	—	3.6	—	—	4.1	—	—
Cyprideis torosa (Jones)	—	—	—	—	—	—	—	—	—	6.7	—
Cypridopsis vidua (O. F. Müller)	—	—	—	—	—	—	—	7.0	6.2	—	—
Herpetocypris reptans (Baird)	—	—	1.6	—	25.6	10.9	—	4.7	—	—	—
Herpetocypris salina (Brady)	—	—	—	—	—	—	—	—	6.2	—	33.3
Ilyocypris bradyi Sars	47.8	—	19.7	—	—	—	—	7.0	—	—	—
Ilyocypris gibba (Ramdohr)	—	—	3.3	—	15.4	34.5	—	4.7	24.7	26.7	—
Ilyocypris inermis Kaufmann	—	—	6.6	—	2.6	—	—	9.3	7.2	6.7	—
Potamocypris foxi Sywula	—	—	—	—	10.3	1.8	—	2.3	7.2	—	—
Proniocypris serrata (Norman)	—	—	—	—	2.6	—	—	—	—	—	—
Total count	23	0[a]	61	12	39	55	0[b]	86	97	15	3

[a] Sand sample.

[b] Sand sample from channel.

Table 10. *The ostracod population of the Woodston Beds in the Peterborough 'L' Section*

(Abundance recorded as percentage of the total number of valves collected from each sample. The occurrence of the Recent Foraminifera Elphidium is shown #.)

	SAA sample number														
species	1309	1288	1289	1290	1291	1292	1293	1294	1295	1296	1297	1301	1303	1304	1306
Candona angulata (Müller)	—	—	—	—	0.6	—	3.1	—	0.4	1.7	1.1	—	—	—	—
Candona compressa (Koch)	—	—	2.3	—	—	—	3.1	—	0.4	0.2	0.3	—	5.7	—	2.9
Candona levanderi Hirschmann	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—	4.4
Candona cf. *lozeki* Absolon	—	—	—	—	—	—	—	—	1.3	1.4	—	—	3.3	—	—
Candona neglecta Sars	9.9	—	—	—	—	—	—	—	—	—	1.1	—	—	—	2.9
Cyclocypris laevis (O. F. Müller)	—	—	—	—	0.3	—	—	—	—	—	—	—	7.3	—	—
Cyprideis torosa (Jones)	1.4	—	84.1	96.3	98.8	99.9	93.8	99.4	96.0	95.9	95.5	100	93.0	—	50.0
Cypridopsis vidua (O. F. Müller)	59.1	—	—	—	—	—	—	—	0.4	—	—	—	—	—	1.5
Cytheromorpha fuscata (Brady)	—	—	13.6	—	—	—	—	—	—	—	—	—	—	—	—
Darwinula stevensoni Brady, Crosskey & Robertson	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Herpetocypris reptans (Baird)	12.7	—	—	—	0.3	0.1	—	—	0.7	—	0.3	—	—	—	—
Herpetocypris salina (Brady)	5.6	—	—	—	—	—	—	—	0.7	0.9	—	—	0.8	—	4.4
Ilyocypris bradyi Sars	—	—	—	—	—	—	—	—	—	—	1.1	—	—	—	—
Ilyocypris cf. *decipiens* Masi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ilyocypris gibba (Ramdohr)	5.6	—	—	3.7	—	—	—	—	—	—	—	—	4.1	—	26.5
Ilyocypris inermis Kaufmann	—	—	—	—	—	—	—	—	—	—	—	—	4.1	—	7.4
Potamocypris foxi Sywula	—	—	—	—	—	—	—	—	—	—	—	—	1.6	—	—
Proniocypris serrata (Norman)	5.6	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
Total count	71	—	44	54	674	713	65	988	892	2238	354	2250	122	—	68
Elphidium							#		#				#		

Table 11. *Coleoptera from Hicks Pit, 1986 section*

(Taxonomic notes: *Hydraena cf. latebricola* Jach; Numerous fragments were found of *Hydraena* of the riparia group of species.The individual species are impossible to separate without the male genitalia. In the Woodston material was a complete abdomen from which P. J. Osborne managed to extract genitalia which are so well preserved that they can without question be placed in the *Hydraena bohemica* Hrb. subgroup from central Europe. They most closely resemble in detailed structure and size *Hydraena latebricola* Jach recently decribed from Jugoslavia (Jach, 1986).Identical genitalia were recovered from Stratum D at Hoxne. A complete account of this species will be published separately. Trichoptera larvae: The identifications are all based on the frontoclypeal apotomes using the excellent photographs in Wilkinson (1980) and the fine line-drawings of Lepneva (1970 and 1971) Whilst this is no substitute for comparison with actual specimens, there can be little doubt that the names given to the fossils are close enough to provide sound palaeontological inferences.)

Depth in cm from surface	115–130	130–145	145–160	160–175	175–195	bulk
Carabidae						
Loricera pilicornis (Fabricius)					2	
Clivina fossor (Linné)					1	
Trechus obtusus Erichson					1	
Bembidion octomaculatum (Geoze)					1	
Bembidion sp.				2		
Pterostichus vernalis (Panzer)					1	
Pterostichus anthracinus (Illiger)					1	
Pterostichus minor (Gyllenhall)			1			
Chlaenius sp.					1	1
Syntomus truncatellus (Linné)					2	
Dytiscidae						
Ilybius sp.					1	
Gyrinidae						
Gyrinus sp.					1	
Hydraenidae						
Hydraena cf. *latebricola* Jach	1	1	5	17	14	
Ochthebius minimus (Fabricius) agg.			1	2	4	
Helophorus sp.				1		
Hydrophilidae						
Coelostoma orbiculare (Fabricius)				1		
Sphaeridium sp.					1	
Cercyon tristis (Illiger)						1
Cercyon sp.			1		4	
Hydrobius fuscipes (Linné)				1		
Limnoxenus niger (Zachach)					1	
Laccobius sp.					1	
Chaetarthria seminulum (Herbst)				1	1	
Orthoperidae						
Corylophus cassidioides (Marsham)					1	
Ptiliidae						
Ptenidium sp.				1	1	
Acrotrichis sp.					1	
Staphylinidae						
Micropeplus staphylinoides (Marsham)					1	
Micropeplus porcatus (Paykull)					2	
Metopsia gallica (Koch) or *M. clypeata* (Mueller)					1	
Xylodromus sp.					1	
Lathrimeum atrocephalum (Illiger)				1		
Trogophloeus sp.				1	1	
Oxytelus rugosus (Fabricius)			1	1	1	
Oxytelus sp.					1	
Platystethius arenarius (Fourcroy)					1	
Stenus sp.				2	1	
Lathrobium sp.					1	
Gyrohypnus angustatus Stephens				1		
Tachinus fimetarius Gravenhorst					1	
Aleocharinae *gen. et sp. indet.*			2	3	8	
Elateridae						
Melanotus sp.					1	
Adelocera murina (Linné)					1	
Throscidae						
Throscus dermestoides (Linné)			1		1	

Table 11 (*contd*)

Depth in cm from surface	115–130	130–145	145–160	160–175	175–195	bulk
Dryopidae						
Dryops sp.			1	5		
Esolus parallelepipedus (Mueller)			1		1	
Oulimnius tuberculatus (Mueller)			4	10	8	
Normandia nitens (Mueller)				2	1	
Georissidae						
Georissus crenulatus (Rossi)					1	
Anobiidae						
Anobium sp.					1	
Scarabaeidae						
Onthophagus sp.			1		1	
Aphodius sp.				1	3	
Chrysomelidae						
Donacia semicuprea Panzer					1	
Scolytidae						
Leperisinus varius (Fabricius)					1	1
Ptelobius vittatus (Fabricius)				1		
Curculionidae						
Otiorhynchus clavipes (Bonsdorff)			1		1	
Notaris scirpi (Fabricius)			1		1	
Curculio sp.			1			
Ceutorhynchus sp.						1
Barypeithes sp.						1
Trichoptera						
Hydropsyche						
Hydropsyche bulbifera McLachlan					1	
Hydropsyche contubernalis McLachlan					1	
Cheumatopsyche lepida Pictet			2	12	5	
Limnephilidae						
Anabolia nervosa Curtis				1	1	
Sericostomatidae						
Notidobia ciliaris (Linné)			3	4	7	
Sericostoma sp.					2	
Megaloptera						
Sialis fuliginosum Pictet			4	2	8	

shingle bottom. The evidence for still or stagnant water is sparse and could be accounted for by quiet backwaters or overbank ponds on the flood plain of the river.

Along the margins of the river were natural water meadows in which grew the sweet grass *Glyceria aquatica* (Linné) the food plant of *Donacia semicuprea* Panzer. This grass would also have been attractive to the large herbivorous mammals the dung of which provided food for *Onthophagus* sp. and *Sphaeridium* sp. and probably also for species of *Aphodius* and *Cercyon*. This swampy ground must have supported the sedges *Scirpus* and *Carex* spp. the food plants of the weevil *Notaris scirpi* (Fabricius).

Several of the scavenging carabid beetles also generally occur in marshy habitats. *Pterostichus vernalis* (Panzer) and *Pterostichus minor* (Gyllenhall) are hygrophiles living in fens and wet meadows, while species of *Chlaenius* are predators on insect larvae, slugs and earthworms, etc. They breed in marshy places often with a luxuriant growth of reeds and sedges (Lindroth 1986). Some of these species, however, hibernate in dry places well away from water so their presence here may not confirm wet conditions.

Many species in this fossil assemblage live in decaying plant debris. These include almost all the carnivorous staphylinid species and *Corylophus cassidioides* (Marsham). Species of *Cercyon* are found in decomposing plant matter and also in the dung of herbivorous mammals. All these species could have lived in the flood refuse of the river.

There is a marked absence of the species that colonise temporary sand banks in rivers, but some of the species recorded live at their muddy margins. *Chaetarthria seminulum* (Herbst) is found under detritus by standing water. *Georissus crenulatus* (Rossi) lives on sandy or muddy banks where its larvae inhabit the uppermost centimetre of the sediment under algal mats. *Bembidion octomaculatum* (Goeze) lives on the silty or sandy margins of ponds. There is some hint from these species that the riparian habitat was not thickly covered by vegetation.

The marshy conditions beside rivers gradually merge with truly terrestrial environments and it is often difficult to allocate insect species to a specific habitat. Thus *Loricera pilicornis* (Fabricius) is a eurytropic species of damp, muddy soils in more or less shaded places in both forest and open country, and often at the margins of open water (Lindroth 1985). *Clivina fossor* (Linné) is also eurytropic, usually occurring in open country on rather wet ground with more or less dense vegetation of grasses and preferably on a clayey soil, never on pure sand (Lindroth 1985). *Trechus obtusus* Erichson is found in moderately humid and usually shaded localities in deciduous forest. *Syntomus truncatellus* (Linné) inhabits open, sun-exposed dry ground preferably with a sparse cover of grasses, such as occurs in dry meadows and open woodland. These carabid species suggest a gradual transition from marsh to light grassy, woodland. Such conditions are also an acceptable habitat for the elaterid beetle *Adelocera murina* (Linné) whose larvae feed at the roots of various plants in meadow-like habitats, the larvae of *Trachys pumilus* Illiger which mine the stems and flower heads of various Labiatae, and species of *Melanotus* whose larvae live on rotten wood or at the roots of plants. *Throscus dermestoides* (Linné) is found in the ground litter in light woodland.

Evidence as to the types of trees present is given by the Scolytidae which breed in galleries excavated under bark. Thus *Leperisinus varius* (Fabricius) normally attacks the trunk and branches of *Fraxinus*, and *Ptelobius vittatus* (Fabricius) is strictly confined to species of *Ulmus* that are already sick, where it can become extremely abundant (Balachowsky 1949). Weevils of the genus *Curculio* include those whose larvae develop inside nuts (e.g. *Corylus*), acorns and galls. *Anobium* is the genus that contains the familiar woodworm or furniture beetle whose larvae drill holes in all manner of fairly dry, old wood. They must have infested dry, dead timber on the woodland floor or the standing boles of dead trees.

(*b*) ***Climatic interpretation***

This insect assemblage indicates temperate conditions. All but two of the Coleoptera are found today living in southern England where they are close to their northern geographic limit. Of the non-British species, the specimen of *Chlaenius* is too incomplete to permit precise identification. It is probably one of the considerable number of species that occur in central Europe today. It is definitely not a Fennoscandian species. The species of *Hydraena* provisionally assigned to the newly described species *latebricola* Jach has so far only been found in Montenegro (Jach 1986).

Amongst the larval Trichoptera, only *H. bulbifera* does not now live in Britain. It has a patchy distribution in central and south eastern Europe extending eastwards into Asia (Wilkinson 1980).

Thus, the climate seems to have been rather warmer than southern England today and with a hint of greater continentality. However, the lack of characteristic Mediterranean species suggests a temperature difference of only one or two degrees.

(*c*) ***The age of the coleopteran fauna***

The fauna from the Woodston Beds is an interglacial assemblage, and has affinities with that from the type locality of the Hoxnian Interglacial. In both cases the highly distinctive species *H. latebricola* is present and so far these are the only localities from which this species has been recovered. Although it is by itself by no means conclusive evidence, the presence of *H. latebricola* gives added support to other lines of evidence suggesting a Hoxnian age.

7. MAMMALIA

(*a*) ***The mammalian fauna***

An indeterminate mammalian rib fragment was found in the Hick 69 section and a rolled vertebra of an indeterminate bovid (*Bos* or *Bison* sp.) was found in the lowest part of the silty sand in the Hicks 86 section. A varied fauna of large mammals has been recorded from the Woodston Beds outcrop and from horizons probably correlating with them. Porter (1861) mentions 'mammoth, ox, horse, deer, rhinoceros and wolf' while Leeds (1956) reported the occurrence of '*Elephas*, *Rhinoceros antiquitatis* and *Bos primigenius*'. All these fossils were recovered from the basal gravel and thus may contain elements from the pre-Woodston Beds land surface as well as contemporary material.

Samples from the Hicks 86 section sorted for Mollusca were also sorted for small mammal material. All the specimens found came from depths below 1.00 m. Six taxa were identified (table 12), all except for the distal radius of a mole (*Talpa* sp.), by their teeth. The other animals were the voles *Clethrionomys glareolus* (Schreber), *Arvicola cantiana* (Hinton), *Pitymys subterraneus* (de Sélys Longchamps) and *Microtus* sp., and the wood mouse *Apodemus sylvaticus* (Linné).

Table 12. *The Mammalia of the Hicks 86 Section*

	Bulk A	Bulk B	1.00–1.20
Apodemus sylvaticus (Linné)			rt lower m1–3 lft upper m2
Clethrionomys glareolus (Schreber)		lft upper m2 lft lower m3	fragment of molar
Pitymys subterraneus (de Sélys Longchamps)			rt lower m1 (fragment)
Arvicola cantiana (Hinton)	rt lower m3*[a]		
Microtus sp.			fragments
Talpa sp.		distal radius	

[a] With posterior bias on enamel thickness.

(*b*) *Palaeoecological indications*

The occurrence together of *C. glareolus* and *A. sylvaticus* suggest evidence of woodland habitats similar to those in which both now live (Currant 1986). *A. cantiana* is the primitive dental morphotype of the living *Arvitola terrestris* Linné, the water vole, and its high relative abundance in Quaternary aquatic environments suggests that it too lived in streams and ponds. Voles of the genus *Microtus* are generally grassland dwellers at present (Stuart 1982) but provide little further information other than at specific level. *Pitymys subterraneus* (de Sélys Longchamps) is an inhabitant of the forest edge and open grassland (Stuart 1982). Moles (*Talpa* sp.), are believed to be native to deciduous woodland, their modern preference for pastureland being a relatively recent opportunistic adaptation.

(*c*) *Age indications from the mammal fauna*

Two aspects of the fauna from Woodston combine to place the deposits in a narrow age band in the Middle Pleistocene. *A. cantiana* is only found in post-Cromerian *sensu stricto* deposits, its earliest occurrence in Britain being at sites like Ostend, Norfolk, Boxgrove, Sussex and Westbury-sub-Mendip, Somerset ['Pink Breccia'-unit 11], the Group 4 assemblages of Currant (1989), representing a major interglacial phase probably equivalent to Cromerian IV of the Dutch sequence. *P. subterranus* indicates an age no younger than the Hoxnian Interglacial corresponding to the Group 3 assemblages of Currant (1989), when this species has its last record in Britain (Stuart 1982).

8. AMINO ACID GEOCHRONOLOGY

Shells of three molluscan taxa, *B. tentaculata*, *Cepaea* sp. and *T. hispida* were collected from the basal layer of the Hicks 86 section and submitted to the Amino-acid Geochronology Laboratory at Royal Holloway and Bedford New College, University of London for analysis. The results of this analysis are set out in table 13. The ratios obtained suggest an age similar to that obtained from bed E of Hoxne but younger than that of Swanscombe (Bowen *et al.* 1989).

9. DISCUSSION

(*a*) *Environmental synthesis*

The diverse faunal and floral evidence indicates that the Woodston Beds were deposited under temperate conditions in the channel and estuary of a large slow-flowing river. Fluvial sedimentation occurred initially with, at first, deposition of gravel as channel bars, and then accumulation of quiet-water sediments with evidence of episodic current activity, suggesting over-bank deposition. Molluscan and insect faunas indicate freshwater environments, but a predominantly estuarine ostracod fauna suggests a direct tidal input. Brackish conditions with tidal channels, mud flats and possibly salt marsh were present at the maximum extent of the marine transgression. The ostracods indicate a much longer period of brackish water conditions than the molluscs, but this may reflect a greater tolerance to changing salinity or a greater ease of transportation from this habitat to the site of deposition. Subsequently, fluvial sedimentation returned initially in quiet water environments, but eventually to deposit the sands and gravels of the Third Terrace of the Nene.

Table 13. *Amino acid ratios from the Hicks 86 Section*

laboratory no.	molluscan species	ratio
Lond-315	*Cepaea* sp.	0.253 ± 0.014
Lond-316	*Trichia hispida*	0.233 ± 0.025
Lond-317	*Bithynia tentaculata*	0.249 ± 0.028
Lond-318	*Cepaea* sp.	0.244 ± 0.005
Lond-319	*Trichia hispida*	0.239 ± 0.022
Lond-320	*Bithynia tentaculata*	0.244 ± 0.030

The fossil evidence suggests that the river was bordered by grassland and marsh with woodland further away. However, trees must have been present near the floodplain to provide the fossil wood in the sediments. The richness and abundance of flora and fauna indicate that the Woodston Beds were deposited during an interglacial. The flora in particular provide good evidence that the sediments were deposited in the early temperate zone of an interglacial *sensu* Turner and West (1968), and the pollen assemblage establishes a correlation with zone Ho II of the Hoxnian Interglacial. The occurrence of the beetle *H. latebricola* only at Woodston and Hoxne, and the close similarity of the insect fauna of the two sites adds weight to the correlation.

It has generally been supposed that the Hoxnian Interglacial was an oceanic episode compared to other Pleistocene interglacials in Britain (Turner 1970). The Woodston flora is consistent with this view, but the molluscs and beetles and to a lesser extent the mammals indicate a climate more continental than today, with several species having present-day core distributions in central Europe.

(*b*) *Sea levels of the Wash*

Most Hoxnian deposits accumulated in isolated lake basins. The Woodston Beds are fluviatile, close to sea level and have unambiguous evidence of a marine incursion. The height of the first marine influence is *circa* 11.00 m O.D. in the 'Type' and 'L' sections and at 11.70 m in the Hicks sections. Because of decalcification and erosion at the top of the sequence, the upper limit of marine conditions is not known, although a marine fauna occurs in less decalcified pockets of sediment at 14.10 m O.D. in the 'L' section and 12.75 m O.D. in the Hicks sections. The only other site in the Wash basin to yield sea level data for the Hoxnian is the Nar Valley (Ventris, 1986; West, 1987)). Here palynological evidence suggests a maximum sea level of *circa* 23 m O.D. for zone Ho III of the interglacial. The earliest evidence for marine conditions in the Nar Valley sequence occurs in zone Ho IIc where marine deposits occur at 2.5 m O.D. At

Woodston also, evidence of marine transgression appears to relate to zone II of the Hoxnian so there would appear to be a 10 m difference in the height of the transgression from the north-east side of the Wash to the south. Several explanations are possible for these height differences. Firstly, if a height difference existed between the two localities in the Hoxnian, surviving evidence of transgression will now be found at different levels, reflecting the progressive encroachment of marine conditions onto higher and higher ground. Secondly, it is possible that the form of the proto-Nene estuary resulted in higher spring tide levels than in the Nar Valley, which would have been closer to the open sea. Thirdly, differential uplift or tectonic warping may have occurred between the Nene and Nar Valleys either in the Hoxnian or subsequently. However, there is no evidence of such tectonic features from any of the terraces of the Nene all of which have similar uninterrupted seaward gradients.

The Hoxnian zone III deposits at Clacton (Turner in Kerney 1971) also show marine influence with a transgression contact at 3.00 m O.D. and continuing estuarine conditions to 9.00 m O.D. This height range is much closer to that of the marine episode at Woodston, but the Clacton transgression occurs at a lower level and in a younger zone than at Woodston, so no exact comparison can be made here and the possibility of differential warping again complicates the correlation of Hoxnian sea levels.

One other supposed Hoxnian site with sea level evidence is Swanscombe. The marine limit at Swanscombe (at Dierden's Pit, Kerney 1971) is *circa* 25 m O.D. and thus 14 m higher than at Woodston. If the two sites are of the same age a difference is again only accountable if warping has taken place.

For a wider and more complete picture of Hoxnian sea levels, more and better dated sites are required. For the present all that it is possible to do is to point out the complications hindering correlation.

(*c*) *Conclusions*

The Woodston Beds of Peterborough were deposited under fully temperate conditions in zone II of the Hoxnian Interglacial. There is evidence of a marine transgression at *circa* 11.00 m O.D. and up to 14.1 m, but the culminating level is not known. Comparison of the pollen flora with that from other pollen-dated Hoxnian sites shows reasonable agreement, and there are additional grounds for correlation with the Hoxnian type site on coleopteran and amino-acid evidence. There are problems of correlation with the molluscan data arising from the lack of ecologically comparable faunas elsewhere.

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REFERENCES

Absolon, A. 1973 Ostracoden aus einigen profilen spät- und postglazialer karbonatablagerungen in Mittel-europa. *Mitt. Staatssammlung Paläont. Hist. Geol.* **13**, 47–93.

Balachowsky, A. 1949 Coléoptères Scolytidae. *Faune Fr.* **50**, 1–320. Paris: Lechevalier.

Bowen, D.Q., Hughes, S.A., Sykes, G.A. & Miller, G.H. 1989 Land-sea correlations in the Pleistocene based on isoleucine epimerization in non-marine Mollusca. *Nature, Lond.* **340**, 49–51.

Briggs, D.J., Coope, G.R. & Gilbertson, D.D. 1985 The chronology and environmental framework of early man in the Upper Thames valley. *Brit. Arch. Rep., Brit. Ser.* **137**, 1–176.

Cain, A.J. 1971 Colour and banding morphs in subfossil samples of the snail *Cepaea*. In *Ecological genetics and evolution* (ed. R. Creed), Oxford: Blackwell.

Cain, A.J. & Currey, J.D. 1968 Studies on *Cepaea* IV. Climate and selection of banding morphs in *Cepaea* from the climatic optimum to the present day. *Phil. Trans. R. Soc. Lond.* B **253**, 483–498.

Cain, A.J., Sheppard, P.M. & King, J.M.B. 1968 Studies on *Cepaea* I. The genetics of some morphs and varieties of *Cepaea nemoralis* (Linné). *Phil. Trans. R. Soc. Lond.* B **253**, 383–396.

Currant, A.P. 1986 Man and the Interglacial faunas of Britain, pp. 50–52. In *The Palaeolithic of Britain and its nearest neighbours: recent trends* (ed. S. N. Collcut), (109 pages.) University of Sheffield: Department of Prehistory and the Archaeology.

Currant, A.P. 1989 The Quaternary origins of the modern British mammal fauna. *Biol. J. Linn. Soc.* **38**, 23–30.

Ellis, A.E. 1969 *British Snails*. Oxford: Clarendon Press.

Elofson, O. 1941 Zur Kenntnis der Marinen Ostracoden Schwedens, mit besonderer Berucksichtigung des Skagerraks. *Zool. Bidr. Upps.* **19**, 215–534.

Fitter, A. 1978 *An atlas of the wild flowers of Britain and Northern Europe*. London: Collins.

Fretter, V. & Graham, A. 1962 *British prosobranch molluscs: their functional anatomy and ecology*. London: Ray Society.

Gilbertson, D.D. & Hawkins, A.B. 1978 The Pleistocene succession at Kenn, Somerset. *Bull. geol. surv. Gt Br.* **66**, 1–44.

Harrison, K. 1935 The March-Nar Sea. *Geol.Mag.* **72**, 257–263.

Holyoak, D.T. & Preece, R.C. 1985 Late Pleistocene

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

interglacial deposits at Tattershall, Lincolnshire. *Phil. Trans. R. Soc. Lond.* B **311**, 193–236.
Horton, A. 1989 *The geology of the Peterborough district. Mem. geol. Surv. U.K.* (44 pages.)
Horton, A., Lake, R.D., Bisson, G. & Coppack, B.C. 1973 The geology of Peterborough. *Rep. Inst. Geol. Sci.*, no. 73/12.
Iversen, J. 1944 *Viscum*, *Hedera*, and *Ilex* as climatic indicators. *Geol. För. Stock. Förh.* **66**, 463–483.
Jach, M.A. 1986 Beschreibung neuer *Hydraena*-arten aus Jugoslawien (Coleoptera, Hydraenidae). *Sonderabdr. Nachricht. Bayer. Ent.* J **35** (3), 65–69.
Keen, D.H., Robinson, J.E., West, R.G., Lowry, F., Bridgland, D.R. & Davey, N.D.W. 1990 The fauna and flora of the March Gravels at Northam Pit, Eye, Cambridgeshire, England. *Geol. Mag.* **127** (5), 453–465.
Kelly, M.R. 1964 The Middle Pleistocene of North Birmingham. *Phil. Trans. R. Soc. Lond.* B **247**, 533–592.
Kendall, C.E.Y. 1913 Notes on some Pleistocene Mollusca in north Huntingdonshire. *J. Conch., Lond.* **13**, 83–91.
Kennard, A.S. 1942 Pleistocene chronology (in discussion). *Proc. Geol. Ass.* **53**, 24–25.
Kennard, A.S. & Woodward, B.B. 1922 The post-Pliocene non-marine Mollusca of the East of England. *Proc. Geol. Ass.* **33**, 104–142.
Kerney, M.P. 1971 Interglacial deposits in Barnfield Pit, Swanscombe and their molluscan fauna. *J. geol. Soc. Lond.* **127**, 69–93.
Kerney, M.P. 1976a A list of the fresh and brackish-water Mollusca of the British Isles. *J. Conch., Lond.* **29**, 26–28.
Kerney, M.P. 1976b *Atlas of the non-marine Mollusca of the British Isles*. Huntingdon: Institute of Terrestrial Ecology.
Kerney, M.P. & Cameron, R.A.D. 1979 *A field guide to the land snails of Britain and north-west Europe*. London: Collins.
Klie, W. 1938 Ostracoda. *Tierwelt Dtl.* **34**, 1–230.
Leeds, E.T. 1956 *The Leeds Collection of fossil reptiles from the Oxford Clay of Peterborough* (ed. W. E. Swinton). (104 pages.) Oxford: Blackwell Scientific Publications.
Lepneva, S.G. 1970 Larvae and pupae of Annulipalpia. In *Fauna of the U.S.S.R.* (*Trichoptera*), vol. II, no. 1, pp. 1–638. Jerusalem: Israel Program for Scientific Translations.
Lepneva, S.G. 1971 Larvae and pupae of Interpalpia. In *Fauna of the U.S.S.R.* (*Trichoptera*), vol. II, no. 2, 1–700. Jerusalem: Israel Program for Scientific Translations.
Lindroth, C.H. 1985 The Carabidae (Coleoptera) of Fennoscandia and Denmark. In *Fauna Entomologica Scandinavica*, Vol. 15, pt 1, pp. 9–224. Leiden and Copenhagen, E. J. Brill.
Lindroth, C.H. 1986 The Carabidae (Coleoptera) of Fennoscandia and Denmark. In *Fauna Entomologica Scandinavica*, Vol. 15, pt 1, pp. 233–497 Leiden and Copenhagen, E. J. Brill.
Lucht, W.H. 1987 *Die Kafer Mitteleuropas Katalog*. Krefeld: Goecke und Evers.
Neale, J.W. 1965 Some factors influencing the distribution of Recent British Ostracoda. *Pubbl. Staz. zool. Napoli* **33** (suppl.), 243–307.
Neale, J.W. & Delorme, L.D. 1985 *Cytheromorpha fuscata* a relict Holocene marine ostracod from freshwater inland lakes of Manitoba, Canada. *Rev. Espan. Micropal.*, XVII, 41–64.
Nüchterlein, H. 1969 Süsswasserostracoden aus Franken: Ein Beitrag zur Systematik und Ökologie der Ostracoda. *Int. Rev. ges. Hydrobiol.*, **54**, 223–287.
Phillips, L.M. 1976 Pleistocene vegetational history and geology in Norfolk. *Phil. Trans. R. Soc. Lond.* B **275**, 215–286.
Porter, H. 1861 *The geology of Peterborough and its vicinity* (126 pages.) Peterborough.
Sparks, B.W. 1961 The ecological interpretation of Quaternary non-marine Mollusca. *Proc. Linn. Soc. Lond.* **172**, 71–81.
Sparks, B.W., West, R.G., Williams, R.B.G. & Ransom, M.E. 1969 Hoxnian Interglacial Deposits near Hatfield, Herts. *Proc. Geol. Ass. Lond.* **80**, 243–267.
Stuart, A.J. 1982 *Pleistocene vertebrates in the British Isles*. London: Longmans.
Trimmer, J. 1854 On some mammaliferous deposits in the valley of Nene, near Peterborough. *Quart. J. geol. Soc. Lond.* **10**, 343–346.
Turner, C. 1970 The Middle Pleistocene deposits at Marks Tey, Essex. *Phil. Trans. R. Soc. Lond.* B **257**, 273–440.
Turner, C. & West, R.G. 1968 The subdivision and zonation of interglacial periods. *Eiszeitalter Gegenw.* **19**, 93–101.
Van Harten, D. 1975 Size and environmental salinity in the modern euryhaline ostracod *Cyprideis torosa* (Jones, 1850), a biometrical study. *Palaeogeogr. Palaeoclimatol. Palaeocol.*, **17**, 35–48.
Ventris, P.A. 1985 Pleistocene environmental history of the Nar Valley, Norfolk. Ph.D. thesis, University of Cambridge.
Vesper, B. 1972 Zur Morphologie und Ökologie von *Cyprideis torosa* (Jones, 1850), unter besonderer Beruck-sichtigung seiner Biometrie. *Mitt. Hamb. zool. Mus. Inst.* **68**, 21–77.
Wagner, C.W. 1957 *Sur les ostracodes du Quaternaire Recent des Pays Bas et leur utilisation dans l'étude géologique des dépôts Holocenes*. The Hague: Mouton and Co.
West, R.G. 1956 The Quaternary deposits at Hoxne, Suffolk. *Phil. Trans. R. Soc. Lond.* B **239**, 265–356.
West, R.G. 1987 A note on the March gravels and Fenland sea levels. *Bull. geol. Soc. Norfolk* **37**, 27–34.
Wilkinson, B. 1980 The use of Caddisfly (Trichoptera) larvae in Palaeoecology. M.Sc. thesis, University of Birmingham.

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APPENDIX 1. STRATIGRAPHIC DESCRIPTIONS OF REPRESENTATIVE SECTIONS IN THE WOODSTON BEDS

(*a*) *Hicks 69*

A trench dug in 1969 at TL 1899 9564 in the Hicks' No. 1 brickyard had a surface level at 12.6 m O.D. and proved the following sequence:

	Thickness/m
Clay, greyish brown mottled with *Cerastoderma edule* (Linné) at base and 20 cm above.	0.88
Cockle Bed, medium to coarse grained, well sorted sand with convex upward valves of *C. edule*, *Ostrea edulis* (Linné) and *Spisula elliptica* (Brown) and sand free pockets of *Hydrobia ventrosa* (Montagu); Rodent teeth and large vertebrate fragments.	0.00–0.06
Clay, greyish brown silty with ?*Cerastoderma*.	0.04–0.06
Shelly sand, pale grey with shell debris and scattered *Cerastoderma*.	0.02–0.06
Clay, greyish brown slightly silty with sand layers and lenses, scattered shell debris bands, probably *Unio*. Becoming more sandy downwards.	0.61
Sand, pale grey with brown mottling, well sorted with abundant shell debris.	0.06–0.07

Clay, brown sandy passing laterally to clayey sand, scattered plant debris and carbonaceous rootlets. Abrupt irregular base. 0.13

Silt, orange brown sandy with sand pockets, shells and shell debris, with plant stems and seeds. Cylindrical ferruginous concretions, possibly after roots or burrows. 0.03

Silt, fine grained humic with large plant fragments and wood, numerous freshwater shells. 0.47

Sands, greyish brown, banded, scattered plant fragments, layer of pebbles at base. Scattered shells.

Gravel, clay bound in top 10 cm with brown clay and and sand pockets. Mostly clean, open work gravel below, with small pebble fragments as matrix. Scattered wood fragments and large bivalves. 0.85

At *circa* 9.2 m O.D. Oxford Clay.

(*b*) *Hicks 86*

In 1986 a trench some 8–10 m to the N of the 1969 section and with a surface height of 12.3 m O.D., was dug to provide additional material for analysis. The sequence was as follows:

Thickness m

Clay, slightly sandy, with a few lenses of fine to medium grained sand, infrequent shell debris orange and pale grey with race nodules. 0.95

Clay, sandy with complete shells and debris, clay pockets and plant debris. 0.20

Sand, slightly clayey in top 7 cm, clayey below. 0.16

Silty clay. 0.16

Sand lens with freshwater shells and wood. 0.00–0.01

Silt with wood fragments. 0.11

Sand, bedded with 1 mm thick clay drapes. Very shelly. 0.19

Silt, sandy with matrix supported flint and quartz pebbles. Increasingly sandy downwards with 4 cm thick stony seam at base. 0.18

At 10.46 m Oxford Clay.

(*c*) *Peterborough 'L' section*

The Woodston Beds were exposed in trenches north of Cow Pasture Farm. The Peterborough 'L' Section [TL 1801 9594] had a surface level of 15.5 m O.D. and proved the following succession:

Thickness m

Clay, weathered with race. 2.40

Interbedded clay and sand laminae up to 0.10m thick. Rare gastropods. 0.07

Clay, grey, laminated. 0.06

Sand, grey, coarse with abundant *C. edule* and gastropods, lenticular channel infill. 0.00–0.35

Sand, dark grey with pale grey shell-rich layers and dark grey carbonaceous partings. Abundant plant and shell debris. Clay seam with *Ostrea* 0.10 m from top. 0.40

Sand, dark grey with felted plant debris interbedded with laminated clay. 0.35

Clay, dark grey with very fine sand wisps and silt partings. Rare sand -filled burrow traces. Very thinly laminated throughout. 0.45

Gravel, well sorted, open, with large unionid shells. 0.40

At *circa* 10.7 m O.D. Kellaways Beds.

(*d*) *Peterborough 'Type' section*

In the Peterborough 'Type' section [TL 1798 9609] 3.1 m of deposits were exposed by a section dug from a surface height of *circa* 14.00 m O.D. The sediments exposed were as follows:

Thickness m

Gravel, yellowish brown clayey gravel with flint and limestone. 1.0-1.13

Clay, grey and brown mottled with rootlets becoming more silty and humic downwards. 1.00

Sand, brownish grey, clayey and silty slightly humic with plant detritus including large wood fragments becoming increasingly common downwards. Shells more abundant downwards with shelly sand with scattered pebbles in the lowest 0.13–0.20 m. Felted plant debris at base infiling channel. 0.43–0.50

Sand, grey coarse clean well-graded with abundant shell debris and shell lenses. Becoming olive grey silty fine sand with plant laths infilling channel at base. 0.20–0.27

Gravel, olive brown to grey, slightly ocherous and oxidized in places. Lenses and beds of clean, well sorted sand with plant debris and shell rich bands and clayey layers of felted plant debris. Cross-stratification in some sand beds with channeled surfaces in places. Large freshwater shells. 0.40

At 10.9 m O.D. Callovian Clay.

(*e*) *Phorpres 1 borehole*

Northwards from the Peterborough 'L' section the base of the gravel rises suggesting that it floors a channel locally. The clay and sand sequence thins as the overlying gravel thickens towards the 'Type' section. Some 40 m north of the 'Type' section the gravels coalesce. A comparable sequence was seen in the Phorpres 1 borehole at TL 1833 9582, which was bored from a surface level of 17.7 m O.D.

Thickness m

Soil and sandy clay 1.01

Ill-sorted gravel with flint and limestone pebbles and seams of chalk-rich sand. 0.97

Clay, yellowish brown, silty. 0.15

Silt, grey, partly oxidized but with carbonaceous streaks in lower part. 0.74

Sand, pale grey, silty bedded with scattered shells
Sand grey and brown banded silty with clay partings, numerous small gastropods. 0.18

Sand, pale brown coarse with fine shell debris. 1.29

Silt, chocolate brown, unbedded, scattered shell and plant debris. 0.33

Gravel, coarse, well-sorted with flint and quartzite pebbles and limestone. Thin clay beds in places. Some shell debris sand. 2.14

At base Oxford Clay at *circa* 10.2 m O.D.