

The Molluscan Fauna of the Middle Pleistocene Interglacial Deposits at Little Oakley, Essex, and Its Environmental and Stratigraphical Implications

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THE MOLLUSCAN FAUNA OF THE MIDDLE PLEISTOCENE INTERGLACIAL DEPOSITS AT LITTLE OAKLEY, ESSEX, AND ITS ENVIRONMENTAL AND STRATIGRAPHICAL IMPLICATIONS

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[Plate 1]

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The molluscan fauna of the interglacial channel deposits at Little Oakley, Essex, U.K., is described. Detailed faunal analyses are presented from three boreholes located at different sites across the palaeochannel. Large-bulk samples (*ca.* 1.5 t), obtained from mechanically excavated pits at one of these sites, have yielded a few additional species and enabled the resolution of several taxonomic problems that result from the fragmentary nature of some of the borehole specimens. The fauna as a whole is fully temperate throughout and indicates the presence of a large, well-oxygenated river, thought to be the ancestral Thames. Mollusca from fringing marsh habitats are also present, together with xerophilous species from dry calcareous

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grassland. Woodland species are virtually absent, suggesting that the river here had a wide, open floodplain. The fauna indicates a Cromerian age and includes the extinct prosobranch *Tanousia* (= *Nematurella* auctt.), which is unknown anywhere in northwest Europe after this interglacial stage. Other noteworthy species include *Sphaerium solidum* (only British Pleistocene record), *Belgrandia marginata*, *Helicella itala* and cf. *Cernuella virgata* (earliest British Pleistocene records), *Trochoidea geyeri* and *Truncatellina cylindrica* (only British Cromerian records). There are significant differences between the faunas at each of the sampling sites, which are thought to reflect mid-channel and marginal facies. This interpretation is in complete accord with the sedimentology and gives strong support for the local palaeogeographical reconstructions. There are also some biostratigraphical changes: *Tanousia* declines upwards and is totally absent in the upper levels of one borehole that is thought to extend later into the interglacial. The significance of this disappearance as caused by either regional (climatic) or local factors is unclear.

1. INTRODUCTION

The existence of fossiliferous deposits at Little Oakley, Essex, U.K., has been known for nearly 50 years (Warren 1940). A. S. Kennard visited the site with S. H. Warren in 1939 and prepared a preliminary report on the Mollusca (Kennard, unpublished manuscript), which had a close affinity to the fauna from the 'Cromer Forest Bed' of West Runton, Norfolk. Kennard also supplied preliminary notes on the Mollusca to Day Kimball and an incomplete faunal list is given in Zeuner (1945, pp. 269–273). Kerney (1959), in an unpublished thesis, re-examined Kennard's material in the British Museum (Natural History) and gave a revised list of Mollusca, but no comprehensive account of the fauna has yet been published.

2. METHODS

The fossiliferous deposit was investigated with a systematic series of boreholes and a few, specially commissioned, mechanically excavated pits. The borehole samples were collected by means of a wing-auger, yielding samples of 10 cm diameter, and these were analysed in detail from three locations (Bridgland *et al.* 1990, figure 1). Samples were dried and after weighing were disaggregated in water. Floating snails and other organic remains were repeatedly decanted and retained in a British standard mesh (BS) no. 60 (0.25 mm) sieve. The remaining sediment was then poured into a second 0.25 mm sieve, washed thoroughly and dried. The dried residues were then passed through a BS no. 30 (0.5 mm) sieve, the fine fractions (less than 0.5 mm) being kept solely for ostracod analyses (Robinson 1990) whereas the Mollusca were picked and counted only from the coarse fraction (greater than 0.5 mm). The standard precautions were taken to avoid counting broken specimens more than once (i.e. by counting only apices or hinge fragments). The results are presented in tables 1 and 2 and plotted graphically on figures 1 and 2, where each species is shown as a percentage of the total Mollusca. Crosses indicate single shells. For the bivalve genera *Sphaerium* and *Pisidium*, the numbers of individual valves were halved before calculation. For *Bithynia*, separate totals are listed for the number of shells and opercula, although the larger value (whether shells or opercula) has been plotted on figure 1 and 2. Where possible, the nomenclature follows Kerney (1976) and Waldén (1976) for the freshwater and land species respectively but for certain extra-British or extinct taxa some familiar names have been substituted for those currently (and

PLEISTOCENE MOLLUSCA AT LITTLE OAKLEY

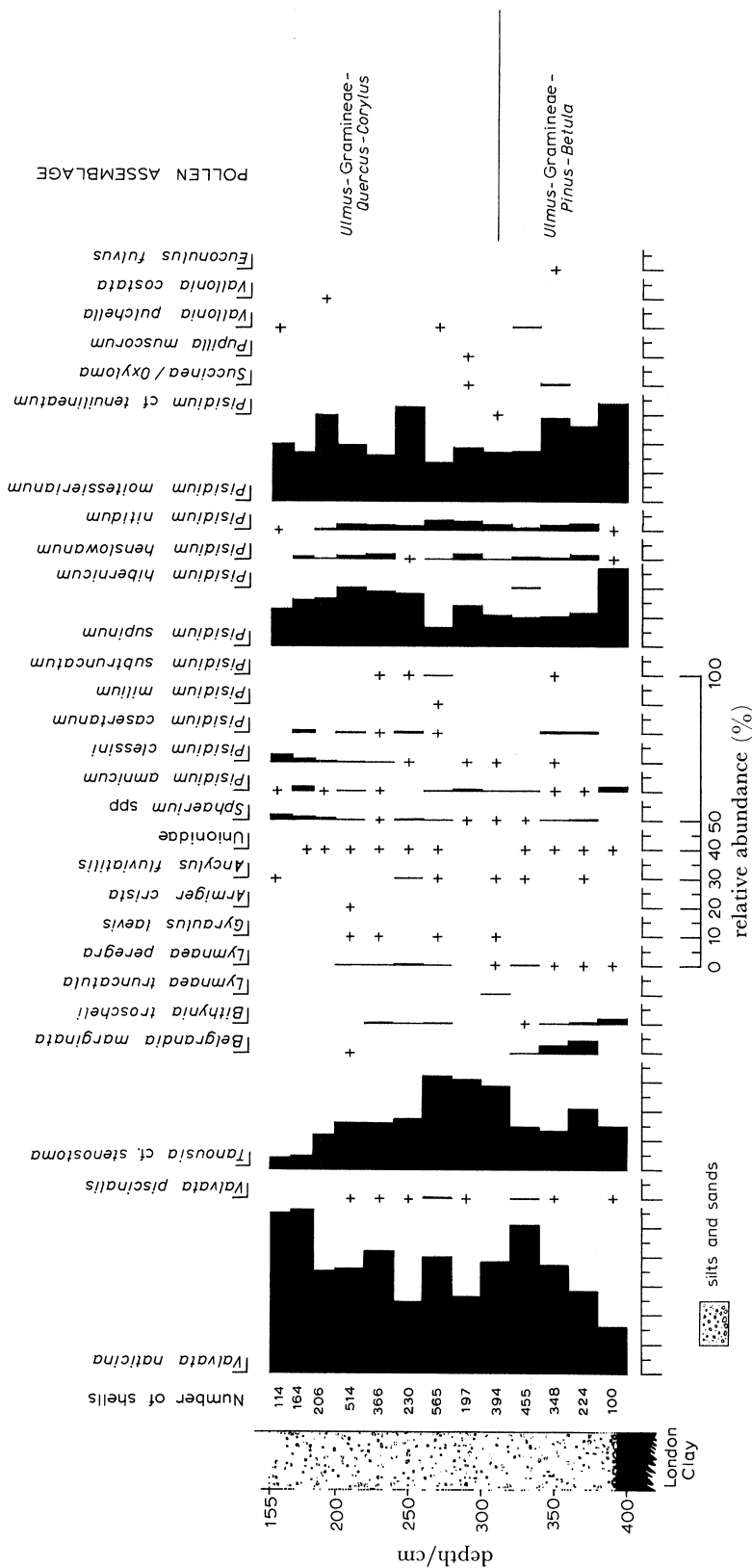


FIGURE 1. Mollusc diagram from borehole LOA.

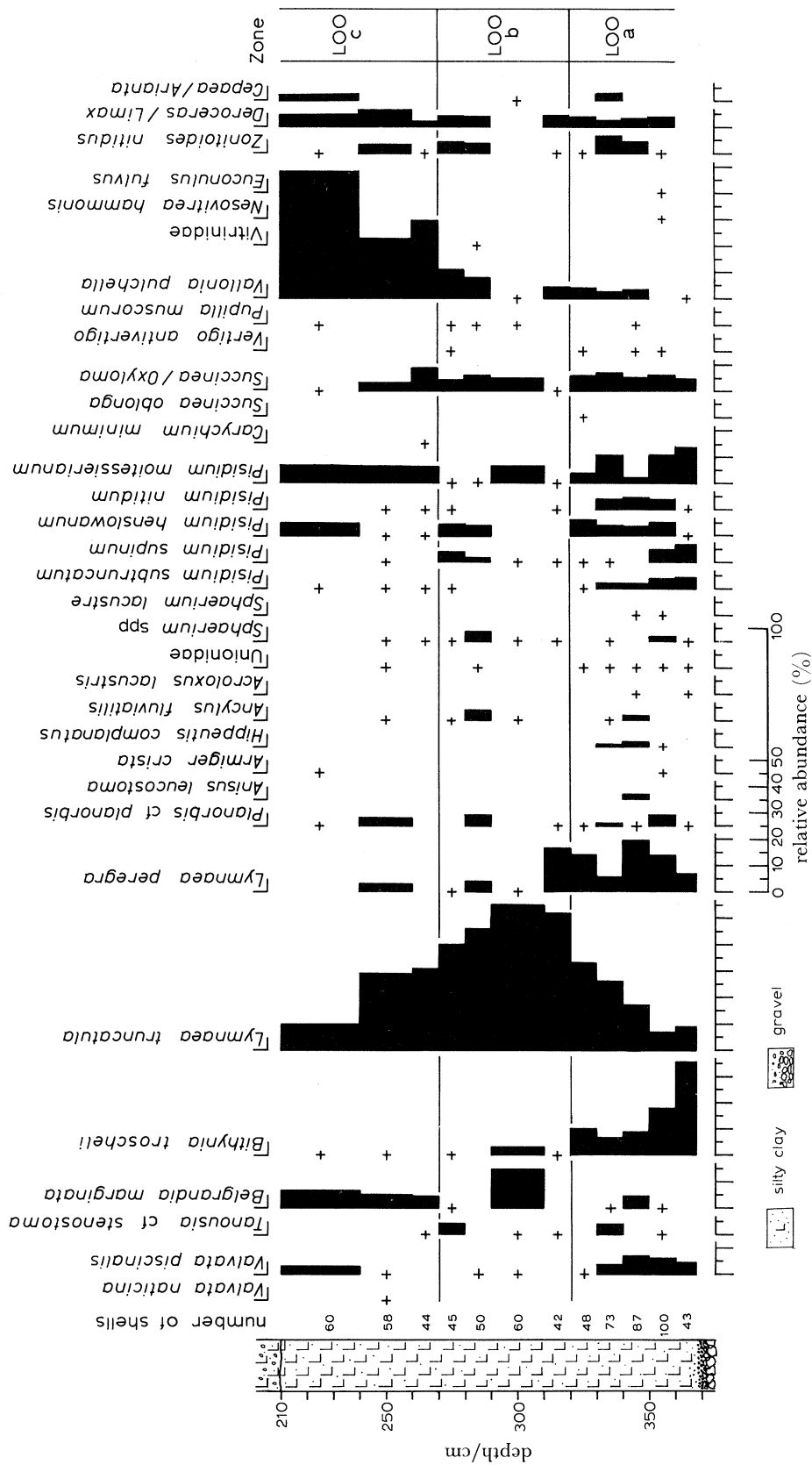


FIGURE 2. Mollusc diagram from borehole LOO.

TABLE 2. MOLLUSCA FROM BOREHOLE LOO

depth (cm)	360-368	350-360	340-350	330-340	320-330	310-320	300-310	290-300	280-290	270-280	260-270	250-260	240-250	230-240	210-230
dry mass of sample (g)	425	475	410	500	500	500	500	500	460	500	500	500	500	500	460
Freshwater species															
<i>Valvata piscinalis</i> (Müller)	2	6	6	3	1	—	—	?1	1	—	—	—	—	?1	1
<i>V. naticina</i> Menke	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Belgrandia marginata</i> (Michaud)	—	1	4	1	—	—	7	2	—	1	2	2	1	3	1
<i>Tanaisia</i> cf. <i>stenostoma</i> (Nordmann)	—	1	—	3	—	—	?1	—	—	2	1	—	—	—	—
<i>Bithynia troscheli</i> (Paasch); shells	4	18	3	5	1	1	1	?1	—	—	—	1	—	1	—
<i>Bithynia opercula</i>	14	18	8	2	5	—	—	—	—	1	—	1	—	—	—
<i>Lymnaea truncatula</i> (Müller)	4	7	15	19	16	22	23	10	23	18	14	5	12	3	3
<i>L. peregra</i> (Müller)	3	14	17	4	7	7	1	—	2	1	—	—	2	—	—
<i>Planorbis</i> cf. <i>planorbis</i> (L.)	1	4	1	1	1	1	—	—	2	—	—	1	?1	—	?1
<i>Anisus leucostoma</i> (Millet)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Armiger crista</i> (L.)	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
<i>Hipppeutis complanatus</i> (L.)	—	1	2	1	—	—	—	—	—	—	—	—	—	—	—
<i>Ancylus fluviatilis</i> Müller	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
<i>Acroloxus lacustris</i> (L.)	1	—	1	—	—	—	—	1	2	1	—	—	—	—	—
Unionidae	+	+	+	+	+	—	—	—	+	—	—	—	—	—	—
<i>Sphaerium lacustre</i> (Müller)	—	1	2	—	—	—	—	—	—	—	—	—	+	—	—
<i>Sphaerium</i> spp.	1	3	—	2	—	—	—	—	3	1	1	—	—	—	—
<i>Psidium subtruncatum</i> Malm	4	8	4	3	2	—	—	1	—	1	1	—	?2	1	—
<i>P. supinum</i> Schmidt	5	9	—	?2	1	2	—	—	1	3	4	2	—	—	—
<i>P. henslowianum</i> (Sheppard)	1	9	5	6	5	—	—	—	3	4	2	—	2	1	3
<i>P. nitidum</i> Jenyns	2	7	7	6	—	1	—	—	—	2	1	1	—	—	—
<i>P. moitessierianum</i> Paladilhe	12	22	4	16	3	1	1	6	1	2	5	1	6	2	5
Terrestrial species															
<i>Carychium minimum</i> Müller	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Succinea oblonga</i> Draparnaud	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
<i>Succinea/Oxyloma</i>	2	6	5	5	3	1	1	2	3	2	4	1	1	—	1
<i>Vertigo antivertigo</i> (Draparnaud)	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Vertigo</i> spp. (probably <i>antivertigo</i>)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pupilla muscorum</i> (L.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Valonia pulchella</i> (Müller)	—	—	—	—	—	—	1	—	1	1	—	—	—	1	—
<i>V. pulchella/excentrica</i>	1	—	—	—	—	—	—	—	1	1	1	1	1	3	—
cf. <i>Vitriobrachium breve</i> (Férussac)	—	—	—	—	—	—	—	1	3	4	12	4	7	12	14
<i>Nesovitretea hammonis</i> (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Zonitoides nitidus</i> (Müller)	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Deroceras/Limax</i>	—	4	2	2	2	1	—	—	2	2	?1	2	—	1	—
<i>Euconulus fulvus</i> agg.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cepaea/Arianta</i>	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1

correctly) used elsewhere in Europe. All the material has been lodged with The University Museum of Zoology, Downing Street, Cambridge.

3. PROBLEMS OF IDENTIFICATION

The preservation of shells was moderately good, although a fair proportion of the bivalves were badly worn. The following points should be noted as regards identification.

Succineidae

All specific determinations should be regarded as tentative.

Larger bivalves

Fragments of larger bivalves belonging to the family Unionidae were easily detected by their nacreous lustre but were impossible to identify to species level. However, complete specimens, some with united valves, were recovered from the excavated pits and show that at least three species are represented. These are discussed under §5 below.

Pisidium henslowanum

Many specimens are grossly thickened and are referable to *P. supinum*, usually regarded as a distinct species. However, the thickened and unthickened forms appear to intergrade and juveniles are impossible to separate. The totals given should therefore be regarded as approximations. Dr M. P. Kerney has kindly checked all my determinations of *Pisidium*.

Cepaea/Arianta

With only one exception, only apical fragments were recovered, so it was impossible to improve upon this identification.

4. ANALYSIS OF FAUNAL CHANGES THROUGH THE PROFILES

The changes in frequency of certain species through the profiles are described below. Full geological descriptions are given in Bridgland *et al.* (1990), whereas the borehole and section logs are lodged with the British Library.

(a) Borehole LOA

This borehole was located near the right-angled bend in Harwich Road, just north of Foulton Hall (TM 22332948). The sediment was a coarse-medium silty sand that was shelly throughout.

The molluscan fauna (figure 1) is dominated throughout by four main species, the prosobranchs *Valvata naticina* and *Tanousia* cf. *stenostoma* and the bivalves *Pisidium supinum* and *P. moitessierianum*. Bivalves in general are abundant, with up to eleven species of *Pisidium* alone. Gastropods, other than the two co-dominant species, are not well represented. The fauna is that of a large, calcareous, well-oxygenated river.

There are no major biostratigraphical changes except that the extinct prosobranch *Tanousia* cf. *stenostoma* declines from its maximum values of ca. 30% (between 260 and 320 cm) to values of less than 5% in the uppermost samples. There is no doubt that this decline is 'real' and not

a statistical artefact, as it is apparent in the absolute numbers as well as the percentage data (table 1). This decline is not accompanied by any other marked faunal changes.

(b) *Bulk samples from the excavated pits LOAC and LOAF*

To gain a clearer picture of both the molluscan and vertebrate faunas, it was decided to open some sections through the channel sediments for bulk sampling. The gravel fraction from such large samples would also provide statistically adequate pebble counts. In October 1984, through the courtesy of the Nature Conservancy Council (G.C.R. unit), a series of pits was dug with a mechanical excavator parallel to Harwich Road (Bridgland *et al.* 1990, figure 1). The first (LOAC) was located immediately adjacent to the site of borehole LOA, whereas LOAF was excavated approximately 25 m to the south. Two further pits (LOAG and LOAH) were excavated and sampled in May 1987. No samples were taken from the other adjacent trial pits.

In both LOAC and LOAF, the surface of the deposit was carefully stripped off in scrapes of *ca.* 25 cm thickness, from which large bulk samples (usually two sacks each weighing *ca.* 25 kg) were taken. Well-preserved unionid valves and large bone fragments were carefully removed in the field. The base of the channel sediments was not exposed in either pit, as levels below 315 cm were beyond the reach of the excavator. Although, from a comparison with borehole LOA, it appears that the basal 85 cm was not recovered, a good series of stratified bulk samples were nevertheless obtained from the main part of the sequence.

The samples were systematically hosed through a pair of large, mounted screens, with mesh sizes of 1 cm (upper) and 1 mm (lower) respectively. Although several minute species would be lost as a result of this coarse sieving, it is simply impracticable to use a finer mesh on such a large volume of sediment. The concentrated residues were dried and carefully searched for molluscan rarities and vertebrate remains (Lister *et al.* 1990). About 1.5 t of sediment was eventually processed in this manner.

The bulk samples yielded many well-preserved adult specimens of species that had only been recognized from fragmentary or juvenile material in borehole LOA. In some instances (e.g. *Sphaerium*) it has been possible not only to give species names to material that could formerly only be assigned to genera but also to give some idea of their relative abundance. The frequency of rodent teeth and certain molluscs varied enormously between samples. Some sacks produced five or six teeth whereas others were totally barren. This suggests that some sorting has occurred and this is discussed in a later section. Reassuringly, the vast majority of the species had previously been encountered in samples from borehole LOA. However, the following species were not present in this borehole and are clearly very rare components of the fauna at this location. The letter refer to the pit, the numbers to the depth in centimetres.

Anisus leucostoma (Millet). Single shells in LOAC 275–295; 235–255; LOAF 235–255; 190–205.

Planorbis planorbis (L.). Single shells in LOAC 255–275; 220–235; LOAF 175–190 (?1).

Gyraulus albus (Müller). Single shell in LOAH 200–225.

Succinea oblonga Draparnaud. Single shells in LOAC 295–315; 235–255 (?1); LOAF 190–205; 175–190; LOAH 325–350, 250–275, 200–225.

Cochlicopa. Juvenile shell in LOAC 235–255; adult specimen in LOAF 235–255 (measuring 6 mm × 2.5 mm).

Truncatellina cylindrica (Férussac). Apertural fragment in LOAH 200–225.

Vertigo antivertigo (Draparnaud). Single shells in LOAF 255–275; 225–235; two specimens in LOAF 235–255.

cf. *Ceriuella virgata* (da Costa). Single half-grown shell in LOAF 205–235.

Helicella itala (L.). Juvenile shells in LOAC 275–295 (?1); LOAC 235–255.

Trochoidea geyeri (Soós). LOAC 275–295 (3); 255–275 (2); 235–255 (1); 165–220 (3); LOAF 255–275 (1); 235–255 (2); 205–235 (4); 190–205 (3); 175–190 (3); LOAG 115–140 (2); LOAH 250–275 (5), 200–225 (10).

Trichia hispida (L.). Apical fragments (with well-developed hair pits) in LOAC 255–275; 235–255; LOAF 190–205; LOAH 200–225.

Cepaea/Arianta. Apex in LOAF 190–205. Fragments of body-whorl with banding from LOAG 115–140 confirm that *Cepaea* is present.

Pisidium obtusale (Lamarck). Single valve in LOAH 325–350.

(c) Borehole LOH

This was located on waste ground in the middle of the village, approximately halfway along Harwich Road (TM 21972928). The sediments were predominantly coarse to medium sands with some silt. Unlike borehole LOA, these sediments were not shelly throughout and it was not possible to plot a mollusc diagram. Consequently detailed counts from this borehole are not presented here. The fauna is very similar to that from borehole LOA with *V. naticina*, *P. supinum* and *P. moitessierianum* again dominating. *Tanousia* cf. *stenostoma* is also frequent but only in the lower levels; indeed it is totally absent above 200 cm. Once again its absence in the upper levels cannot be explained as the result of low counts since a large shelly bulk sample (ca. 25 kg) from a temporary section 20 m away, also did not yield a single *Tanousia*. The pollen diagram for this borehole (Gibbard & Peglar 1990, figure 2) suggests that the uppermost levels extend later into the interglacial and that they are younger than any other part of the Little Oakley Silts and Sands so far studied.

The decline and disappearance of *Tanousia* in the upper part of the sequence therefore appears to be a 'real' event with potential biostratigraphical significance (see Gibbard & Peglar 1990, figure 2). Because the composition of the rest of the fauna and the lithology remains unchanged, the reason is unlikely to be due simply to the changing regime of the river. Moreover, explanations invoking a climatic cause seem equally unlikely because of the palynological evidence, so the problem must remain open.

(d) Borehole LOO

This was located on a patch of open ground almost halfway along Seaview Avenue at TM 22202925. Unlike the deposits recovered from the other boreholes, the predominant sediments here were silts and clays, with sand only becoming an important component in the basal levels. Although shells were present throughout, they were not abundant and the overall totals per sample are low. Consequently, it has been necessary to summate totals from certain contiguous levels for plotting on figure 2 although the full data is given in table 2. Despite the low numbers, which account for the discontinuous and irregular records for certain species, a clear pattern is nevertheless apparent. The sequence has been divided into three zones as follows:

LOOa 320–370 cm

The assemblage from this zone is more diverse than those from the two subsequent zones and contains relatively greater frequencies of aquatic taxa and is particularly rich in gastropods (*Bithynia troscheli* and *Lymnaea peregra*).

LOOb 270–320 cm

The frequencies of the amphibious snail *Lymnaea truncatula*, that had been increasing throughout the preceding zone, reach their maximum values (40–50%) in this zone. Truly aquatic taxa show a slight decline.

LOOc 210–270 cm

This zone is characterized by the marked expansion of terrestrial snails (e.g. *Vallonia pulchella*) that inhabit marsh environments. The relative frequency of *Lymnaea truncatula* declines, suggesting that conditions were becoming drier.

5. NOTES ON SELECTED SPECIES

A revised list of Mollusca from Little Oakley is given in table 3. Species in square brackets have been recorded erroneously in the past from the Little Oakley channel deposits. The locations of the critical sites referred to in the text are shown in Bridgland *et al* (1990).

[*Viviparus* sp. A small fragment of body-whorl with a trace of a band was referred to this taxon by A. S. Kennard (unpublished manuscript) and Kerney (1959). It is indeterminate even at generic level].

Valvata piscinalis (Müller). All specimens belong to a rather small form (figure 6†) similar to that found in the 'Upper Freshwater Bed' at West Runton and to which Kennard (1944, p. 147) applied the name *V. andreana* Menzel.

Valvata naticina Menke. Abundant at Little Oakley (figure 5†). In Britain it is also known from two Norfolk sites, Sidestrand (? Cromerian) and Trimmingham (Cr IIa) (Sparks 1980) and Sugworth, Berkshire (Gilbertson 1980), as well as from the upper part of the Swanscombe aggradation which is thought to be Hoxnian in age (Kerney 1971). *V. naticina* occurs today over a wide area of central and eastern Europe (S. and E. Germany, Czechoslovakia, Poland, Austria, Hungary, Rumania and European Russia) (Ehrmann 1933; Ložek 1964) although it is extinct in Britain.

Belgrandia marginata (Michaud). The presence of this species (figure 8), characteristic of interglacials in N.W. Europe, constitutes its earliest known occurrence in the British Pleistocene. It is not known with certainty from the 'Cromer Forest Bed' of the Norfolk coast and does not occur at West Runton (*contra* Ellis 1969, p. 80). Sandberger's (1880, pp. 99–100) record for the Cromerian is erroneous since his '*B. nana*' was obtained from a much later channel deposit at Mundesley (Reid 1882, p. 118–119), that has recently been shown to be Ipswichian (Phillips 1976).

Tanousia cf. *stenostoma* (Nordmann). The taxonomy of this prosobranch genus has been the subject of a series of recent papers. British authors have conventionally referred to this genus as *Nematurella* but Schlickum & Schütt (1971) showed that it is generically distinct and

† FIGURES 5–13 appear on plate 1.

PLEISTOCENE MOLLUSCA AT LITTLE OAKLEY

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TABLE 3. COMPLETE REVISED LIST OF MOLLUSCA FROM THE LITTLE OAKLEY SILTS AND SANDS

(A.S.K./S.H.W., Kennard/Warren collections in the BMNH; LOA complex, Borehole LOA and excavated pits LOAC, LOAF, LOAG and LOAH.)

	A.S.K./ S.H.W.	LOA complex	Borehole LOO
Freshwater species			
<i>Valvata piscinalis</i> (Müller)	×	×	×
<i>V. naticina</i> Menke	×	×	×
<i>Belgrandia marginata</i> (Michaud)	×	×	×
<i>Tanousia</i> cf. <i>stenostoma</i> (Nordmann)	×	×	×
<i>Bithynia troscheli</i> (Paasch)	×	×	×
<i>Lymnaea truncatula</i> (Müller)	×	×	×
<i>L. peregra</i> (Müller)	×	×	×
<i>Planorbis planorbis</i> (L.)	—	×	×
<i>Anisus leucostoma</i> (Millet)	×	×	×
<i>Gyraulus laevis</i> (Alder)	×	×	—
<i>G. albus</i> (Müller)	—	×	—
<i>Armiger crista</i> (L.)	×	×	×
<i>Hippeutis complanatus</i> (L.)	—	×	×
<i>Ancylus fluviatilis</i> Müller	×	×	×
<i>Acroloxus lacustris</i> (L.)	—	—	×
<i>Unio pictorum</i> (L.)	?×	×	—
<i>U.</i> cf. <i>tumidus</i> Philipsson	×	×	—
<i>U. crassus</i> Philipsson	×	×	?×
cf. <i>Anodonta cygnea</i> (L.)	—	×	—
<i>Sphaerium corneum</i> (L.)	×	×	?×
<i>S. solidum</i> (Normand)	×	×	?×
<i>S. lacustre</i> (Müller)	×	×	×
<i>Pisidium amnicum</i> (Müller)	×	×	—
<i>P. clessini</i> Neumayr	×	×	—
<i>P. casertanum</i> (Poli)	×	×	—
<i>P. personatum</i> Malm	×	—	—
<i>P. obtusale</i> (Lamarck)	—	×	—
<i>P. milium</i> Held	—	×	—
<i>P. subtruncatum</i> Malm	×	×	×
<i>P. supinum</i> Schmidt	×	×	×
<i>P. henslowanum</i> (Sheppard)	×	×	×
<i>P. hibernicum</i> Westerlund	—	×	—
<i>P. nitidum</i> Jenyns	×	×	×
<i>P. moitessierianum</i> Paladilhe	×	×	×
<i>P.</i> cf. <i>tenuilineatum</i> Stelfox	—	×	×
Terrestrial species			
<i>Carychium minimum</i> Muller	×	—	×
<i>Succinea oblonga</i> Draparnaud	—	×	×
<i>Succinea/Oxyloma</i>	×	×	×
<i>Cochlicopa lubrica</i> (Müller)	×	×	×
<i>Truncatellina cylindrica</i> (Férussac)	—	×	—
<i>Vertigo antivertigo</i> (Draparnaud)	—	×	×
<i>Pupilla muscorum</i> (L.)	×	×	×
<i>Vallonia costata</i> (Müller)	—	×	—
<i>V. pulchella</i> (Müller)	×	×	×
<i>V. excentrica</i> Sterki	×	—	—
cf. <i>Vitrinobrachium breve</i> (Férussac)	×	—	×
<i>Vitrea crystallina</i> (Müller)	×	—	—
<i>Nesovitrea hammonis</i> (Ström)	—	—	×
<i>Zonitoides nitidus</i> (Müller)	—	—	×
<i>Deroceras/Limax</i>	—	—	×
<i>Euconulus fulvus</i> agg	—	×	×
cf. <i>Cerņuella virgata</i> (da Costa)	—	×	×
<i>Helicella itala</i> (L.)	—	×	—
<i>Trochoidea geyeri</i> (Soós)	×	×	—
<i>Trichia hispida</i> (L.)	—	×	—
<i>Cepaea/Arianta</i>	—	×	×

proposed the new genus *Lithoglyphulus* to accommodate it, together with two other taxa. Schlickum (1974) subsequently synonymized *Lithoglyphulus* with Servain's genus *Tanousia* which has priority by many years.

Several species belonging to the genus *Tanousia* still inhabit parts of Yugoslavia but in N.W. Europe only two extinct species have been referred to this genus. *Tanousia runtoniana* (Sandberger) was originally described from the 'Upper Freshwater Bed' at West Runton (Sandberger 1880) whereas the type locality of *T. stenostoma* is from Pleistocene deposits at Gudbjerg, Fyn, Denmark (Madsen & Nordmann 1901). Sections are no longer available at Gudbjerg and the age of these deposits has not been determined with precision (Rosenkrantz 1945), although they are thought to be early Middle Pleistocene (cf. Jessen 1927).

Schlickum & Schütt (1971) and Schlickum (1974) give comparative descriptions in the belief that the form from Little Oakley is *T. runtoniana*. However, the Little Oakley specimens do not match West Runton shells very closely despite Kennard's (unpublished manuscript) assertion that they 'cannot be separated from *runtoniana* even as a variety'. However, even Kennard commented on the 'abnormal growth' of some Little Oakley specimens which he supposed had been parasitized by trematodes known to cause growth abnormalities in several prosobranchs. The chief differences between *T. runtoniana* and *T. stenostoma* from their respective type localities can be summarized as follows:

1. *T. runtoniana* is narrower in outline whereas *T. stenostoma* has an inflated body-whorl and a much broader and more conical shell.
2. In *T. runtoniana* the whorls increase more slowly.
3. In *T. runtoniana*, the upper part of the last whorl is slightly but distinctly detached from the wall of the preceding whorl, leaving a deep cleft whereas in *T. stenostoma* the parietal wall does not stand away from the preceding whorl but is attached along its length.
4. When viewed laterally, the top of the outer wall of the peristome of *T. runtoniana* turns down sharply along the suture a short distance behind the aperture, corresponding with the point of detachment of the last whorl. In *T. stenostoma* there is no downturning along the suture, which remains level (figures 4 and 7).
5. The growth lines of *T. runtoniana* are more pronounced than those of *T. stenostoma*, particularly towards the aperture.

Using these criteria, specimens from Little Oakley resemble Danish *T. stenostoma* more closely than they do *T. runtoniana*, a conclusion already reached by Kerney (1959). Table 4 compares measurements of *T. runtoniana* from West Runton and *T. stenostoma* from Gudbjerg with those of Little Oakley shells. From these measurements it can be seen that the latter are intermediate in size and shape, with the differences in breadth being more significant than those in height. Thus whereas the mean height of the Little Oakley shells differs from those of the other two populations by no more than 5.3%, the breadths show much greater differences (figure 3). The Little Oakley shells are on average 8.9% broader than *T. runtoniana* from West Runton but 17% narrower than *T. stenostoma* from Gudbjerg, the last being some 31.2% broader than *T. runtoniana* from West Runton. Thus the breadths of the Little Oakley population are closer to those of *T. runtoniana* than Danish *T. stenostoma* (figure 3), despite the fact that in other respects (e.g. apertural characters) they match *T. stenostoma*. In other words, the Little Oakley shells appear to be a small, narrow form of *T. stenostoma* with the last whorl smaller in relation to the spire (figure 4). It is just possible that they may represent another, undescribed, taxon but a final decision on this point is deferred until further comparisons can be made.

PLEISTOCENE MOLLUSCA AT LITTLE OAKLEY

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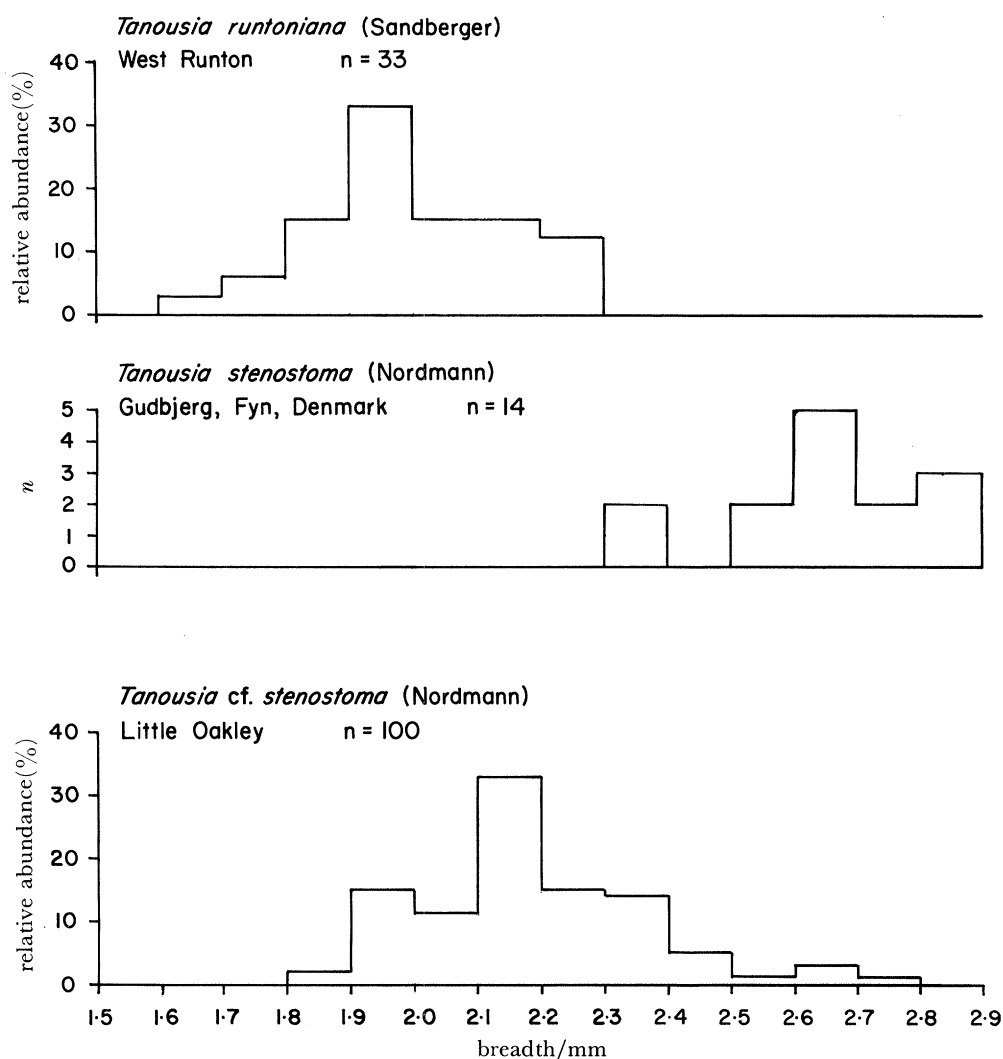


FIGURE 3. Measurements of the breadths of *Tanousia* from Little Oakley compared with those of *T. runtoniana* and *T. stenostoma* from their respective type localities.

TABLE 4. MEASUREMENTS OF *TANOUSIA* FROM LITTLE OAKLEY COMPARED WITH SPECIMENS OF *T. RUNTONIANA* (SANDBERGER) AND *T. STENOSTOMA* (NORDMANN) FROM THEIR RESPECTIVE TYPE LOCALITIES

(Measurements were made optically with a microscope and graticule eyepiece and are accurate to ± 0.05 mm.)

	n	\bar{x}	height mm		breadth mm		
			s.d	range	\bar{x}	s.d.	range
<i>Tanousia runtoniana</i> West Runton, Norfolk ^a	33	3.72	0.24	3.20–4.47	2.02	0.16	1.67–2.27
<i>Tanousia stenostoma</i> Gudbjerg, Fyn, Denmark ^b	14	4.12	0.24	3.72–4.56	2.65	0.16	2.36–2.90
<i>Tanousia cf. stenostoma</i> Little Oakley, Essex ^c	100	3.90	0.28	3.27–4.93	2.20	0.17	1.87–2.73

^a C. Reid coll. BMNH (24 shells); J. Reeve coll. Norwich Castle Museum (9 shells).

^b A. S. Kennard coll. BMNH: 8 shells (G.83721); Rijks Geologische Dienst (Haarlem): 6 shells.

^c A. S. Kennard coll. BMNH.

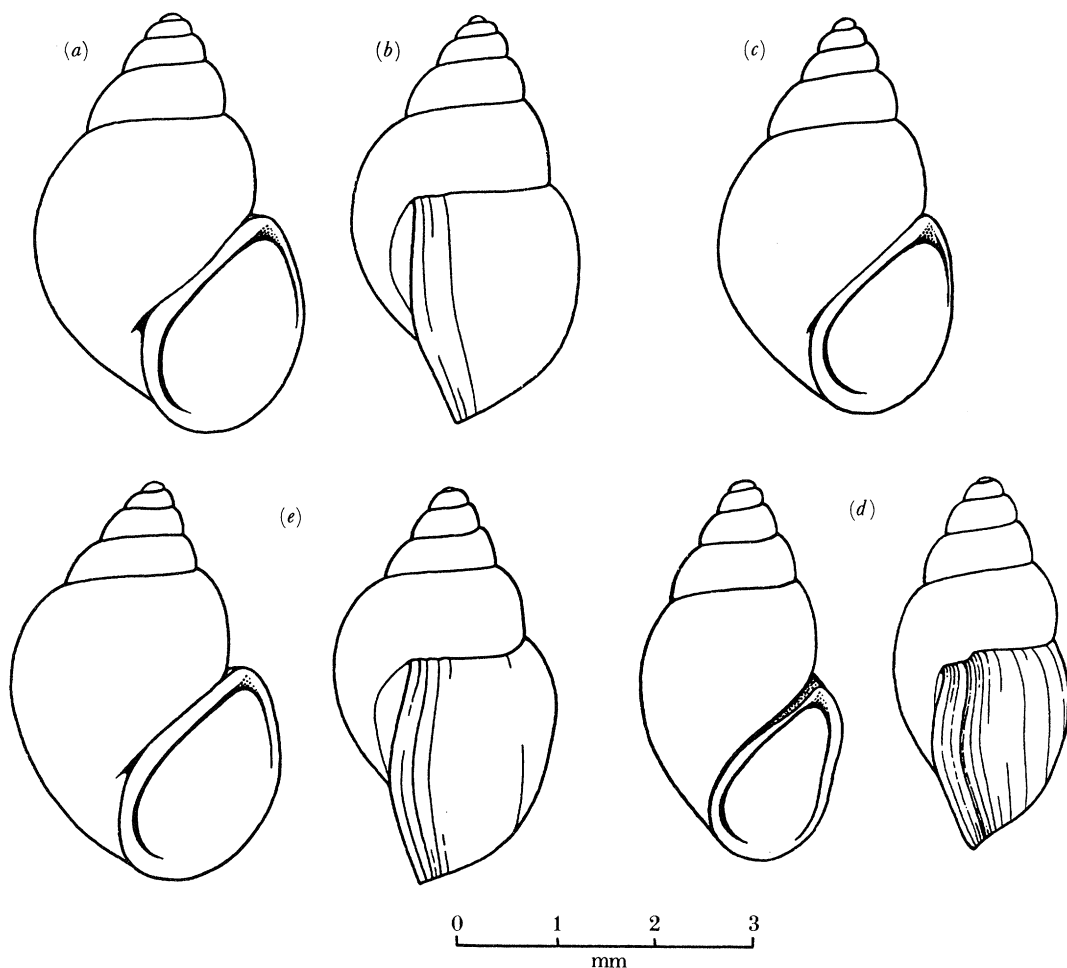


FIGURE 4. *Tanousia* from Little Oakley (a–c) compared with *T. runtoniana* (d) from the ‘Upper Freshwater Bed’, West Runton, Norfolk, and *T. stenostoma* (e) from the ‘Middle Pleistocene’ of Gudbjerg, Fyn, Denmark; BMNH, Kennard Collection (ex V. Nordmann Coll.) G83721. Drawings by Dr M. P. Kerney.

Gilbertson (1980) also recorded *T. runtoniana* from Sugworth, Berkshire where, like most sites, it occurred at low frequency. I have been able to examine only two shells from this locality, one not even fully mature and the other with apertural damage. Close examination of the upper part of the apertures, however, does suggest that they are indeed *T. runtoniana*, although it is desirable to obtain more complete adult shells to confirm this.

Through the courtesy of Mr T. Meijer (Rijks Geologische Dienst, Haarlem) I have been able to compare the Little Oakley shells with several other *Tanousia* populations from N.W. Europe. Thus Tesch’s (1944) record of *T. runtoniana* from a borehole through marine Tiglian deposits on the Isle of Schokland is an error for *Hydrobia ulvae*. Moreover, Tesch’s shell of ‘*Nematurella stenostoma*’, again from Lower Pleistocene marine deposits from a borehole near Dordrecht, is also very probably misidentified although the specimen is now lost. Mr T. Meijer (personal communication) has however recorded a few specimens of *T. runtoniana* from interglacial deposits at Bavel (type Bavelian), thought to date from the late Lower Pleistocene (Zagwijn 1985). This therefore appears to constitute the earliest Dutch record of *T. runtoniana* although there is one additional record from a North Sea borehole (file number L10-6: 47.26–47.70 m

below sea-bottom) through deposits of Cromerian interglacial III or IV age (associated with *Pisidium clessini* and *Macoma balthica*). Schlickum (1974) cites French records of *T. runtoniana* from the 'Isle-les-Villenoy, Bois de l'Épinette' in the 'Moyenne terrasse, Mindel II?', which are said to be smaller and slightly narrower than Little Oakley specimens. Three shells in the Senckenberg Museum, Frankfurt, F.R.G. (registration numbers SMF 266489/3), collected by Puisségur from here, have slightly stronger spiral microsculpture than specimens from Little Oakley (T. Meijer, personal communication). Although *T. stenostoma* has been reported from the Russel Tiglia pit at Tegelen (Freudenthal *et al.* 1976), Mr T. Meijer (personal communication) now considers it best, in view of the crushed nature of the shells, to regard these as specifically indeterminate. Thus *T. stenostoma* is not known with certainty from the Dutch Quaternary.

In 1939 Tesch described a new species of *Nematurella* from the Lower Pleistocene (Tiglian) from boreholes at Tegelen and Rosmalen as *N. minima* (Tesch 1939, p. 60). This has recently been shown to be conspecific with *Tournouerina belnensis* (Delafond & Depéret), a genus apparently distinct from *Tanousia* (Schlickum 1971, 1978).

The belief that Little Oakley shells are *T. runtoniana* has led to considerable confusion so that it has become necessary to completely revise all European *Tanousia* identified as '*runtoniana*'. This work is beyond the scope of the present paper and must remain for the future.

The occurrence of *T. stenostoma* at Little Oakley is the first British record although Kerney (1959) also recorded *T. cf. stenostoma*, as well as *T. runtoniana*, from the 'Upper Freshwater Bed' at West Runton. Kennard & Woodward (1914) had previously listed it without comment 'from the Cromerian' but had mistakenly regarded *stenostoma* as merely a junior synonym of *runtoniana* (Kennard & Woodward 1926, p. 26).

Bithynia troscheli (Paasch). All *Bithynia* shells were clearly referable to this species and no trace of *B. tentaculata* was detected. The opercula also all seemed to match those of *B. troscheli* (cf. Meijer 1985, pp. 77–82). British authors have formerly referred to this species as *B. inflata* (Hansén) but Paasch's name has priority. In N.W. Europe *B. troscheli* has been recorded from the Dutch Tiglian and most interglacials up to and including the Last (Ipswichian). It is closely allied to *B. leachii* (Sheppard), the form that currently occurs in the British Isles but unknown there before the Flandrian. However, it differs from *B. leachii* in being generally rather larger and distinctly broader in relation to its height. Much debate has surrounded the validity of this separation but most authorities regard *B. troscheli* as a distinct species that still inhabits parts of northern and eastern Europe (Ehrmann 1933).

Unionidae. At least three, and possibly four, species of large mussel were present in the material collected from the mechanically excavated pits. The commonest species was *Unio crassus* (figure 13) and several well-preserved specimens with valves united were recovered still in positions of life. Other, more elongate, shells were clearly *Unio pictorum*, others were tentatively referred to *U. tumidus* and one very fragmentary specimen from LOAF 255 cm, measuring at least 11.5 cm × 6 cm has been tentatively referred to *Anodonta cygnea* on size alone. This shell seemed to be thinner than that of *Margaritifera auricularia*, the only other possible species that reaches these proportions.

Sphaerium. Three species of *Sphaerium* have now been recorded from Little Oakley. Most of the specimens (except those of *S. lacustre*) recovered from the boreholes are too fragmentary to be named to species level. However, all adult and half-grown shells of this genus were carefully picked from the large bulk samples collected from the excavated pits. The occurrence of both

S. corneum and *S. solidum* had now been confirmed. The presence of *S. solidum*, which outnumbers *S. corneum* by about 5 to 1, is particularly noteworthy as this constitutes its only known occurrence in the British Pleistocene. Its presence in the Hoxnian at Swanscombe (Kimball *in* Zeuner, 1945, p. 273; Davis 1953; Castell *in* Ovey, 1964) has not been confirmed and is very probably based on misidentifications of the heavily thickened form of *S. corneum* that Kennard called *S. bulleni*, a name he initially applied to Little Oakley *S. solidum* (A. S. Kennard, unpublished manuscript). Examples of *S. solidum* from Little Oakley have been previously figured by Ellis (1978, plate ix, figures A–B) but although they show the characteristic trigonal shape, they are worn and the strongly concentric striation is poorly preserved. Better specimens from Little Oakley are here figured alongside those of *S. corneum* (figures 11 and 12). In the Quaternary of N.W. Europe, *S. solidum* is known from the Dutch Tiglian and most subsequent Middle and Late Pleistocene interglacials. Its modern range is in central and eastern Europe, extending northwards to the southern Baltic (Estonia) and eastwards to the Urals. It is local in The Netherlands, Belgium and northern France and has only recently been discovered in Britain in the River Witham in Lincolnshire (Redshaw & Norris 1974).

Pisidium personatum Malm. A single valve is present in the Warren collection among a batch of specimens determined by S. P. Dance.

Pisidium cf. *tenuilineatum* Stelfox. A single worn valve (borehole LOA 300–320) has been tentatively referred to this species by Dr M. P. Kerney. If correct, this would represent its earliest known occurrence in the British Pleistocene.

[*Carychium ovatum* Sandberger. Listed by Kimball *in* Zeuner (1945). Now considered to be conspecific with *C. minimum*.]

Truncatellina cylindrica (Férussac). A new record from the British Cromerian although known from the Norwich Crag.

[*Discus rotundatus* (Müller). Listed by Kerney (1959) on the basis of shells in the Kennard collection. Although correctly named they appear to be somewhat better preserved than most of the Little Oakley fossils and they may well be contaminants.]

cf. *Vitrinobrachium breve* (Férussac). Two shells belonging to the Vitrinidae are present in the Kennard/Warren collections from Little Oakley. A. S. Kennard (unpublished manuscript) noted that they were ‘near to *elongata* Draparnaud’ and were listed as this species by Kimball *in* Zeuner (1945). *V. elongata* is a synonym of *Semilimax semilimax* (Férussac), a species that had been recorded from West Runton and a few other British Middle Pleistocene interglacial deposits. Holyoak & Preece (1986) have recently shown that these fossils, including those from Little Oakley, are much closer to *Vitrinobrachium breve* than to *Semilimax semilimax*. Fragments of another specimen were recovered from borehole LOO 280–290 cm.

DESCRIPTION OF PLATE 1

Scanning electron micrographs (figures 5–8) and light photomicrographs (figures 9–13) of selected shells from Little Oakley.

FIGURE 5a, b. *Valvata naticina* Menke. LOAC 270–295.

FIGURE 6a, b. *Valvata piscinalis* (Müller). LOAC 235–255.

FIGURE 7a, b. *Tanousia* cf. *stenostoma* (Nordmann). LOAC 235–255.

FIGURE 8. *Belgrandia marginata* (Michaud). LOAF 255–275.

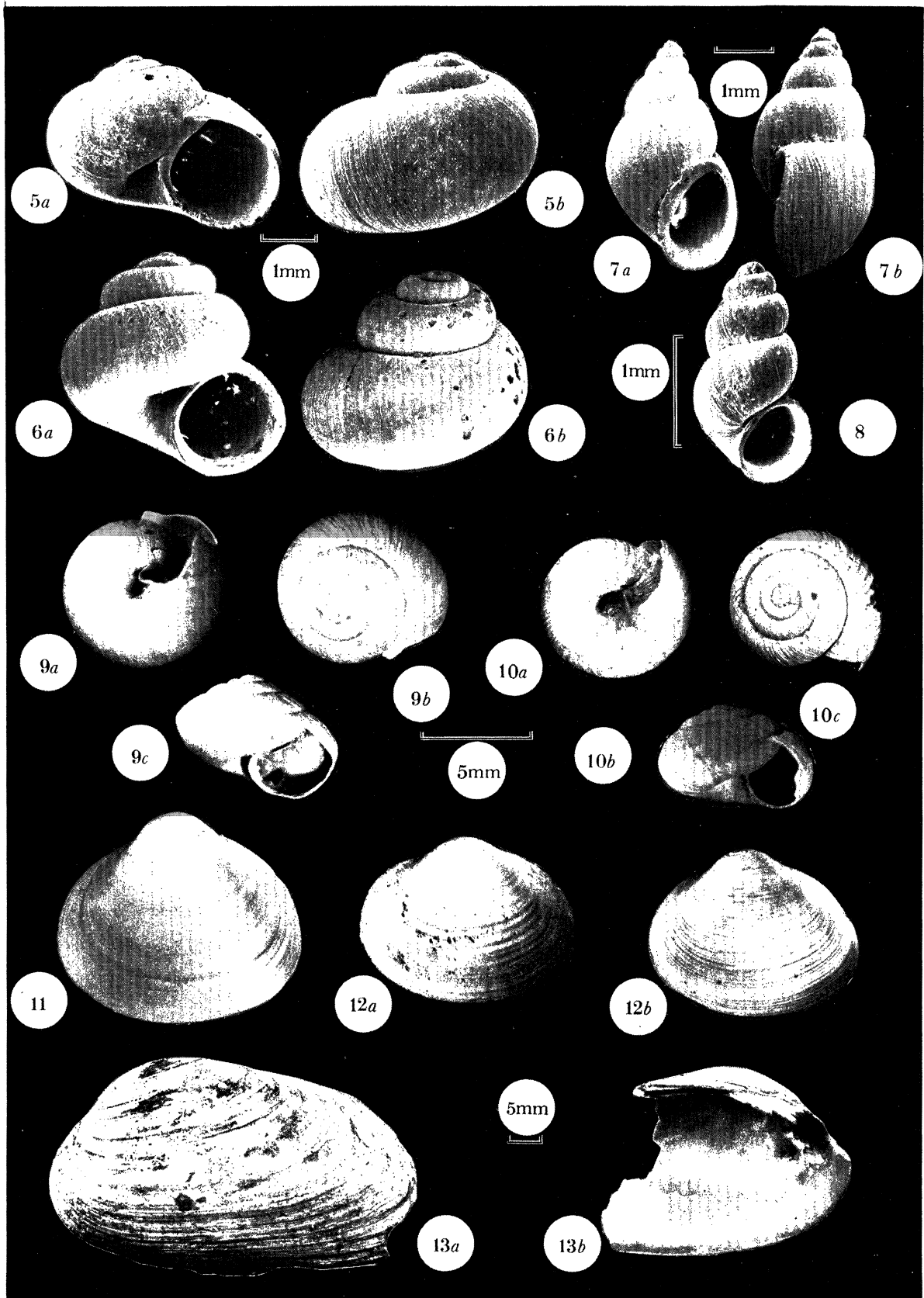
FIGURE 9a–c. cf. *Cernuella virgata* (da Costa). LOAF 225–235.

FIGURE 10a–c. *Trochoidea geyeri* (Soós). LOAC 165–220.

FIGURE 11. *Sphaerium corneum* (L.). LOAC 235–255.

FIGURE 12. *Sphaerium solidum* (Normand). (a) LOAC 255–275 (b) LOAC 225–235.

FIGURE 13a, b. *Unio crassus* Philipsson. LOAC unstratified.



FIGURES 5-13. For description see opposite.

(Facing p. 402)

cf. *Cermeuella virgata* (da Costa). A single half-grown shell lacking banding, closely resembling this species, was recovered from the excavated pit LOAF 205–235 cm (figure 9). If correctly identified this represents the earliest British Pleistocene record of this species.

Helicella itala (L.). The earliest record from the British Pleistocene although it is known from much older deposits on the continent.

Trochoidea geyeri (Soós). The Kennard collection contains eight juvenile shells that Kennard (unpublished manuscript) tentatively referred to *Helicopsis striata* (Müller). Several further specimens, including a few adult shells, were recovered from the excavated pits and suggest that *T. geyeri* is involved rather than the morphologically similar *H. striata* (cf. Sparks 1953). Peripheral banding was still preserved on a few shells (figure 10). These constitute the only British Cromerian records of this central and southern European xerophile.

[*Candidula crayfordensis* Jackson. Listed by Kimball in Zeuner (1945) but clearly an error for *Trochoidea geyeri*.]

Several other species are present in boxes of partly sorted material labelled ‘Little Oakley’ in the British Museum (Natural History). These include the land snails *Aegopinella nitidula*, *Cepaea nemoralis* and *Trichia plebeia* and the aquatic snails *Valvata cristata*, *Lymnaea stagnalis* and *Bathymorphalus contortus*. The land snails appear to be modern contaminants but the status of the latter are equivocal; they may have come from ‘the patch of highly calcareous white marl’ mentioned by S. H. Warren & A. G. Davis (unpublished manuscript). Their presence at Little Oakley requires confirmation.

6. ENVIRONMENTAL IMPLICATIONS

The molluscan fauna from Little Oakley is dominated by freshwater species which indicate that the channel sediments were deposited by a large, well oxygenated, calcareous river upstream of any tidal influence. The frequencies of *Pisidium supinum* and *P. moitessierianum*, together with *P. amnicum* and *P. clessini*, are particularly characteristic of large lowland rivers. Moreover, all the *P. casertanum* belong to the strongly thickened *ponderosum* form, again indicative of fluvial conditions. There is strong geological evidence to suggest that the river was indeed the ancestral, pre-diversion Thames (Bridgland *et al.* 1990). The molluscan fauna, comprising over 50 taxa, is fully temperate in character throughout and is diagnostic of the middle parts of an interglacial in Britain.

There are significant differences between the assemblages from boreholes LOA and LOH and those from borehole LOO. The assemblages from the first two are similar in being composed largely of bivalves, with gastropods, other than *Valvata naticina* and *Tanousia*, occurring rather infrequently. In borehole LOO, in which the total counts are much lower, both the diversity and frequency of gastropods is significantly higher. Indeed the mean gastropod:bivalve ratio from LOA is 1.45 ± 0.61 compared with 5.27 ± 2.39 from LOO. Moreover the gastropods present in LOO suggest much quieter, shallower, plant-rich conditions. *Lymnaea peregra* and *L. truncatula* are much commoner and the river limpet *Ancylus fluviatilis* is here joined by the lake limpet *Acroloxus lacustris*. There is also a complete reversal in the frequency of the *Valvata* species such that *V. naticina* is here recorded only from a single shell whereas *V. piscinalis* dominates. These differences are thought to reflect depositional facies within the river. Thus sediments from boreholes LOA and LOH accumulated under relatively high-energy conditions in mid-channel, whereas those from LOO were deposited in a quieter

marginal environment. This conclusion gains support from the sedimentology with the former two boreholes producing much coarser sediments (chiefly medium–fine sands) than LOO (largely silts and clays).

Although the Mollusca from LOO broadly reflect marginal conditions, there are significant changes within the profile suggesting a shallowing sequence to the point where hygrophilous land snails (e.g. *Vallonia pulchella*) make up a substantial part of the fauna.

Land snails otherwise only occur at low frequency. They are clearly derived from two quite different sources. First, there are the marsh species (e.g. *Vallonia pulchella*, *Zonitoides nitidus*, *Vertigo antiverlugo* and the Succineidae), relatively frequent in the upper part of LOO and occurring as occasional shells in the other boreholes, which are flushed from marginal habitats. Second, there are the xerophilous species of dry calcareous grassland (e.g. *Trochoidea geyeri*, *Helicella itala*, cf. *Cerņuella virgata*, *Truncatellina cylindrica* and *Pupilla muscorum*). Such species are frequently found in fluvial sediments where their occurrence is often explained as due to bank collapse caused by the lateral erosion of the river (e.g. Sparks 1964). Incorporation by such means would also account for the large differences between bulk samples in the frequency of xerophilous taxa and rodent teeth, although fluvial sorting would also be an important factor. Woodland species are virtually absent, suggesting that the river here had a wide, open floodplain. This conclusion is in complete accord with the palynological evidence where high values of Gramineae and herb taxa occur throughout (Gibbard & Peglar 1990).

7. THE AGE OF THE DEPOSITS AND COMPARISONS WITH OTHER FOSSIL FAUNAS

The molluscan fauna of Little Oakley points strongly to an age earlier than the Hoxnian Stage since it is quite different from fluvial assemblages of this age described from Swanscombe and Clacton (Kerney 1971). A broadly Cromerian age is suggested by the presence of the genus *Tanousia*, found nowhere in N.W. Europe later than the Cromerian, and also by the occurrence of *Bithynia troscheli* to the exclusion of *B. tentaculata*. The latter species, normally common in all temperate post-Cromerian freshwater deposits, is unknown from the Cromerian stratotype at West Runton and all other British Cromerian sites except Trimingham (Sparks *in West* 1980). Earlier published records of *B. tentaculata* from West Runton, based largely on the identifications of opercula, have all proved to be erroneous (Sparks *in West* 1980, p. 26). The absence of *Corbicula fluminalis* is another feature that characterizes British Cromerian sites although it is known, like *B. tentaculata*, from still older deposits. Kerney (1977) provides a succinct summary of the chief malacological differences between various interglacials in Britain.

Knowledge of molluscan faunas from the British Cromerian is restricted to those of the pre- and early temperate substages (Cr I–II) from West Runton, together with a few other less well studied sites along the Norfolk and Suffolk coasts (Sparks *in West* 1980) and that of the late temperate substage (Cr III) from Sugworth, Berkshire (Gilbertson 1980; Preece 1989). One of the most striking differences between these sites and Little Oakley is the abundance of *Tanousia* at the latter. Indeed at some levels in LOA, it exceeds 30% of the fauna, its highest recorded frequency from any site in N.W. Europe. Two explanations have been advanced to account for this abundance. A. S. Kennard (unpublished manuscript) used it as evidence to suggest that Little Oakley might be somewhat older than the ‘Cromer Forest Bed’ at West Runton, where *Tanousia* never exceeds 3%. Kerney (1959), on the other hand, though that *Tanousia* might be a brackish-water species and that its abundance at Little Oakley might be due

to weakly brackish conditions. Neither explanation seems likely as *Tanousia* is known nowhere else at such frequency and the ostracods provide no evidence of brackish conditions (Robinson 1990). This and the other faunal differences are probably best explained in terms of contrasting depositional environments, rather than invoking difference in age or brackishness. Thus most of the sediments at Little Oakley accumulated under high-energy conditions than those of either West Runton or Sugworth. There are several species of land snail recorded from Little Oakley that constitute either the earliest Pleistocene (*Helicella itala*, cf. *Ceriuella virgata*) or only Cromerian records (*Truncatellina cylindrica*, *Trochoidea geyeri*) from Britain. These have no stratigraphical importance and in all cases constitute taxa that inhabit dry calcareous grassland, an environment poorly represented at all other British Cromerian sites. Leaving these facies differences apart, the overall nature of the mollusca fauna at all these sites exhibits a broad similarity.

These faunal characteristics therefore suggest an age no later than the Cromerian. A maximum age is much harder to estimate as most British pre-Cromerian Quaternary deposits are marine in origin. Nevertheless non-marine shells still occur consistently, albeit at very low frequency, in the Lower Pleistocene Crags of East Anglia. Despite the fact that several hundred non-marine shells have now been obtained, no specimens of *Valvata naticina*, *Bithynia troscheli* or *Unio crassus* have even been recorded from British pre-Cromerian deposits. However, it is clear from a comparison with the Dutch sequence that there are enormous gaps in the British Lower and Middle Pleistocene succession (West 1980; Zagwijn, 1985; Mayhew & Stuart 1986).

Recent work by Mr T. Meijer on both museum material and on recently collected shells from the Dutch Lower and Middle Pleistocene have greatly clarified aspects of faunal history. Thus whereas in The Netherlands *B. troscheli* occurs in several pre-Cromerian interglacials including the Tiglian, *V. naticina* has not been recorded there with certainty before the Cromerian. Moreover, as mentioned earlier, most of the Dutch Tiglian records of *Tanousia* have proved to be either erroneous or specifically indeterminate. The earliest record of *T. runtoniana* comes from the Bavel interglacial which is thought to be late Lower Pleistocene (Zagwijn 1985). The extensive molluscan fauna from Bavel (T. Meijer, unpublished data) differs markedly from that of Little Oakley and other British Cromerian sites in having more extinct taxa, consistent with its much earlier age.

There is, however, a similarity between the Little Oakley assemblages and the fauna (T. Meijer, unpublished data) from the Noordbergum borehole (58.45–60.20 m.o.m.), now equated with the 'Interglacial IV' (*sensu* Zagwijn) and provisionally correlated with the Cromerian stratotype at West Runton. The chief differences are the absence of *Tanousia* and presence there of *B. tentaculata* but otherwise the match is close, despite the fact that the fauna from Noordbergum is derived from estuarine or shallow marine sediments. No information exists on the molluscan faunas from the three earlier interglacials of the 'Cromerian Complex' in The Netherlands. These are distinguished on the basis of palynology alone and each is known only from one or two boreholes (Zagwijn *et al.* 1971; Zagwijn 1985). This ignorance precludes further comparison with the more complete Dutch sequence, although correlation with 'Interglacial I' can be eliminated on both palynological (Gibbard & Peglar 1990) and palaeomagnetic evidence (Bridgland *et al.* 1990), whereas 'Interglacial II' also has rather different vegetational characteristics. The available evidence suggests that Little Oakley belongs to the latter part of the 'Cromerian Complex' and correlation with Noordbergum ('Interglacial IV') and West Runton (Cromerian *sensu stricto*) seems probable although not certain (cf. Kolfshoten 1988).

I acknowledge the help received from Dr M. P. Kerney and Mr T. Meijer, who have both allowed me to quote from their unpublished work. I thank Dr P. L. Gibbard and Dr D. R. Bridgland for help in the field and Dr A. M. Lister and Mr J. Clayden for assistance in processing the substantial volume of sediment from the excavated pits, which were financed by the Nature Conservancy Council (G.C.R. Unit). Thanks are also due to Dr A. J. Sutcliffe and Mr J. Cooper of the Department of Palaeontology, British Museum (Natural History), to Diana Smith of Norwich Castle Museum and to Mr T. Meijer of the Rijks Geologische Dienst (Haarlem) for allowing me to examine material in their care. Dr D. T. Holyoak commented on an earlier draft.

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FIGURES 5-13. For description see opposite.