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THE PALAEOECOLOGY OF MIDDLE PLEISTOCENE MOLLUSCA FROM SUGWORTH, OXFORDSHIRE

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CONTENTS

This paper describes the non-marine Molluscan faunas of riverine interglacial deposits from Sugworth, near Oxford. The faunal assemblages studied indicate the former presence of a large, well oxygenated river, a proto-Thames, fringed with marsh and flowing through a fully wooded, temperate interglacial landscape. Freshwater, riverine taxa predominate, with variations in the molluscan assemblages principally reflecting local changes associated with the river shifting its course. Derivation, transportation and winnowing are thought to be important in the formation of the assemblages. The balance of available evidence indicates that the deposits should be assigned to Zone CrIIIb of the Cromerian interglacial. Declines in both the numerical abundance of specimens per sample and the species numbers per sample, noted through the profile, *may* have an underlying climatic cause.

1. Introduction

The riverine interglacial deposits at Sugworth Lane, near Oxford (SP 45132007) were exposed during the construction of the Abingdon bypass in 1972 and 1973. The deposits occur in four channels, up to 200 m in width, that are eroded into Kimmeridge Clay (Jurassic), and are overlain by up to 2 m of pebbly clay interpreted as a solifluction deposit. The fossiliferous channel infill was up to 5 m thick. The upper surface of the fossiliferous deposits was at 91 m o.d., some 39 m above and 2 km to the east of the modern floodplain of the River Thames. In a preliminary note the deposits were attributed to a large river, the proto-Thames, fringed with marsh, flowing from north to south through fairly densely wooded terrain in a fully temperate interglacial climate (Briggs *et al.* 1975). They were referred to the Cromerian interglacial, and, in the subsequent, more detailed, stratigraphic study by Shotton *et al.* (1980), more specifically assigned to Zone CrIIIb of that interglacial.

2. METHODS

This paper records a palaeoecological study of the non-marine Mollusca found in profile D at the site, of which a full description is given in Shotton *et al.* (1980). It was sampled by Dr K. Crabtree in 1973. A vertical series of samples, each 1.5 to 2.0 kg, were taken at 0.1 m intervals. Sample D0 corresponds to 0 to 0.1 m, D10 to 0.1 to 0.2 m, etc., from the base of the sequence. The samples were divided, with 1 kg of each being investigated for its molluscan remains and the remainder being studied by Dr E. Robinson for their ostracod faunas.

The samples were washed through a 0.5 mm. sieve and examined under a binocular microscope. Normally, only apical fragments or, in less abundant taxa, single identifiable parts such as lip fragments, have been counted. The numbers of single valves of lamellibranchs found have been halved in table 1 to represent the number of individuals present. Odd numbers have been rounded upwards. Opercula of *Bithynia inflata* (Hansén) have been recorded separately from the number of shells of this taxon and are excluded from column totals and from subsequent percentage frequency calculations. The molluscan fauna at each level are shown in table 1, and the variation in the composition of the assemblages illustrated in figures 1 and 2. Figure 2 also reveals variations in the abundance of ecological groupings recognized in the faunas and the presence or absence and ratios of *Bithynia* shells to opercula. In the upper parts of the section, the numbers of specimens per sample falls to very low levels, rendering interpretation both difficult and unreliable, as figures for percentage composition are prone to wide fluctuations depending upon the presence or absence of small numbers of other taxa. Such samples containing less than 30 individuals per sample (excluding opercula) are distinguished in figures 1 and 2. Nomenclature for land Mollusca follows that of Waldén (1976) and for freshwater Mollusca, the list set out by Kerney (1976).

3. IDENTIFICATION

Many of the robust, thicker shelled taxa are excellently preserved. However, there are several problems of identification with other groups. First, there has been extensive breakage, fragmentation and abrasion in the riverine environment. This is especially true of the terrestrial molluscs. Secondly, the large numbers of juveniles present have caused many difficulties, especially with the more problematic groups such as the Pisidia.

The stratigraphically critical species *Valvata goldfussiana* Wüst and *Nematurella runtoniana* (Reid) are well represented. The present material is almost identical to the extensive collections of these two species, largely from West Runton, held in the British Museum (Natural History). The shells of *Bithynia* are all referable to *Bithynia inflata*, extinct in Britain; however, the opercula found are more typical of those of the modern *Bithynia tentaculata* (Linné). This feature was also noted by Sparks (1963) in his studies of molluscs from the Cromer Forest Bed in East Anglia.

The identifications of all Pleistocene Succineidae must be regarded as tentative (Kerney 1971). While there is some variation in form, the Sugworth specimens are probably referable to the common holarctic *Oxyloma pfeifferi* (Rossmässler). The shells listed as *Vallonia* spp. are juveniles or apical fragments. *Vallonia excentrica* Sterki has not been identified in the mature specimens, but it may be present in the juveniles or fragments, in which it is not readily distinguished from *Vallonia pulchella* (Müller). There have been no finds of the southeast European taxon *Vallonia enniensis* Gredler, which is known from the Cromer Forest Bed and subsequent interglacials in Britain.

The identifications of distinct species of the slug *Deroceras* must be treated with caution since the morphology of their degenerate shells is known to be an unreliable guide to species. The relatively long, tubular shells of the Clausiliidae have proved especially vulnerable to river transport.

The more intact of the specimens examined are closely comparable with specimens attributed to *Clausilia pumilia* C. Pfeiffer, identified from the Cromer Forest Bed, that are held in the British Museum (Natural History). Examination of other apical fragments suggests that further taxa in the Clausiliidae are also present, but are not determinable with certainty.

The specimens of *Cepea* and *Unio* are similarly very fragmented; however, for the Unionidae, there are some excellently preserved valves that are referable to *Unio crassus* Phillipson. This species is extinct in Britain but still found in continental Europe. The *Anodonta* is represented by a small hinge fragment only. The variation in shell form of the specimens of *Pisidium henslowanum* (Sheppard) parallels that found in the species in the Hoxnian deposits at Swanscombe by Kerney (1971). Many valves are grossly thickened and on strict morphological grounds could be referred to *Pisidium supinum* Schmidt. However, at Sugworth, as at Swanscombe, the thickened and unthickened specimens appears to intergrade and no satisfactory separation can be made.

4. PROBLEMS OF INTERPRETATION

The reconstruction in broad outline and local detail of the environments represented by the molluscan assemblages necessitates consideration of two groups of factors:

(*a*) the particular depositional environment of this river eroding through Kimmeridge Clay;
(*b*) analysis of the present and past ecological tolerances of the taxa found.

First, riverine deposits may collect molluscan remains from a variety of habitats, several of which may not be aquatic. Molluscs may enter the river sediment from overhanging vegetation, from bank collapse, from soil and bank erosion and from the partially fluid, upstream, river bed deposits, as well as by the collection of shelly remains of those individuals from the living assemblage at the particular depositional environment. Opportunities for selective winnowing or deposition are many and complex, depending upon chance and upon the more identifiable factors associated with the river's flow régime, bed stability and lateral shifts. The ratio of shells to opercula of *Bithynia inflata* may aid interpretation. The thick, flat opercula are more prone to winnowing by running water than are the larger shells, and may be more resistant to destruction (Sparks 1961; Kerney 1971; Gilbertson & Hawkins 1978). However, care must be exercised in analysis since opercula are known to split, even while under microscope examination (Sparks 1961). Nevertheless, when opercula significantly outnumber preserved shells, it may indicate that relatively small molluscan remains have been introduced into the area as sediment.

TABLE 1.

Sugworth, sample D	0	10	30	50	70	90	100	110	130	150	170	190	200	210	230	250	270	290	300	310	330	350	370	390	400	410	430	450	470	total
Viviparus sp.	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Valvata cristata Müller	1	1	—	1	—	—	8	—	—	—	—	—	—	—	—	2	—	4	—	—	—	—	—	—	—	—	—	—	—	17
Valvata piscinalis (Müller)	43	227	120	204	27	18	172	24	111	60	15	109	62	8	13	16	25	37	4	3	6	1	1	—	—	—	—	—	—	1306
Valvata naticina Menke	5	15	15	4	—	—	—	1	4	—	?1	14	—	—	1	8	4	7	—	—	—	—	1	—	—	—	—	—	—	80
Valvata goldfussiana Wüst	—	14	3	10	—	—	6	1	15	11	1	14	14	—	—	1	1	—	6	—	1	2	—	—	—	—	—	—	—	100
Nematurella runtoniana (Reid)	—	4	—	2	—	—	—	—	—	3	—	4	1	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	17
Marstoniopsis scholtzi (Schmidt)	1	4	—	—	—	—	—	—	—	—	—	1	1	5	—	3	—	8	1	—	—	—	—	—	—	—	—	—	—	24
Bithynia inflata (Hansén)	3	10	2	13	—	—	38	1	31	1	1	5	12	1	3	4	1	2	2	—	—	—	—	—	—	—	—	—	—	130
Bithynia opercula	14	32	16	25	18	8	101	23	39	14	7	18	5	10	2	15	6	26	1	5	3	2	—	—	4	3	1	3	—	401
Carychium minimum Müller	1	—	—	?1	—	—	3	—	—	—	—	1	—	—	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	9
Carychium tridentatum (Risso)	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Lymnaea truncatula (Müller)	—	4	—	—	—	—	3	—	3	1	—	—	4	—	2	—	5	—	2	—	—	—	—	—	—	—	—	—	—	24
Lymnaea palustris (Müller)	—	—	—	—	—	—	—	—	?1	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Lymnaea stagnalis (Linné)	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Lymnaea peregra (Müller)	4	15	16	5	4	2	18	3	16	2	—	4	1	1	—	6	2	4	4	—	—	—	—	—	—	—	—	—	—	107
Planorbis planorbis (Linné)	—	1	1	—	—	—	3	1	—	—	—	1	—	1	—	—	2	10	—	—	—	—	—	—	—	—	—	—	—	20
Planorbis leucostoma (Millet)	—	—	—	1	—	—	3	—	—	—	—	—	1	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	7
Anisus vortex (Linné)	—	—	—	—	—	—	7	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	10
Bathyomphalus contortus (Linné)	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	5
Gyraulus laevis (Alder)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1
Gyraulus albus (Müller)	8	63	32	53	6	8	171	1	22	12	2	17	12	1	5	7	22	18	8	1	2	—	—	—	—	—	—	—	—	471
Armiger crista (Linné)	10	25	9	29	—	—	10	1	1	1	—	3	4	12	17	14	7	29	4	2	—	—	—	—	—	—	—	—	—	178
Hippeutis complanata (Linné)	—	2	—	—	2	—	7	—	—	—	—	—	—	—	—	—	—	5	1	—	—	—	—	—	—	—	—	—	—	17
Ancylus fluviatilis (Linné)	63	216	93	185	38	8	107	24	200	166	1	117	99	53	62	82	67	58	24	35	15	—	3	1	1	—	10	—	—	1728
Acroloxus lacustris (Linné)	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	1	—	1	—	—	—	—	—	—	—	—	4
Oxyloma cf. *pfeifferi* (Rossmässler)	—	?1	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	4
Succinea spp.	2	6	—	2	6	—	2	1	2	5	2	1	2	—	—	3	1	—	1	—	—	—	—	—	—	—	—	—	—	36
Cochlicopa lubrica (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
Vertigo antivertigo (Draparnaud)	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Vertigo augustior Jeffreys	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1

Sugworth, sample D	0	10	30	50	70	90	100	110	130	150	170	190	200	210	230	250	270	290	300	310	330	350	370	390	400	410	430	450	470	total
Vertigo spp.	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Vallonia costata (Müller)	—	—	4	1	—	—	—	—	2	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12
Vallonia pulchella (Müller)	3	4	—	3	4	—	8	3	2	2	—	3	5	3	2	4	—	—	4	2	—	—	—	—	—	—	1	—	—	53
Vallonia spp.	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Discus rotundatus (Müller)	1	1	—	1	1	1	—	—	—	1	—	—	2	4	—	1	1	—	—	1	—	2	—	—	—	—	—	—	—	17
Vitrea sp.	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Aegopinella spp.	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Zonitoides nitidus (Müller)	—	1	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Limax sp.	—	—	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Deroceras laeve (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	?1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Deroceras agreste (Linné)	—	—	—	—	—	—	—	—	—	?1	—	—	—	—	—	—	2	—	—	—	—	1	1	—	—	—	—	—	—	5
Deroceras reticulatum (Müller)	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	1	—	1	—	5
Clausilia pumila C. Pfeiffer	—	?2	?2	—	—	—	—	—	—	?2	—	?2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	?8
Clausilia spp.	—	3	3	6	—	1	1	2	3	2	1	4	2	1	1	—	1	1	—	—	—	—	—	—	—	—	1	—	—	33
Trichia hispida (Linné)	3	4	2	?1	—	—	7	—	1	6	—	2	1	—	1	3	1	—	—	—	—	—	—	—	—	—	—	—	—	32
Cepea spp.	—	1	—	1	—	—	—	—	1	1	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	8
Unio crassus Philipsson	—	—	—	1	—	—	—	—	—	1	1	—	2	—	—	—	2	—	2	—	—	—	—	—	—	—	—	—	—	9
Unio sp.	1	1	—	1	1	—	—	—	2	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Anodonta sp.	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Sphaerium corneum (Linné)	2	2	2	2	1	1	2	—	3	1	—	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19
Sphaerium lacustre (Müller)	—	—	—	—	—	—	—	—	—	1	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Pisidium amnicum (Müller)	2	—	2	2	—	2	2	—	3	1	—	3	2	—	—	2	—	—	2	—	—	—	—	—	—	—	—	—	—	23
Pisidium clessini Neumayr	2	8	4	5	2	1	5	2	6	3	3	7	7	1	1	1	2	3	1	2	3	—	—	1	—	—	1	—	—	71
Pisidium casertanum (Poli)	2	—	—	1	—	—	1	—	—	—	?1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	6
Pisidium obtusale (Lamarck)	2	—	—	2	—	—	—	—	—	—	—	—	1	1	—	—	1	3	—	—	—	—	—	—	—	—	1	—	—	11
Pisidium milium Held	—	—	—	—	—	1	—	—	—	—	1	—	—	—	1	—	1	—	—	—	1	—	—	—	—	—	—	—	—	5
Pisidium subtruncatum Malm	9	5	1	2	1	—	4	—	2	—	—	—	2	1	—	1	3	1	1	—	?1	—	—	—	1	—	1	—	—	36
Pisidium henslowanum (Sheppard)	74	321	111	184	52	14	10	21	63	33	7	55	64	45	73	67	76	253	24	32	54	3	3	1	5	2	41	2	—	1690
Pisidium nitidum Jenyns	33	182	51	46	34	7	14	8	21	6	10	95	57	25	46	49	27	97	7	12	7	1	3	—	1	—	4	—	—	843
Pisidium pulchellum Jenyns	—	?1	—	—	?1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Pisidium moitessierianum Paladilhe	1	7	1	—	—	—	2	—	—	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14
total	276	1154	474	772	181	64	621	94	519	325	47	470	365	173	234	281	268	547	105	91	91	13	12	3	8	3	61	3	0	7255

Similarly, very low ratios of opercula to shells suggest loss of small molluscan remains downstream.

The sediments themselves present problems. They are faulted and reveal evidence of lateral shifts in the position(s) of the major channel(s). In the thick sequence of relatively homogenous, reworked Kimmeridge Clay, minor breaks in the sequence, due to faulting or to fluctuations in the river bed erosion/sedimentation rates, are difficult to satisfactorily identify. Consequently, individual samples may integrate deposits of slightly different character or deposits originally separated by a hiatus in the sequence.

Analysis of the frequency curves for several species through profile D, e.g. *Ancylus fluviatilis* in figure 1, indicates several breaks of unknown duration in the sequence. These were sometimes followed by periods of local stability, or, on other occasions, by progressive environmental change. Similarly, the ratios of *Bithynia* opercula to shells demonstrate large fluctuations which appear to be related to variations in shell input and loss. This variability in the pattern of shell derivation, transportation and loss indicates we must expect considerable variability in the faunal content of samples within and between profiles, and that much of this variability is attributable to essentially random processes. The most noticeable horizon present was a layer of *in situ* valves of *Unio crassus* at 1.9–2.0 m (D190–D200), which indicated a temporary phase of river bed stability. Interestingly, it is characterized by the highest ratio of *Bithynia* shells to opercula, suggesting net loss of smaller molluscan remains, and by the highest representation of terrestrial species. These results are found, to a reduced extent, at sample D300, and serve to re-emphasize the importance of complex interactions between erosion and deposition in determining the nature of the assemblages found. However, the expected relation between evidence of the most rapid, shallow flow (from the maximum representation of *Ancylus*) and the greatest representation of terrestrial gastropods does not hold in the sequence. This is presumably the result of a tendency of the terrestrial gastropods either to float or to fragment relatively rapidly.

Secondly, many molluscan taxa tolerate a much wider range of environmental conditions than those held characteristic of their 'normal' or optimal conditions. For example, Kerney (1971) has shown that while *Vallonia costata* (Müller) is commonly regarded as a typical dry grassland snail, in the Hoxnian interglacial conditions at Swanscombe it appears to have been part of a light scrubland community. Additionally, at Sugworth, one is sufficiently far back into the Pleistocene to seriously question whether the physiological tolerances of the Sugworth species might be significantly different from their descendants.

Comparisons between the mutual behaviour of the still extant taxa present through the sequence indicate that their populations fluctuate with respect to each other in a manner that is acceptable for palaeoecological interpretation, since it is predictable from knowledge of their contemporary ecological requirements. For example, variations in the relative abundance of the most important species, *Ancylus fluviatilis* and *Valvata piscinalis*, and of *Gyraulus albus* Müller and the smaller lamellibranchs support this crucial methodological point.

Ancylus fluviatilis favours fast flowing rivers, streams or the wave zones of lake shores. *Valvata piscinalis* is more of a lake species, occurring in greatest number in quieter, deeper water, at 1.5 to 2.0 m below the surface (Ökland 1964). At Sugworth this inverse relation holds in profile D. The highest frequencies of *Ancylus fluviatilis* are associated with comparatively low frequencies of *Valvata piscinalis*, indicating the presence of a faster flowing, shallower water riverine facies, while quieter, deeper water facies are marked by higher percentages of *Valvata piscinalis* with low frequencies of *Ancylus fluviatilis*.

Thirdly, in samples D0–D50, D90–D120, and D290–D310 there are population fluctuations between the most abundant of the filter feeding lamellibranchs, *Pisidium henslowanum* (Sheppard) and *Pisidium nitidum* Jenyns, which may be hampered by rich aquatic plant life, and the gastropod *Gyraulus albus*, which would have been better suited to such plant rich habitats. In samples D90–D120 and D290–D310, fluctuations between these three species suggest that aquatic plant growth especially fluorished when flow rate at this location was increasing and river depth decreasing.

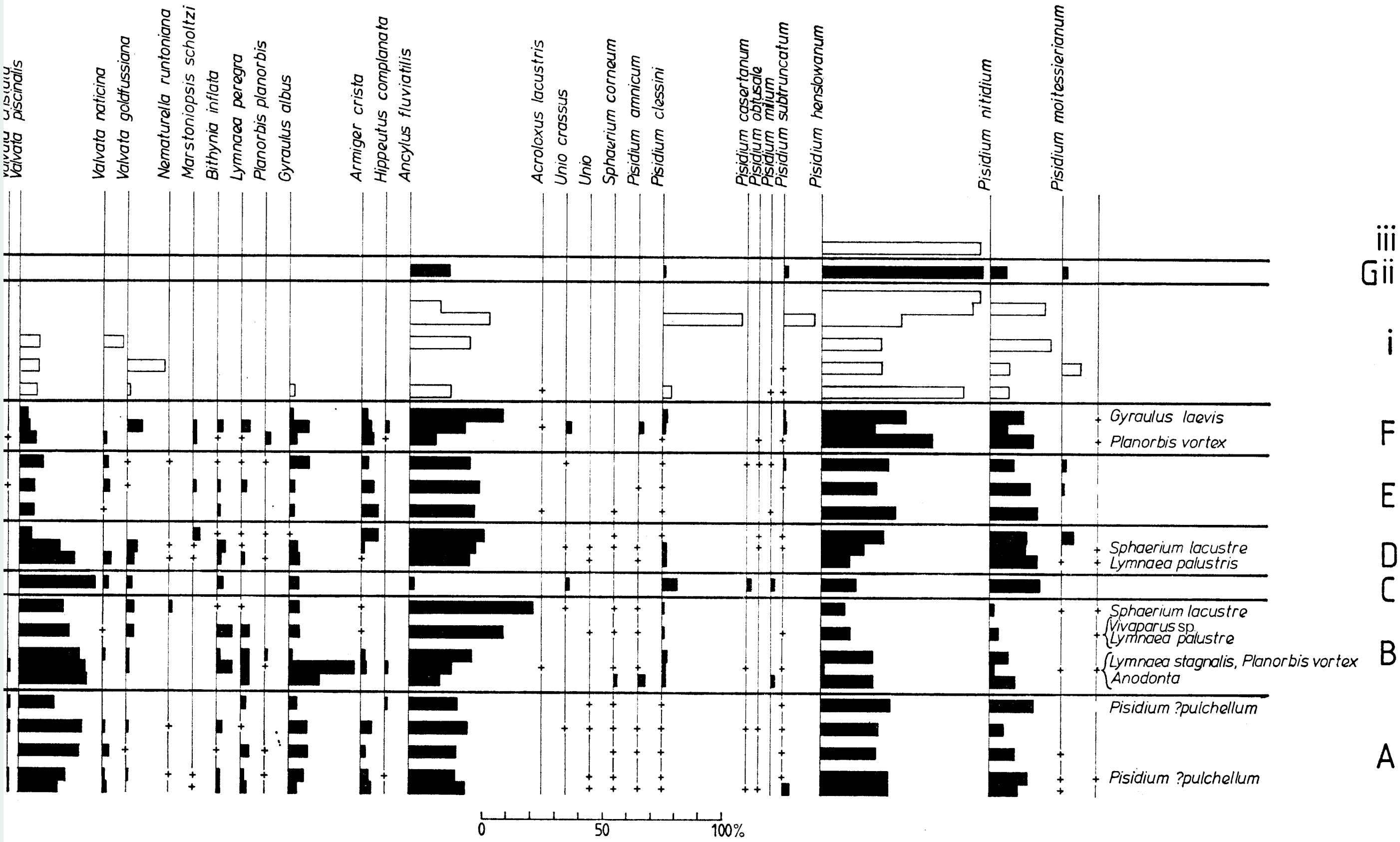

FIGURE 1. Freshwater Mollusca as percentage of total Mollusca: + represents less than 1 %. White bars are at levels where the total number of specimens is very small.

The ecological requirements of those species now extinct in the British Isles or totally extinct can be generally inferred from a comparison of their behaviour in assemblages with those species more certainly known, bearing in mind the many problems of transportation, destruction etc. *Valvata naticina* and *Valvata goldfussiana* are present in low but consistent percentages, and were probably associated with similar habitats to *Valvata piscinalis*. *Bithynia inflata* behaves in a manner to be expected from the contemporary *Bithynia tentaculata*, essentially similar to *Valvata piscinalis*. *Marstoniopsis scholtzi* has a fairly close parallel in *Armiger crista*, which would have favoured plant rich, fringing aquatic habitats. The section revealed that *Unio crassus* was most abundant with stable river bed conditions and rapid flow, while the abundance of *Pisidium clessini* follows trends in the populations of *Ancylus fluviatilis*, suggesting a preference for rapid flow. Frequencies of *Nematurella* are too low for satisfactory interpretation.

5. ENVIRONMENTAL RECONSTRUCTION

(*a*) *Local ecological changes*

All samples with an adequate number of specimens for satisfactory palaeoecological analysis (D0–330; D430) indicate the former presence of a large, well oxygenated, calcareous river in a temperate climate. The much less abundant marsh and terrestrial fauna suggest that the river was fringed with marsh in a tree covered interglacial landscape. The abundance of riverine, aquatic plant life appears to have varied with flow rate and depth over this location. No major regional environmental changes are apparent from the composition of the molluscan faunas.

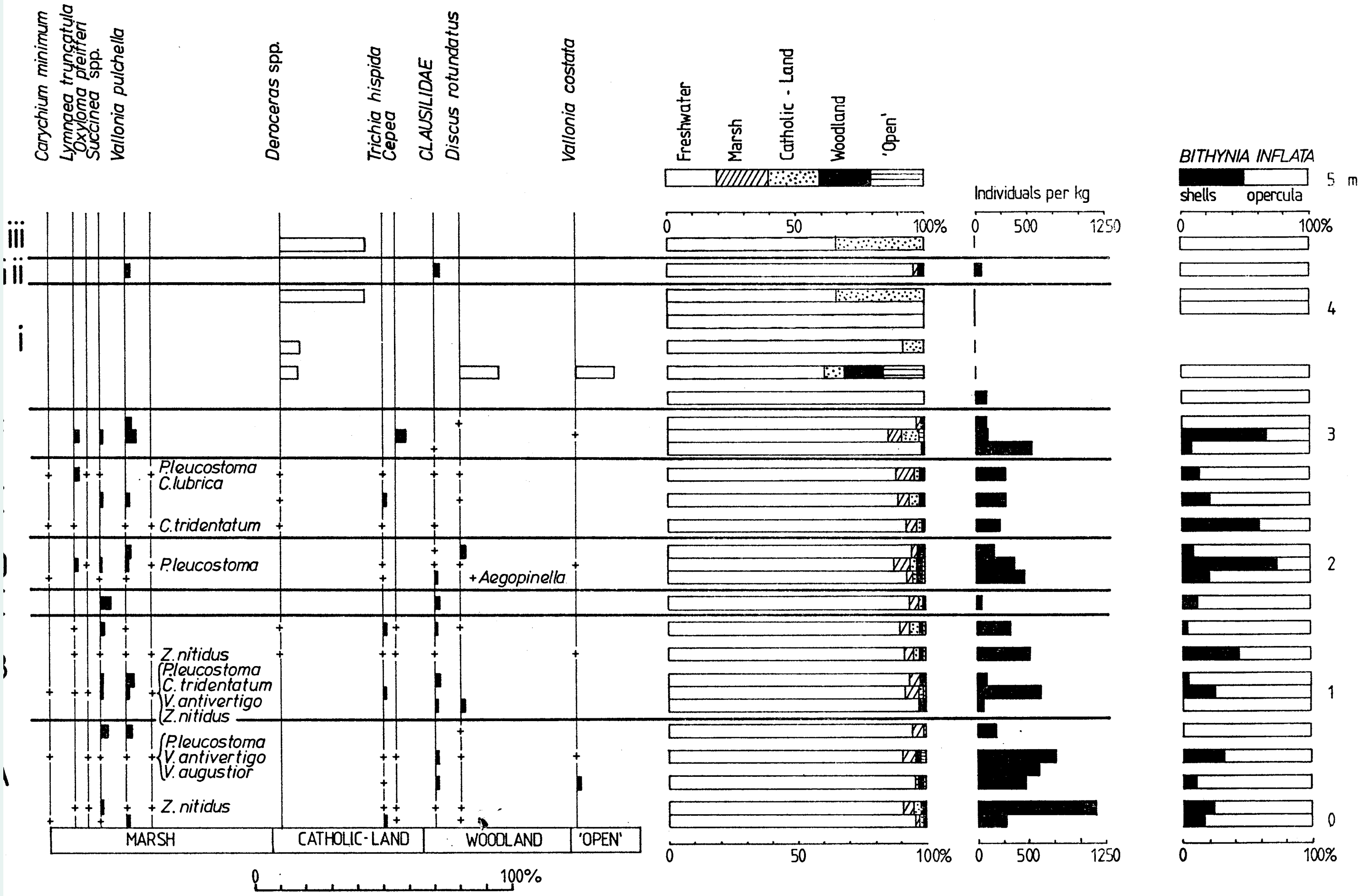

FIGURE 2. Land Mollusca as percentage of total Mollusca.

It is useful to consider the faunal assemblages in terms of Sparks's (1961) broadly defined molluscan groupings. The great majority of the specimens are freshwater and belong to 'moving water group' of rivers, streams and lakes. *Pisidium moitessierianum* Paladilhe is particularly characteristic of fully temperate climates and large rivers (Sparks & West 1959; Kerney 1971). Other members of this grouping include *Valvata piscinalis*, *Lymnaea stagnalis* (Linné), *Ancylus fluviatilis*, *Anodonta* sp. and the Pisidia group, *Pisidium amnicum* (Müller), *Pisidium clessini*, *Pisidium henslowanum*, and *Pisidium nitidum*.

Individuals belonging to other general groupings are much less abundant. The 'ditch' group, nowadays favouring clean, shallow, plant rich habitats is represented by *Valvata cristata* Müller, *Planorbis planorbis* (Linné), *Planorbis vortex* (Linné) and *Acroloxus lacustris* (Linné). The freshwater catholic group, with their tolerance of all but the most unfavourable 'slum' habitats, include *Lymnaea palustris* (Müller), *Lymnaea peregra* (Müller), *Armiger crista* (Linné), *Gyraulus albus*, *Bathyomphalus contortus* (Linné), *Hippeutus complanata* (Linné), *Sphaerium corneum* (Linné) and *Pisidium milium* Held. The slum group probably occupied small, ephemeral pools subject to seasonal drought on the floodplain. They are very spasmodically represented by very low numbers of *Lymnaea truncatula* (Müller), *Planorbis leucostoma* (Millet), *Sphaerium lacustre* (Müller), *Pisidium casertanum* (Poli) and *Pisidium obtusale* (Lamarck).

TABLE 2. LOCAL MOLLUSCAN ECOLOGICAL ASSEMBLAGE ZONES RECOGNIZED IN PROFILE D, SUGWORTH

Zone Giv. *Pisidium henslowanum*, *Deroceras* spp. (uncertain)
Zone Giii. *Ancylus fluviatilis*, *Pisidium henslowanum* (flowing water)
Zone Gii. *Ancylus fluviatilis*, *Pisidium henslowanum*, and *Deroceras* spp. (uncertain)
Zone Gi. *Valvata piscinalis*, *Pisidium henslowanum* and *Ancylus fluviatilis* (uncertain)
Zone F. *Ancylus fluviatilis* increasingly dominant, dominant *Pisidium henslowanum* (flowing water)
Zone E. *Ancylus fluviatilis* and *Pisium henslowanum* codominant (flowing water) Hiatus
Zone D. *Ancylus fluviatilis*, *Pisidium henslowanum* rise to dominance, *Valvata piscinalis* declines, relative bed stability (shallowing, flowing water), minor derivation, notable horizon of *Unio crassus*, terrestrial species most abundant
Zone C. *Valvata piscinalis* dominant, *Ancylus fluviatilis* rare (deeper, quieter water)
Zone B. *Ancylus fluviatilis* increasingly dominant (faster flowing, shallower water)
Zone A. *Valvata piscinalis*, *Ancylus fluviatilis*, *Pisidium henslowanum* equally abundant; relative faunal stability (moderately deep but flowing water)

Terrestrial species are poorly represented in the assemblages. This is probably as a result of effective distance of the depositional environment from terrestrial habitats, rather than any lack of terrestrial habitat. Species favouring marsh habitats are most common and include *Carychium minimum* Müller, all the Succineids, *Cochlicopa lubrica* (Müller), the *Vertigo* spp. and *Zonitoides nitidus* (Müller). Taxa of a wider ecological tolerance constitute the terrestrial 'catholic' group, which comprises *Deroceras* spp., *Trichia hispida* (Linné) and the fragmented Cepeas. Indications of woodland casting shade are given by the consistent, if low numbers, of *Discus rotundatus* and the Clausiliidae. The notable dry land species present is *Vallonia costata*, which may have been a member of a light wood or scrub community.

The changing proportions of the principal ecological groupings present through profile D are shown in figure 2. In this sequence, the faunas indicate the dominance of quieter, deeper water, or of shallower, faster flowing facies. There is a consistent, if numerically small, indication of fringing marsh and woodland bordering the river. There are no indications of any open or bleak landscapes.

Consideration of the ecological requirements of the principal riverine species present, *Ancylus fluviatilis*, *Valvata piscinalis* and *Pisidium henslowanum*, enables the profile to be divided into a series of purely local, molluscan, ecological assemblage zones, which correspond to local facies changes experienced at the site. These may be separated by local hiatuses in the sequence, usually identified through sudden changes in the percentage abundance of various elements in the assemblages. These assemblage zones are somewhat arbitrarily identified, some on the basis of a direction of ecological change, i.e. a gradual shift towards a deeper, quieter water facies, while other zones represent comparatively stable environmental conditions. The zonation is almost totally explicable in terms of change of river discharge and depth, associated with lateral shifts of the major channel(s) about profile D (table 2). It does not necessarily imply variations in total river discharge.

The upper samples from D350–D470, with the exception of D430, cannot be satisfactorily interpreted. The molluscan assemblage of D430 suggests temperate, riverine conditions, with fringing marsh and woodland, as typically occurred below D350. The other samples are principally composed of *Ancylus fluviatilis*, *Pisidium henslowanum* and *Pisidium nitidum*, with occasional remnants of *Deroceras* spp., which can assume very large percentages in these numerically small samples. Differential destruction is not an adequate explanation for many notable absentees, since the relatively fragile *Pisidia* appear to have survived. Curiously, the trend towards higher percentage representations of marsh at the expense of riverine species, apparent in the upper part of the sequence, is associated with dramatically lower species representations. These upper faunas might be derived from the more readily winnowable shells from earlier riverine deposits. An alternative explanation of the notable lack of individuals per sample and of the species diversity might be made in terms of considerably increased siltation rates, involving largely sterile sediment.

(*b*) *Climate*

There is no evidence for major climatic change from the study of the molluscan remains in the profile. Many of the taxa present are climatically very tolerant. No species associated with cold Pleistocene environments or forest recession were noted. There are a number of species present that are of temperate, southern affinities, *Vertigo augustior*, *Discus rotundatus*, *Pisidium moitessierianum*, and several, *Valvata naticina*, *Clausilia*(?)*pumila* and *Unio crassus*, with central or eastern European affinities, which might suggest a certain element of climatic continentality compared to the present day Oxfordshire. However, much more information is needed on the factors, other than climate, influencing dispersal during the Upper Pleistocene, before continentality can be inferred from their presence at Sugworth.

It is possible that a gradual climatic deterioration is one of the underlying causes of two of the most notable aspects of figures 1 and 2: the gradual overall decline in population numbers per sample, which culminates in the samples D350 and above, and the faunal impoverishment above this level. Possible changes in siltation rate may be linked to this background change. Nevertheless, if such deterioration did occur, its extent at this stage was relatively minor, as specimens of the thermophilous lamellibranch *Pisidium moitessierianum* and woodland indicators still occur in sample D430.

6. DATING

The known stratigraphic ranges of freshwater, non-marine molluscan taxa thought significant for dating interglacial deposits in southern England have recently been reviewed by Kerney (1977, tab. 3.1). Kerney points out that, while such faunas are moderately well known from the Hoxnian and Ipswichian interglacials, in the Cromerian they are principally known from only two sites in East Anglia, at West Runton (Zeuner 1959; Sparks 1963) and at Little Oakley (Kerney 1959). Information on pre-Cromerian interglacials is limited to the finds of early workers such as Reid (1890), which are not, as yet, related to any pollen zonation.

Nevertheless, with these important limitations in mind, the balance of available evidence still indicates that the Sugworth deposits should be assigned to the Cromerian interglacial. *Nematurella runtoniana* is only known from the Cromerian interglacial, while *Valvata goldfussiana* is known from the Cromerian interglacial, from the pre-Cromerian Weybourne Crag (Reid 1890; Zeuner 1959) and from Tegelen of the Netherlands (Freudenthal *et al.* 1976), indicating a *minimum* age of Cromerian.

These two taxa are unknown from the later interglacials. A *maximum* age of Cromerian is also suggested by the presence at Sugworth of the following taxa, which have not as yet been identified in deposits older than Cromerian: *Valvata naticina*, *Bithynia inflata*, *Marstoniopsis scholtzi* and *Unio crassus*.

The presence of thermophilous species, the absence of taxa associated with climatically 'cold' conditions or with treeless landscapes, coupled with the general richness of the fauna, indicate that the fauna does not belong to Zones CrI or CrIV of that interglacial. The general decline in the number of species per sample and in species numbers per sample, and the possibility of an ultimately climatic cause, indicate that the deposit post-dates any climatic optimum in the Cromerian interglacial and is best attributed to later phases of the temperate interglacial substage Cromerian Zone CrIII, probably Zone CrIIIb.

Kerney (1977) has pointed out certain parallels between the Cromerian and Hoxnian interglacials. The present molluscan data may indicate that maximum species diversity in both interglacials was not attained until substages Zones HoIII and CrIII, respectively. In the Hoxnian interglacial, maximum species diversity is related to the relatively late arrival of the species of central and southern European affinities (Kerney 1971), a point originally observed by Kennard (1942*a*, *b*). Kennard suggested that these data provided evidence for the relatively late linkage of the Thames and Rhine river systems. Unfortunately, currently available stratigraphic and palaeobiogeographic data are insufficient to pursue these concepts further.

7. Conclusions

The riverine deposits recently exposed at Sugworth, near Abingdon, Oxfordshire, present a complex aggradation of a large, well oxygenated, calcareous river, a proto-Thames, fringed with marsh and flowing through a well wooded landscape in a fully temperate climate. The molluscan evidence indicates that the deposit collected during the Cromerian interglacial, probably substage CrIIIb.

Lateral shifts in the river channel have caused a series of minor facies variations to be present in the profile studied. These variations principally reflect changes in water depth and flow rate. The molluscan assemblages indicate the presence in the profile of local depositional hiatuses and of derivation, transportation and winnowing of the fauna. A general, if poorly defined, fall in specimens per sample and in species per sample through the deposit are not fully understood, but may reflect early stages in a climatic deterioration.

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