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MOLLUSCAN AND PLANT BIOSTRATIGRAPHY OF SOME LATE DEVENSIAN AND FLANDRIAN DEPOSITS IN KENT

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Sequences of calcareous slope and spring deposits (mainly tufa) are described from two localities in Kent (Folkestone and Wateringbury). They contain rich faunas of terrestrial Mollusca, allowing a detailed reconstruction of the local environments. The faunal changes also reveal an underlying common pattern, ascribed largely to the effects of climate and migration. Eight biostratigraphical assemblage zones are proposed, applicable to deposits of this general character in the area of southern England. The base of each zone is defined as follows:

zone y first appearance of a molluscan fauna, dominantly of *Pupilla*, *Vallonia* and *Vitrina*;
zone z expansion of *Abida* and *Trichia*;
zone a decline of *Pupilla*, appearance of *Carychium* and *Aegopinella*;
zone b expansion of *Carychium* and *Aegopinella*, occurrence of *Discus ruderatus*;
zone c expansion of *Discus rotundatus*, suppression of *Discus ruderatus*;
zone d expansion of *Oxychilus cellarius*;
zone e re-expansion of *Vallonia*;
zone f appearance of *Helix aspersa*.

Botanical evidence (pollen and seeds) and some radiocarbon dates allow a partial correlation of the zones with the standard Godwin pollen zones of the Late Devensian (late-glacial) and the Flandrian.

1. INTRODUCTION

In July 1968 a trial pit made by Kent County Council Highways Department below the Chalk escarpment at Sugarloaf Hill, Folkestone, revealed a sequence of Late Devensian and Flandrian spring and slope deposits containing molluscs, plant remains and beetles. In view of the potential importance of the site in linking molluscan and vegetational changes further sections were opened in 1969 for more detailed study.

The early Flandrian Wateringbury tufa was first described forty years ago (Brown 1939). In 1975–6 a much more detailed investigation was made, revealing strong biostratigraphical similarities with the deposits at Folkestone.

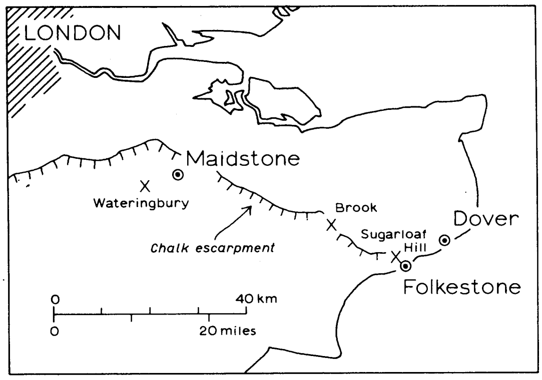

FIGURE 1. Location of sites.

2. METHODS OF INVESTIGATION

(*a*) *Mollusca*

The following extraction procedure was adopted. After drying, each sample was disaggregated in water. Floating snails and other organic fragments were repeatedly decanted and retained in a British Standard mesh (B.S.) no. 30 (0.5 mm) sieve. The remaining sediment was poured into a second B.S. no. 30 sieve, washed thoroughly, dried, and divided into arbitrary fractions (B.S. sieves 8, 12, 16 and 22). Picking of the finer fractions was carried out under a binocular microscope, by means of a black sorting tray marked with white lines so that the field of view could be tracked efficiently. All apical fragments (gastropods) or umbonal hinge fragments (bivalves) were extracted, identified and counted. Nomenclature and taxonomic order follow Waldén (1976) and Kerney (1976*a*).

The results are presented as histograms of percentage frequency (figures 5, 9, 11). Crosses indicate single shells. Aquatic species (*Pisidium*, *Lymnaea*) and obligatory swamp species (*Carychium minimum*, Succineidae, *Vertigo antivertigo*, *V. genesii*, *V. moulinsiana*, *V. angustior*, *Zonitoides nitidus*) have been excluded from the main summation total and are shown as a percentage of the sum of the remaining land species. For *Pisidium*, the numbers of individual valves were halved before calculation. *Cecilioides acicula* has also been excluded from the main total. Owing to the subterranean habits of this species, which can penetrate along rootlets and shrinkage cracks in calcareous soils to a depth of at least 2 m, it is difficult to know to what extent the shells recovered are contemporary with the deposits; obviously fresh (glassy) shells were ignored but it is possible that all are intrusive.

For the sake of simplicity, many terrestrial species have been grouped into ecological categories 'A' and 'B'. Roughly, those in group 'A' are catholic species of wide tolerance, living in open ground, marshes, and coniferous and deciduous woods (*Cochlicopa*, *Columella*, *Vertigo substriata*, *Punctum*, *Vitrina*, *Vitrea*, *Nesovitrea*, *Deroceras/Limax*, *Euconulus*, *Arianta/Cepaea*). Those in group 'B' are more critical in their requirements, being commonest in deciduous woods and similar well shaded places (*Carychium tridentatum*, *Acanthinula*, *Ena*, *Aegopinella*, Clausiliidae, *Helicigona*). *Carychium* and *Aegopinella* make up the greater part of this second group.

Some points concerning identification are briefly considered below.

Columella. Determinations of *C. columella*, *C. edentula* and *C. aspera* were checked by Dr C. R. C. Paul.

Vallonia. In the Wateringbury diagram (figure 9) *V. pulchella* and *V. excentrica* are plotted separately. Since juveniles are indistinguishable, the procedure adopted was to divide and assign all immature shells exactly in proportion to the numbers of identifiable adults present in each sample.

Milax. Well grown internal shells of milacid slugs are distinctive by reason of their central nucleus and bilateral symmetry. Undoubted shells of *Milax* occur in the hillwash at Folkestone and an attempt has been made to separate *Milax* quantitatively at this site. But there is a good deal of variation and the distinction from Limacidae (*Deroceras*, *Limax*) is by no means clear-cut, especially in juveniles.

Trichia. The numbers given for *T. hispida* and *T. striolata* are approximations. Specimens below *ca*. 2 mm are hard to distinguish, though *T. striolata* tends to have a slightly larger protoconch and sparser hair pits on the initial whorls.

Arianta and *Cepaea*. It has proved impossible to separate apices quantitatively. The presence of either or both of these genera is, however, usually clear from shell fragments bearing characteristic microsculpture. Lip fragments are also distinctive.

(*b*) *Plant remains*

The accumulation of tufa may permit the preservation of three general categories of plant fossils, all of which were encountered during the present investigations. The first and most characteristic of these are leaf, stem and moss impressions, where finely crystalline calcium carbonate has been deposited on plant surfaces, leaving very detailed and delicate casts. Normally the original cellular material has disappeared completely, having been oxidized or broken down by microorganisms under the typical conditions of fluctuating water level at the surface of these spring deposits. In some tufa or travertine deposits, but not in those considered here, quite thick beds consisting of densely packed leaf impressions or calcified moss banks can occur.

Less commonly, under conditions of very rapid deposition and permanent waterlogging, the actual plant material may be preserved almost intact, particularly if seeds, for example, are totally encased within tufaceous nodules. This category of preservation is well represented at Folkestone and Wateringbury.

A third category of remains consists of pollen and spores. Although a great deal of work has been carried out on the palynology of Flandrian fen and bog deposits in Britain, that of tufas has been virtually ignored. It has been considered that two major drawbacks exist concerning the pollen analysis of such deposits. First, it is widely held that alkaline environments are markedly less favourable to pollen preservation than the neutral to acid conditions found in bogs and in many lakes. Faegri & Iversen (1975, p. 180) state: 'The acidity of the substrate is also of great importance for preservation of exines. In raw humus ('mor') pollen grains may be excellently preserved even under relatively dry conditions, whereas they may be rather badly corroded in alkaline deposits, even if preservation conditions in general have been favourable. This may be partly due to a bacteriostatic (and fungistatic?) effect of the acid medium.' Although there may be some truth in this statement, pollen preservation in the highly calcareous marls of East Anglian Breckland meres and of small lakes in the Burren of western Ireland (W. A. Watts, personal communication) is excellent, so that alkaline conditions *per se* are not detrimental.

The second problem is that tufas almost invariably form under conditions of fluctuating water level. The exines of pollen and spores appear to be notably susceptible to oxidation under conditions of alternate wetting and drying. Under such stressful conditions differential destruction takes place. This has been the subject of debate and experiment (see, for example: Andersen 1970; Havinga 1964, 1967) but because of the predominance of interest in oligotrophic peat bogs and lakes such studies have concerned themselves almost exclusively with conditions of neutral to low pH. As far as we are aware no work has been done on the relative resistance of different pollen and spore types to decay or bacterial attack under alkaline conditions such as those that prevail in the neighbourhood of tufa-forming springs or in marl-producing lakes.

The most noticeable feature of the pollen assemblages at Folkestone and Wateringbury is the large number of grains that defy identification because they are too badly corroded, crumpled or broken. The proportion of identifiable to unidentifiable grains is recorded on the diagrams for each level. It must be assumed that an incalculable but probably considerable amount of pollen and spores has been destroyed, so that only a residual assemblage is actually being studied. In addition, serious differential destruction of taxa has certainly taken place. In view of the paucity of evidence with regard to pollen preservation under alkaline sediment conditions, it seems worthwhile to record observations made on the samples from these sites.

The pollen percentages are based on counts of grains that it was possible to identify with certainty. It follows that there is a bias not only in favour of taxa that occur in abundance or are particularly resistant, but also in favour of those that tend to corrode in a characteristic way or have prominent shapes or features that render identification possible, even when their exines are in an advanced state of decay. *Pinus*, for example, with its saccate grains, certainly falls into the last class, though it also seems to be rather resistant to corrosion in any case. The arci of *Alnus* grains and the deeply invaginated pores of *Tilia* ensure that these grains can be recognized when almost all surface pattern has been lost. *Ulmus* grains could generally be recognized because of the persistent nature of their rugulate sculpture pattern. The triporate grains of *Betula* and *Corylus* tend to decay in rather different ways. In *Betula* the surface of the exine becomes etched and featureless but the annular nature of the pores remains visible. In *Corylus* the pores become indistinct, but very often, though not always, the corroded surface of the grain takes on a verrucate appearance. These differences greatly reduce the difficulties of identifying triporate grains. The Gramineae pollen that was encountered fell into two classes: smaller grains which could be identified from their single pore quite easily, even when corroded, and larger grains which crumpled up almost completely, presumably as their walls became thinned and less rigid. These could sometimes be identified if they could be moved sufficiently on the slide to reveal the presence of the pore. The most difficult pollen grains to identify with certainty were those of Cyperaceae and *Quercus*. It should be noted at this stage that within any particular pollen sample the range of preservation of grains of individual taxa was broad. Thus in samples where, for example, *Quercus* was only represented by shadowy, barely identifiable grains, the occasional perfectly preserved grain occurred, leaving no doubt about the occurrence of the taxon at that level. The problem with identifying Cyperaceae grains is their lack of well defined features or sculpture, so that when slightly corroded they resemble featureless unidentifiable corroded grains of other taxa. The same is true of *Quercus*, but the general condition of the pollen grains of this taxon, at levels where it was most abundant, does suggest that it is particularly susceptible to corrosion and likely to be severely under-represented in the diagrams.

Havinga (1964) studied the corrosion susceptibility of pollen of different tree taxa to artificial oxidation, and related the results to the condition of pollen in sandy soils. He arranged the common tree genera in the following sequence of increasing susceptibility to corrosion: *Tilia*, *Alnus*, *Corylus*, *Betula*, *Carpinus*, *Ulmus*, *Quercus*, *Fagus*, *Fraxinus*. Later (Havinga 1967), he studied the destruction of pollen grains in biologically active soils and recorded a different sequence: *Quercus*, *Fraxinus*, *Tilia*, *Betula*, *Fagus*, *Carpinus*, *Ulmus*, *Alnus*, *Corylus*. Andersen (1970) also found that in the mor soils of Danish forests *Quercus* grains appeared to be markedly less subject to corrosion than were those of *Corylus*. In the absence of experimentation it is not possible to produce a comparable list for the environments considered here. Comment can only be based on the general condition of pollen grains in the tufa samples and on comparisons with other pollen diagrams from southern England that cover the same timespan; these are very few in number and from rather different environments.

The general conclusion is that in tufaceous deposits the order of susceptibility of pollen grains to corrosion, whether by oxidation or microbiological activity, is the reverse of that suggested by Havinga (1967) and by Andersen for biologically active soils. *Corylus* appears to be generally rather resistant to corrosion, even allowing for the fact that, at Folkestone at least, it was probably over-represented because of trees growing virtually on the site. *Pinus* also seems to be relatively resistant. On the other hand, *Quercus* is exceedingly susceptible. These conclusions are also supported by the results of pollen analysis of calcareous soils beneath prehistoric earthworks (Dimbleby & Evans 1974), which suggest that pollen of *Corylus*, Compositae (Liguliflorae) and fern spores are particularly resistant to decay.

Plant macrofossils have been extracted in two ways from the sediments under consideration. Ideally, as from the tufa deposits from pit 1 at Folkestone, samples of known volume were decalcified in a basin of 0.7 M HCl and screened with plenty of water through a series of sieves. Each size fraction was then examined carefully under a binocular microscope and all identifiable plant fragments were picked out, sorted, determined and then stored in small phials containing a mixture of glycerine, alcohol and formalin. Procedures for handling and identification are given in more detail by Dickson (1970). Sample B from Folkestone and certain samples from Wateringbury were also treated in this way.

Other plant macrofossils, notably those from sample A at Folkestone and from the main sequence of samples at Wateringbury, were picked out either during extraction of the Mollusca or from the residues from such extraction. In either case these samples had been oven-dried and sieved. In this process certain plant fossils, particularly leaves, may be destroyed because they become very brittle when dried. Seeds may be overlooked if totally encased in tufa, and there is a possibility of small and very light seeds being lost during the sieving and drying operations. All in all, it is better to use wet-sieving techniques wherever possible.

The samples for pollen analysis were largely prepared by standard techniques. They were, however, also treated with sodium pyrophosphate, $Na_4P_2O_7$, as described by Bates *et al.* (1978). This greatly reduces the amount of material to be digested in HF but it may also be applied at later stages of the preparation procedure to remove any persistent fine-grained inorganic debris. Acetolysis was by boiling for 30 min in a 20 : 1 solution of CH_3COOH and concentrated H_2SO_4, followed by oxidation (cold) over 2–5 h in a 4.5 : 8 : 0.75 mixture of aqueous $NaClO_3$, CH_3COOH and concentrated H_2SO_4. Finally the residues were heated for about 5 min in 100 g/l NaOH and washed repeatedly in distilled water before mounting either in silicone oil, via tertiary butyl alcohol, $(CH_3)_3COH$, or directly in safranin-stained glycerine jelly. This rather gentle 'Godwin' acetolysis procedure followed by oxidation is more time-consuming than the widely used Erdtman acetolysis, but yields far more satisfactory results for these sediments. There is no evidence that this treatment is any more corrosive to pollen grains than is the Erdtman method, provided that the duration of oxidation is carefully controlled, and the removal of other forms of organic detritus thereby achieved is more efficient. The oxidation treatment described must follow and not precede the acetolysis (cf. variations of this technique described by Brown (1960, pp. 27, 29–30)) and should on no account be used in conjunction with the Erdtman acetolysis, which then does cause considerable loss of pollen.

3. Folkestone

(*a*) *Location and stratigraphy*

The site (National Grid reference TR 220379) lies on the Cretaceous Gault Clay at the mouth of an escarpment coombe (Holywell Coombe) immediately west of Sugarloaf Hill. The coombe contains several springs, drainage from which becomes entirely subsurface for a distance of some 500 m (figure 2). In November 1969 three closely adjacent pits were cut with a mechanical excavator as near as possible to the site of the original trial pit in the axis of the valley floor about 300 m below the springs and about 110 m north of the new bypass road (Churchill Avenue). The general relationship of the deposits is shown in figure 3. The water table lies at about 1.5 m from the surface and pumping was necessary to allow examination. In spite of this, rapid collapse of the unshored sides of the pits tended to occur due to the free movement of water through the permeable basal deposits above the Gault Clay.

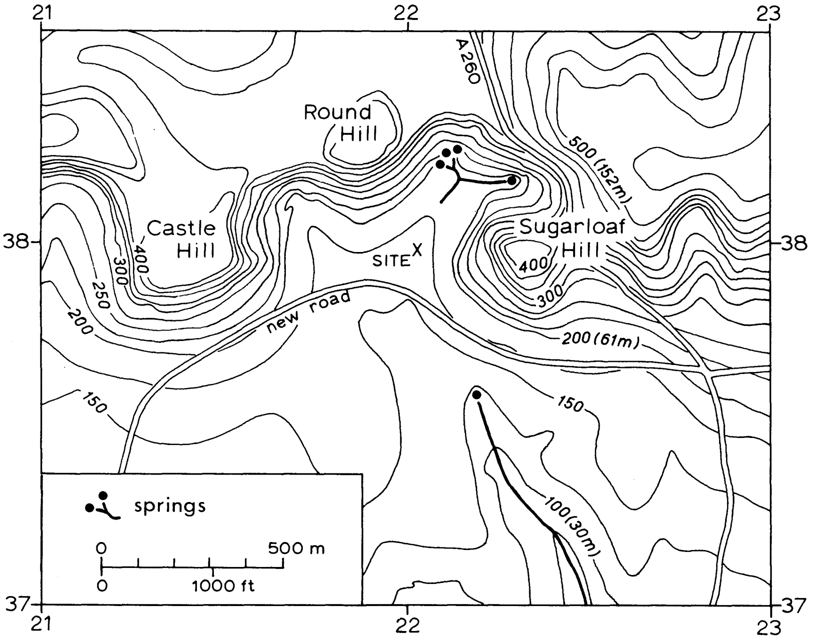

Figure 2. Holywell Coombe, Sugarloaf Hill, Folkestone (contours in feet (1 ft ≈ 0.305 m)). National Grid 1 km coordinates are marked.

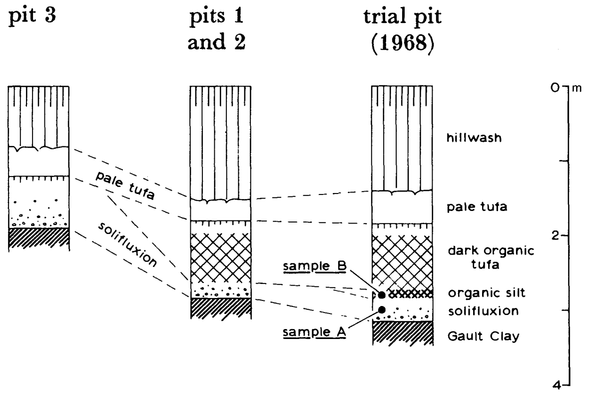

Figure 3. Sections seen in 1968 and 1969 excavations, Holywell Coombe, Folkestone (TR 220379).

Pits 1 and 2 showed a similar stratigraphy. A sediment monolith removed from pit 1 (figure 4) was measured as follows (top 75 cm below ground level).

depth/cm	
0–75	brown (Munsell 10YR 5/3) humic chalk silt with scattered stones (hillwash), slightly darker in basal 20 cm; base irregular
75–91	pale yellow (2.5Y 7/4) soft nodular tufa
91–94	greyish brown (2.5Y 5/2) organic clayey silt
94–104	pale yellow (2.5Y 7/4) soft nodular tufa
104–113	light brownish grey (2.5Y 6/2) slightly organic clayey chalk silt, passing down into
113–121	light grey (2.5Y 7/2) tufaceous chalk silt, passing down into

depth/cm	
121–160	greyish brown (2.5Y 5/2) tufaceous organic chalk silt, with scattered tufa nodules and much wood debris, including hazel (*Corylus*) nuts, passing down into
160–190	tufaceous organic silt as above, but tufa nodules larger and more abundant, and locally forming lenses of well sorted tufa gravel
190–210	clastic chalk and flint gravel
210+	grey Gault Clay

Much of the tufa is in the form of nodules, possibly algal in origin, up to about 5 cm across and having a concentric laminated internal structure. Frequently there is a nucleus consisting of a shell or plant fragment.

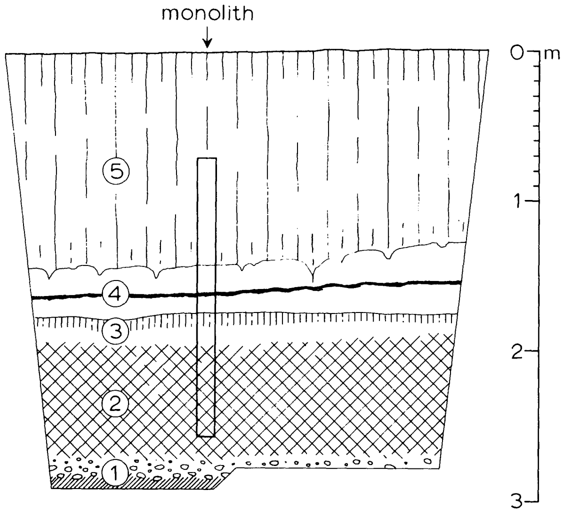

Figure 4. South face of pit 1, Folkestone, November 1969. (1) Gault Clay with veneer of solifluxion gravel; (2) dark silty nodular tufa with much vegetable debris; (3) tufaceous chalky silt, grey towards top; (4) pure tufa with dark organic seam; (5) humic chalky silt (hillwash).

The original trial pit of July 1968 exposed a section similar to that described above. But at one point near the base there was seen:

> dark tufaceous organic chalk silt with tufa nodules (as pit 1, 121–190 cm); dark organic silt without tufa nodules (sample B; ^{14}C Q-1508), 10 cm; grey chalk silt with chalk pebbles and plant fragments (sample A; ^{14}C St-3409), 30 cm; chalk and flint gravel on Gault Clay (as pit 1, 190–210 cm).

Small bag samples (samples A and B) proved to be rich in macroscopic plant remains. Unfortunately these horizons could not be relocated in the 1969 excavations, in which there everywhere appeared to be a hiatus at this level (figure 3).

At pit 3 the deposits were thinner, the upper tufa (layer 4, figure 4) having overlapped the lower, more organic layers to rest directly on Devensian chalky solifluxion (figure 3). The stratigraphy of a monolith block was as follows (top 65 cm below ground level).

depth/cm	
0–15	brown chalk silt (hillwash)
15–50	pale nodular tufaceous silt

depth/cm	
50–53	greyish brown organic clayey chalk silt
53–57	pale nodular tufaceous silt
57–80	pale (5Y 7/2) 'cheesy' chalk silt with scattered small chalk pebbles; top 15 cm darker (5Y 6/2) and penetrated by rootlet cavities
80–125	as above, but coarser and more pebbly
125+	veneer of iron-stained flint and chalk gravel on Gault Clay

(*b*) *Mollusca*

The results of the molluscan analyses are listed in tables 1 and 2, and partially displayed in figure 5. Preservation is on the whole very good. Some valves of *Pisidium* from the lower waterlogged layers have their organic periostracum preserved.

TABLE 1. MOLLUSCA, PIT 3, AND 1968 TRIAL PIT, FOLKESTONE

depth/cm	100–110	90–100	80–90	75–80	70–75	65–70	sample A, 1968 (St-3409)	sample B, 1968 (Q-1508)
dry mass of sample/g	1525	1455	1380	760	745	725	—	—
Carychium minimum Müller	—	—	—	—	—	—	—	6
Carychium tridentatum (Risso)	—	—	—	—	—	—	—	1
Lymnaea truncatula (Müller)	1	4	9	—	—	—	8	—
Catinella arenaria (Bouchard-Chantereaux)	—	9	5	—	—	1	—	1
cf. *Oxyloma pfeifferi* (Rossmässler)	4	5	5	1	—	—	—	1
Cochlicopa spp.	4	5	8	3	2	1	2	7
Columella columella (Martens)	—	—	—	—	1	3	?1	—
Vertigo pusilla Müller	—	—	—	—	—	—	—	1
Vertigo antivertigo (Draparnaud)	—	—	—	—	1	—	—	1
Vertigo genesii (Gredler) seg.	1	1	1	—	2	—	—	—
Abida secale (Draparnaud)	20	22	12	6	7	24	15	2
Pupilla muscorum (Linné)	9	24	17	9	14	22	21	2
Vallenia costata (Müller)	19	25	18	9	13	4	7	2
Vallonia pulchella (Müller)	4	1	—	2	1	2	1	2
Vallonia pulchella/excentrica	16	8	11	6	6	8	5	3
Punctum pygmaeum (Draparnaud)	13	14	13	5	2	3	7	4
Vitrina pellucida (Müller)	3	3	1	1	4	—	—	3
Vitrea cf. *contracta* (Westerlund)	—	—	—	—	—	—	—	2
Nesovitrea hammonis (Ström)	7	2	5	1	3	8	1	3
Aegopinella nitidula (Draparnaud)	—	—	—	—	—	—	—	3
Zonitoides nitidus (Müller)	—	—	—	—	—	—	—	1
Deroceras spp.	12	3	4	5	8	9	1	8
Euconulus fulvus (Müller) agg.	2	2	2	1	2	1	1	5
Helicella itala (Linné)	2	—	—	—	—	—	—	—
Trichia hispida (Linné)	16	23	43	44	49	81	53	9
Arianta arbustorum (Linné)	1	1	1	2	1	1	3	5
Pisidium casertanum (Poli)	2	1	1	—	—	—	—	7
Pisidium tenuilineatum Stelfox	—	—	—	—	—	—	—	1

Sample A, 1968 *trial pit*, *and pit 3*, *110–65* cm

The basal chalky solifluxion silts above the Gault Clay contain a fauna of unmistakably late-glacial type, characterized by *Catinella arenaria*, *Columella columella*, *Vertigo genesii*, *Abida secale*, *Pupilla muscorum*, together with large numbers of *Trichia hispida*. The Mollusca indicate both dry hillsides with a patchy cover of herbaceous vegetation, and wet swampy ground, the latter

TABLE 2. MOLLUSCA, PIT 1, FOLKESTONE

depth/cm	175–180 (St-3395)	155–160	145–150	135–140 (St-3411)	125–130	116–120	112–116	108–112	104–108	99–104	94–99	91–94	St-3410 (Pit 2)	85–91	80–85	65–70	60–65	45–50	30–35	15–20	0–5
dry mass of sample/g	605	615	610	600	630	790	775	810	760	875	790	750	—	765	790	1100	1075	830	1005	950	1050
Pomatias elegans (Müller)	—	—	—	—	—	—	—	—	1	8	3	3	2	2	2	47	56	22	11	10	13
Acicula fusca (Montagu)	—	—	—	—	—	—	—	—	—	—	1	95	32	10	8	—	—	—	—	—	—
Carychium minimum Müller	24	59	43	79	53	33	19	127	156	36	10	83	47	7	5	1	3	—	—	1	—
Carychium tridentatum (Risso)	53	129	99	165	58	59	27	139	1016	190	52	454	373	32	43	35	34	1	1	1	—
Lymnaea truncatula (Müller)	5	10	10	24	13	11	5	13	2	—	—	6	3	2	1	2	2	—	—	4	6
Succinea oblonga Draparnaud	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	7	3
cf. *Oxyloma pfeifferi* (Rossmässler)	—	1	1	2	5	1	6	19	9	8	7	7	8	1	10	3	2	—	—	—	—
Cochlicopa spp.	10	17	14	20	4	14	10	40	72	25	7	16	16	3	3	20	39	9	4	6	1
Columella columella (Martens)	5	2	4	6	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Columella edentula (Draparnaud)	3	7	6	3	1	5	6	30	27	7	2	14	6	1	—	1	—	—	—	—	—
Columella columella/edentula	4	—	1	14	1	1	2	2	1	—	—	3	1	1	—	—	—	—	—	—	—
Vertigo pusilla Müller	12	19	13	16	10	17	5	7	23	9	2	23	9	3	1	—	—	—	—	—	—
Vertigo antivertigo (Draparnaud)	1	—	—	?1	?1	1	5	41	2	1	?1	—	2	—	—	—	—	—	—	1	—
Vertigo substriata (Jeffreys)	2	4	4	6	—	5	9	50	16	4	5	20	8	—	2	—	—	—	—	—	—
Vertigo pygmaea (Draparnaud)	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	11	11	6	9	22	9
Vertigo genesii (Gredler) seg.	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Vertigo moulinsiana (Dupuy)	—	1	—	—	3	2	4	5	1	—	—	2	—	—	—	—	—	—	—	—	—
Vertigo alpestris Alder	—	—	?1	2	1	1	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—
Vertigo angustior Jeffreys	1	3	4	5	1	2	3	55	20	1	—	—	—	—	—	—	—	—	—	—	—
Abida secale (Draparnaud)	4	5	2	5	3	3	2	1	—	3	1	—	—	—	—	1	—	—	—	—	—
Pupilla muscorum (Linné)	4	11	3	10	5	8	3	—	1	2	1	—	1	—	—	28	13	3	5	15	3
Leiostyla anglica (Wood)	—	—	—	—	—	—	—	—	—	—	—	63	26	8	14	1	—	—	—	—	—
Lauria cylindracea (da Costa)	7	9	8	27	10	17	8	5	6	3	2	2	?1	1	—	—	—	—	—	—	—
Vallonia costata (Müller)	23	62	46	49	31	30	10	16	19	7	2	2	3	4	3	275	211	51	22	27	5
Vallonia pulchella (Müller)	1	1		1	1	1	1	—	—	—	—	—	—	—	—	—	1	5	12	7	6
Vallonia excentrica Sterki				—	—	—	—	—	—	—	—	—	—	—	—	22	17	11	5	3	2
Vallonia pulchella/excentrica	9			5	2	4	2	1	—	3	—	—	3	1	2	57	52	41	62	35	52
Acanthinula aculeata (Müller)	1			8	4	1	—	4	10	50	13	13	15	2	2	20	3	—	1	—	—
Spermodea lamellata (Jeffreys)				—	—	—	—	—	—	1	2	181	83	37	46	—	—	—	—	—	—
Ena obscura (Müller)				1	1	1	1	—	1	—	—	—	2	—	—	—	—	—	—	—	—

Punctum pygmaeum (Draparnaud)	18	14	16	20	12	11	6	13	37	6	1	12	17	2	2	7	4	1	1	6	2
Discus ruderatus (Férussac)	1	2	1	2	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Discus rotundatus (Müller)	—	—	—	—	—	—	—	1	55	290	58	215	168	30	36	44	23	3	2	1	2
Vitrina pellucida (Müller)	3	2	—	1	1	2	—	—	—	4	1	3	1	—	1	—	—	1	1	—	—
Vitrea crystallina (Müller)	36	96	63	99	53	59	33	97	331	46	12	39	95	2	3	6	1	2	—	—	1
Vitrea contracta (Westerlund)	4	21	10	13	17	6	7	6	61	39	4	13	33	3	6	13	4	1	17	6	6
Nesovitrea hammonis (Ström)	17	27	15	31	12	10	2	14	76	13	4	3	5	—	—	4	2	—	—	—	—
Aegopinella pura (Alder)	2	15	14	15	6	10	4	21	57	49	20	32	19	15	18	12	7	—	—	—	1
Aegopinella nitidula (Draparnaud)	23	57	40	54	31	23	16	48	228	225	90	433	171	68	59	43	50	7	4	1	—
Oxychilus cellarius (Müller)	—	—	—	—	—	—	—	—	—	98	46	124	56	29	27	9	8	—	2	3	1
Oxychilus alliarius (Miller)	—	—	—	—	—	8	6	15	58	1	—	1	2	—	—	—	—	—	—	—	—
Zonitoides nitidus (Müller)	5	2	10	10	5	4	6	10	6	5	1	3	1	—	1	—	—	—	—	—	—
Milax sp.	—	—	—	—	—	2	1	2	19	37	4	19	16	12	19	95	102	46	52	24	12
Deroceras/Limax spp.	26	13	2	3	3	1	1	25	18	57	10	28	11	18	19	69	67	24	40	73	31
Euconulus fulvus (Müller) agg.	6	10	5	8	3	9	5	22	15	7	5	10	9	2	2	—	—	—	—	—	—
Cecilioides acicula (Müller)	—	—	—	—	—	—	—	—	—	1	2	1	—	1	2	19	22	3	16	42	16
Cochlodina laminata (Montagu)	—	—	—	—	—	—	—	—	1	3	1	1	4	—	1	3	5	?1	?2	—	—
Macrogastra rolphii (Turton)	—	—	—	—	—	—	—	—	—	—	—	—	?1	—	—	1	1	—	—	—	—
Clausilia bidentata (Ström)	7	10	5	12	8	5	5	3	26	42	10	16	7	5	4	11	5	6	1	2	3
Balea perverea (Linné)	—	—	—	—	—	—	—	—	—	2	1	2	3	1	3	—	—	—	—	—	—
Helicella itala (Linné)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	7	3
Monacha cartusiana (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	?1	—	4	—	—
Monacha cantiana (Montagu)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	7
Trichia hispida (Linné)	19	26	17	33	7	24	8	2	9	11	3	14	9	6	5	113	107	51	51	67	65
Trichia striolata (Pfeiffer)	—	6	9	15	26	17	6	8	48	54	11	8	14	1	1	90	205	63	25	19	38
Helicigona lapicida (Linné)	—	—	—	—	—	—	—	—	—	—	1	1	3	1	1	3	1	1	1	1	1
Arianta arbustorum (Linné)	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	—	×	—
Arianta/Cepaea spp.	8	20	8	12	7	5	4	7	27	46	14	70	23	8	13	33	31	19	7	3	1
Cepaea sp.	×	×	—	×	—	×	×	×	×	×	×	×	×	×	—	×	×	×	×	×	×
Helix aspersa Müller	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Pisidium casertanum (Poli)	2	45	51	67	278	109	95	238	20	27	6	11	4	1	1	1	—	—	—	—	1
Pisidium personatum Malm	53	220	192	372	224	176	32	143	23	26	10	12	10	—	—	—	—	—	—	—	—
Pisidium milium Held	—	—	—	—	1	—	8	34	2	10	14	26	1	1	3	—	—	—	—	—	—
Pisidium subtruncatum Malm	—	—	—	—	102	1	12	19	—	77	172	61	1	1	—	—	—	—	—	—	—
Pisidium nitidum Jenyns	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—
Pisidium tenuilineatum Stelfox	3	32	33	13	28	86	29	16	—	—	1	—	1	—	5	—	—	—	—	—	—

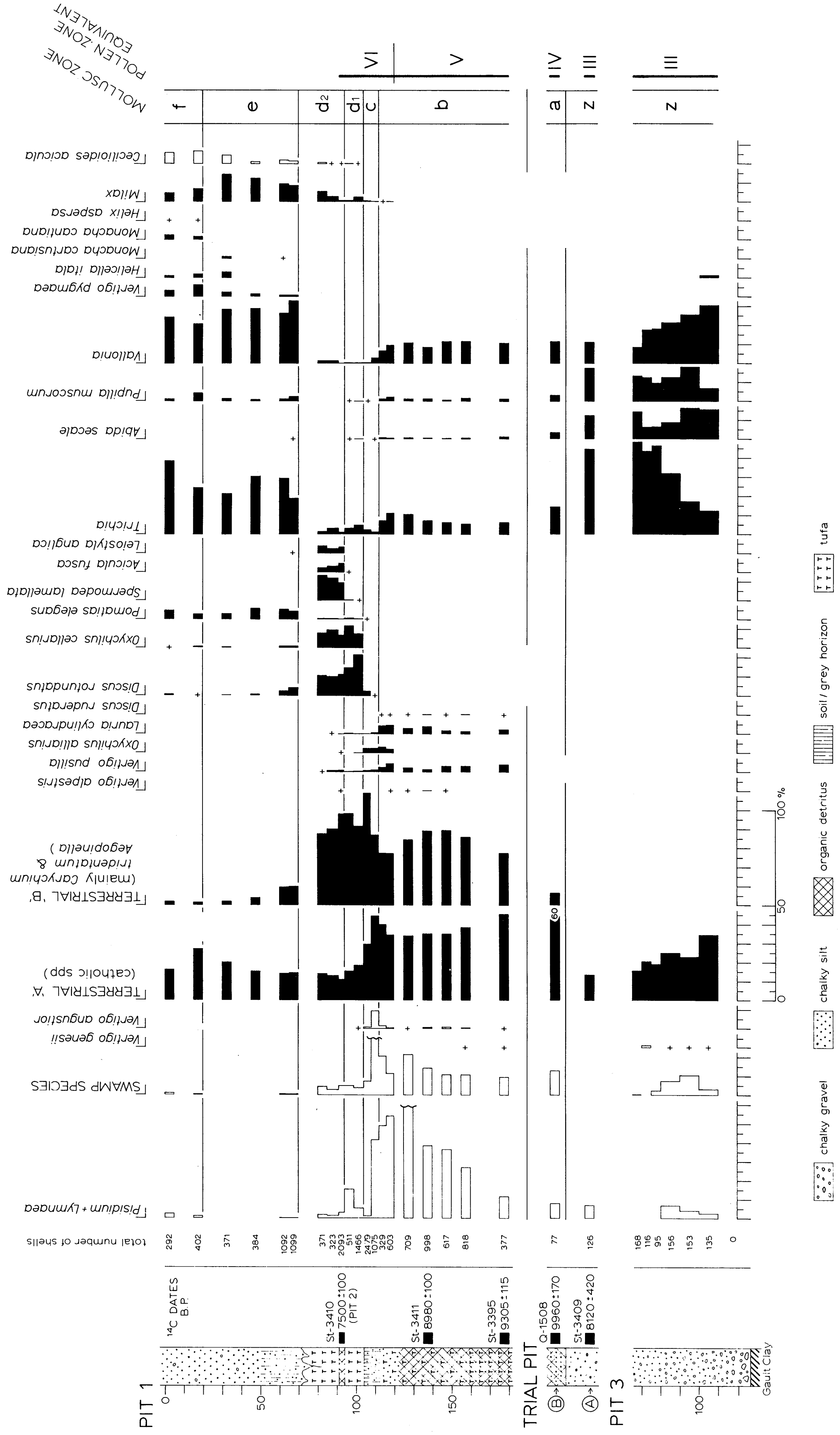

FIGURE 5. Molluscan diagram, Folkestone.

evidently occupying the floor of the valley. The marsh snails *Vertigo genesii* and *Catinella arenaria* are boreo–alpine species virtually extinct in Britain, and are today characteristic of calcareous flushes in highland areas of Scandinavia. Both are common in Late Devensian sediments of suitable facies in southern Britain.

The nature and significance of the late-glacial molluscan fauna are discussed more fully in Kerney (1963) and in Kerney *et al.* (1964), where most of the species are illustrated.

Sample B, 1968 *trial pit*

The Mollusca of the overlying horizon of organic silt (sample B) show a decline of the more characteristic open ground late-glacial elements (*Pupilla*, *Abida*, *Trichia*) and an increase to a value of 60 % of the species of the catholic terrestrial group 'A'. This suggests the development of a more stable and abundant vegetational cover, to the disadvantage of species adapted to broken ground. Clearly this is to be linked with the ending of solifluxion, as reflected in the lithological change from mineral to organic deposits. The environment remained relatively open, although *Carychium tridentatum* and *Aegopinella nitidula*, species with woodland affinities (terrestrial group 'B'), make their appearance. Swampy conditions continue.

Pit 1, 180–112 cm

The fauna is a mixture of dry ground, marsh and aquatic species. Freshwater Mollusca (mainly *Pisidium*) are most common in this division, especially above 130 cm. The *Pisidium* fauna indicates both swampy ground (*P. casertanum*, *P. personatum*) and more permanent water (*P. milium*, *P. subtruncatum*, *P. tenuilineatum*). The occurrence of *P. tenuilineatum* is particularly noteworthy. This rare species is known also from early Flandrian tufas at Brook, Kent (Kerney *et al.* 1964), and at Totland Bay, Isle of Wight (Preece 1979). Marsh species are also common and the marsh heliophile *Vertigo angustior* is consistently present. *Vertigo genesii* and *Columella columella* survive in small numbers from the Late Devensian.

The main body of dry ground species suggests a thin woodland cover. *Vertigo pusilla*, *Lauria cylindracea* and *Discus ruderatus* are characteristic elements of the fauna. The open ground species *Vallonia costata* occurs at a value of about 10 %, and *Pupilla muscorum* and *Abida secale* are present in small numbers. All of these will live in patches of broken stony soil in dry open woods, and it is perhaps significant that the obligatory grassland species *Vallonia excentrica* does not occur.

Pit 1, 112–80 cm

Swampy conditions continue, though the purely aquatic element declines markedly. It is interesting to note the sharp peak in *Vertigo angustior* at the beginning of this division: this clearly reflects a transient development of boggy grassland occurring at the change from open, flooded swamp to shaded marsh.

The dry-ground fauna changes in character. *Discus rotundatus* appears and rises to high values, followed by *Oxychilus cellarius*. *Carychium tridentatum* is abundant. The open-ground species (*Vallonia costata*, *Pupilla muscorum*, *Abida secale*) become rare. All this suggests the development of a more closed forest cover.

Above 94 cm there is a great expansion of *Acicula fusca*, *Leiostyla anglica* and *Spermodea lamellata*, and a total disappearance of the open-ground genera *Pupilla* and *Abida*. This reinforces the evidence for closed forest, probably of high humidity. *Leiostyla* and *Spermodea* have markedly western, oceanic distributions in the British Isles at the present time, and are virtually extinct in southern England (Kerney 1976*a*, maps 78 and 86).

Pit 1, 70–0 cm

The Mollusca reflect a dramatic reversion to open ground. *Vallonia* forms 25–30% of the assemblages, together with *Pupilla muscorum*, *Vertigo pygmaea*, *Monacha cartusiana* and *Helicella itala*. The abundance of *Trichia* is reminiscent of the late-glacial environment. *Pomatias elegans*, which appears sparsely in the forest zone below, increases in numbers, which suggests the development of broken ground with scrub. Shade-demanding species (*Discus rotundatus*, *Carychium tridentatum*, *Acicula fusca* etc.) decline or disappear. *Milax*, which today tends to be strongly synanthropic, is common, and above 20 cm the introduced mediterranean snails *Monacha cantiana* and *Helix aspersa* also occur.

The slightly but significantly higher values for *Discus rotundatus*, *Carychium tridentatum*, *Aegopinella* and other shade-demanding species in the buried soil below 60 cm may reflect the former existence of woodland on this land surface, at a period after tufa formation had ceased.

The frequency of *Vallonia pulchella* and the appearance of *Succinea oblonga* in the upper part of the hillwash suggest increasing dampness. *S. oblonga* is now a rare species in Britain, with a specialized liking for bare muddy surfaces in open situations.

(*c*) *Plant remains*

Sample A, 1968 *trial pit*

This sample failed to yield pollen and spores but contained much coarse plant detritus, especially small stem fragments of woody and herbaceous plants, plant cuticle and mosses, as well as fruits and seeds (table 3). The combination of well preserved plant macrofossils and virtual absence of pollen is not uncommon from drift-muds of glacial age. A probable explanation is that plant detritus, together with silt and frost-shattered chalk, was washed down from the open hillside behind the site and accumulated in shallow temporary pools, or even puddles, at the foot of the slope. These pools tended to dry out frequently, which resulted in oxidation of the pollen, but, with the periglacial climate limiting fungal and bacterial activity, some of the coarser plant detritus survived long enough to be buried and preserved in a waterlogged condition by further influxes of downwashed inorganic sediment.

The plant macrofossil assemblage from this horizon is both diverse and well preserved, with the exception of leaves, which probably became fragile and badly broken when the sample was dried out after collection. It clearly represents plant communities from several different habitats, but notably from the steep dry slopes of the coombe cut into the Lower Chalk and from its marshy floor underlain by Gault Clay.

Remains of forest trees are entirely lacking, and the evidence suggests a late-glacial landscape of open heathland with dwarf shrubs, a discontinuous cover of herbaceous vegetation and a fair amount of bare ground. Damper ground along the spring line at the foot of the Chalk escarpment supported tall herb vegetation, willow scrub and freshwater marsh.

The most abundant shrub remains are those of *Betula nana*, dwarf birch. Today *B. nana* has a distribution of arctic–alpine type in northern and central Europe. Over much of its range it is found either in subalpine dwarf shrub-heath or in a tundra-type vegetation on mineral soil with dwarf arctic–alpine herbs and shrubs. Although other low-growing shrubs, such as *Juniperus*, *Empetrum* and *Arctostaphylos* occur in the assemblage, the presence of a number of

TABLE 3. PLANT MACROFOSSILS FROM 1968 TRIAL PIT, FOLKESTONE

Sample A	
shrubs and dwarf shrubs	
Arctostaphylos uva-ursi (L.) Spreng.	1 fruitstone
Betula nana L.	56 fruits; 1♀ cone scale; 2♂ cones; 1 entire leaf + several fragments
Empetrum sp.	1 fruitstone
cf. *Empetrum* sp.	1 fruitstone (immature?)
Juniperus communis L.	2 leaf tips
Salix spp.	1 capsule; 67 bud scales; 1 leafy bud; leaf fragments
herbs	
Anthriscus sylvestris (L.) Hoffm.	1 fruit
Arenaria ciliata L.	20 seeds
Armeria maritima (Mill.) Willd.	1 calyx
Carex aquatilis Wahlenb. or *bigelowii* Torr. *ex* Schwein	20 biconvex nutlets
Carex spp.	5 trigonous nutlets
Cerastium alpinum L. or *arvense* L.	1 seed
Chrysanthemum leucanthemum L.	2 fruits
cf. *Conopodium majus* (Gouan) Lor. & Barr.	1 fruit
Helianthemum canum (L.) Baumg.	7 leaf fragments
Hieracium pilosella agg.	2 fruits
Papaver sp. (sect. Scapiflora)	2 seeds
Ranunculus aconitifolius L.	12 achenes
Rumex sp. (sg. *Rumex*)	3 fruits
Silene cf. *acaulis* L.	10 seeds
Silene vulgaris (Moench) Garcke agg.	70 seeds
Stellaria neglecta Weihe	15 seeds
Stellaria sp.	1 immature seed
Taraxacum officinale agg.	1 fruit
Thalictrum cf. *minus* L.	2 fruits
Valeriana sp.	1 fruit
Viola sp. (sg. *Viola*)	4 seeds
mosses	
Crataneuron commutatum (Hedw.) Roth var. *commutatum*	very abundant
Pohlia sp.	frequent
fungal fruiting bodies ('*Geococcum*')	frequent
Sample B	
trees and shrubs	
Betula nana L.	1 fruit; 1 cone scale
Betula spp. (trees)	60 fruits; 17♀ cone scales
Populus sp.	70 bud scales
Prunus padus L.	3 fruitstones
Salix spp.	2 buds
mosses	
Eurhynchium striatum (Hedw.) Schimp.	frequent
Homalothecium lutescens (Hedw.) Robins.	frequent
fungal fruiting bodies ('*Geococcum*')	occasional

herbaceous taxa that are quite characteristic of Devensian full and late-glacial floras from many sites in Britain suggests that it was vegetation of the latter type that dominated the slopes at Folkestone. *Empetrum* and *Arctostaphylos* tend to be calcifuge and are unlikely to have been growing on the chalky slope itself, but there may have been patches of acid soil on the top of the escarpment. *Empetrum* seeds were also recorded from the late-glacial deposits at Dover Hill, Folkestone, less than 2 km away (Kerney 1963).

Among the herbs, members of the Caryophyllaceae were particularly conspicuous and included *Silene vulgaris*, *Arenaria ciliata*, *Cerastium* and probably *Silene acaulis*. *Armeria*, *Helianthemum canum* and *Papaver*, arctic poppy, are typical components of this vegetation, as no doubt were grasses and sedges, although it has not been possible to demonstrate the presence of the former with certainty. *Chrysanthemum leucanthemum* and *Hieracium pilosella* are interesting additions to this picture. From the marsh and tall herb communities are recorded *Rumex*, *Anthriscus sylvestris*, *Stellaria neglecta*, *Valeriana*, *Ranunculus aconitifolius* and also *Carex* spp.

Together the botanical and molluscan evidence suggest that this plant assemblage is of Younger Dryas age. It is of importance because there are very few comparable lists of plant macrofossils of this age, particularly from southern Britain, and, indeed, because of the critical geographical location of the site, so close to the present European mainland. One characteristic of the late-glacial flora, which it demonstrates well, is the mixture of arctic–alpine plants and those having, today, a more southerly distribution, as has been discussed in detail by Godwin (1975).

Notes on individual plant taxa

Juniperus communis. Juniper is represented by two leaf fragments. Its occurrence is of interest in lending further support to Iversen's (1954) now widely accepted hypothesis that *Juniperus* was abundant in Younger Dryas vegetation, at least in a non-flowering state, so that it was able to respond immediately and flower freely with the onset of the Flandrian climatic amelioration.

Anthriscus sylvestris. Godwin (1975) lists only Cromerian and Ipswichian interglacial records for this species and refers to its 'doubtful status in the British Isles today'. There now seems to be little reason to query its native status in the British flora.

Arenaria ciliata. Bell (1968) studied seeds of a range of species of *Arenaria* by scanning electron microscopy and showed that they could be distinguished by their epidermal cell patterns. Several seeds from Folkestone examined in this way all proved to have cell patterns almost identical with those in Bell's photographs of *A. ciliata* from a wide geographical range of localities.

Chrysanthemum leucanthemum. This species is now being recognized as a member of Devensian open-ground plant communities. It was found in Middle Devensian deposits at Thrapston, but, apart from that, Godwin lists only Flandrian occurrences from archaeological contexts. The two fruits recovered are, therefore, the first late-glacial records for the British Isles.

Hieracium pilosella. This aggregate species has only one previous fossil record, from the Ipswichian interglacial, and so this too is new to the late-glacial vegetational record.

Papaver sp. (section Scapiflora). This taxonomically complex group of poppies covers not only the widespread species *P. alpinum* of the Alps and central Europe and *P. radicatum* of the Scandinavian mountains and the Arctic, including Iceland, but also a whole range of endemic species in isolated regions. No representatives of this group are native today in the British Isles. The fossil seeds from Folkestone closely resemble reference material of *P. radicatum* but an insufficient range of seeds of other species was available for comparison. Similar seeds are known from Devensian full-glacial deposits at Great Billing, Northants., and Barnwell Station, Cambridge (Morgan 1969; Bell & Dickson 1971), and there is another record of Younger Dryas age from Scotland (Conolly 1957).

Ranunculus aconitifolius. This too is a species today not native in the British Isles. It now occurs in montane areas of central Europe, where it grows in marshes and by streamsides. It too has Middle Devensian records for several sites in Britain, notably the Lea valley, Barnwell Station and Earith, and so is well recognized as a member of the Devensian 'full-glacial' flora, but this is the first evidence of its persistence into Younger Dryas times.

Stellaria neglecta. This is an unexpected addition to the late-glacial flora. Today it is a plant of shaded habitats, such as wood margins and stream banks, with a generally southerly distribution in western and central Europe, extending north into southern Sweden and Scotland. However, it is one of the more abundant elements in the Folkestone assemblage, and so was probably growing on damp ground close to the site of deposition.

Sample B, 1968 *trial pit*

Although this sample consisted very largely of coarse organic detritus, again no fossil pollen or spores were recoverable. The plant macrofossils, however, provide the first evidence for woodland conditions, probably still of a rather open nature. In strong contrast to sample A, most of the plant remains identified belong to tree species. Most abundant are those of tree birches and poplar, pioneer colonizers of open ground, with light, wind-dispersed seeds. Unfortunately, plant remains from this horizon were not well preserved, and both the winged fruits and cone scales were so damaged that it was not possible to identify them to species level with certainty, but the range of variation suggests that both *B. pendula* and *B. pubescens* were present. The bud scales of *Populus* were identified by their characteristic cell pattern, the epidermal cells being very thick-walled with small stellate lumina. *P. tremula*, the aspen, has been recorded from a number of late Devensian and early Flandrian deposits (Godwin 1975), but the characteristic catkin scales, on which specific identification is commonly made, were not recovered here. *Prunus padus*, bird cherry, is now uncommon in southeast England but more frequent in northern and western Britain. Willows were also present. Open turf on the chalky slopes is suggested by the occurrence of the moss *Homalothecium lutescens*.

Both plant macrofossil and molluscan evidence suggest for this sample a Flandrian Pre-boreal age, equivalent to Godwin's pollen zone IV, and this will be shown to be supported not only by the further studies at Wateringbury but also by radiocarbon dating of wood fragments from this sample.

Pit 1

Both pollen and plant macrofossils were recovered from the bottom metre of tufaceous sediments in pit 1, particularly where they were most organic. Above the prominent organic seam within the upper tufa (91–94 cm) no trace of plant materials was found. Either they were not preserved here or have been destroyed by subsequent oxidation.

The pollen diagram for this pit is presented as figure 6 and the plant macrofossil list as table 4. In this case it is most convenient to consider both together.

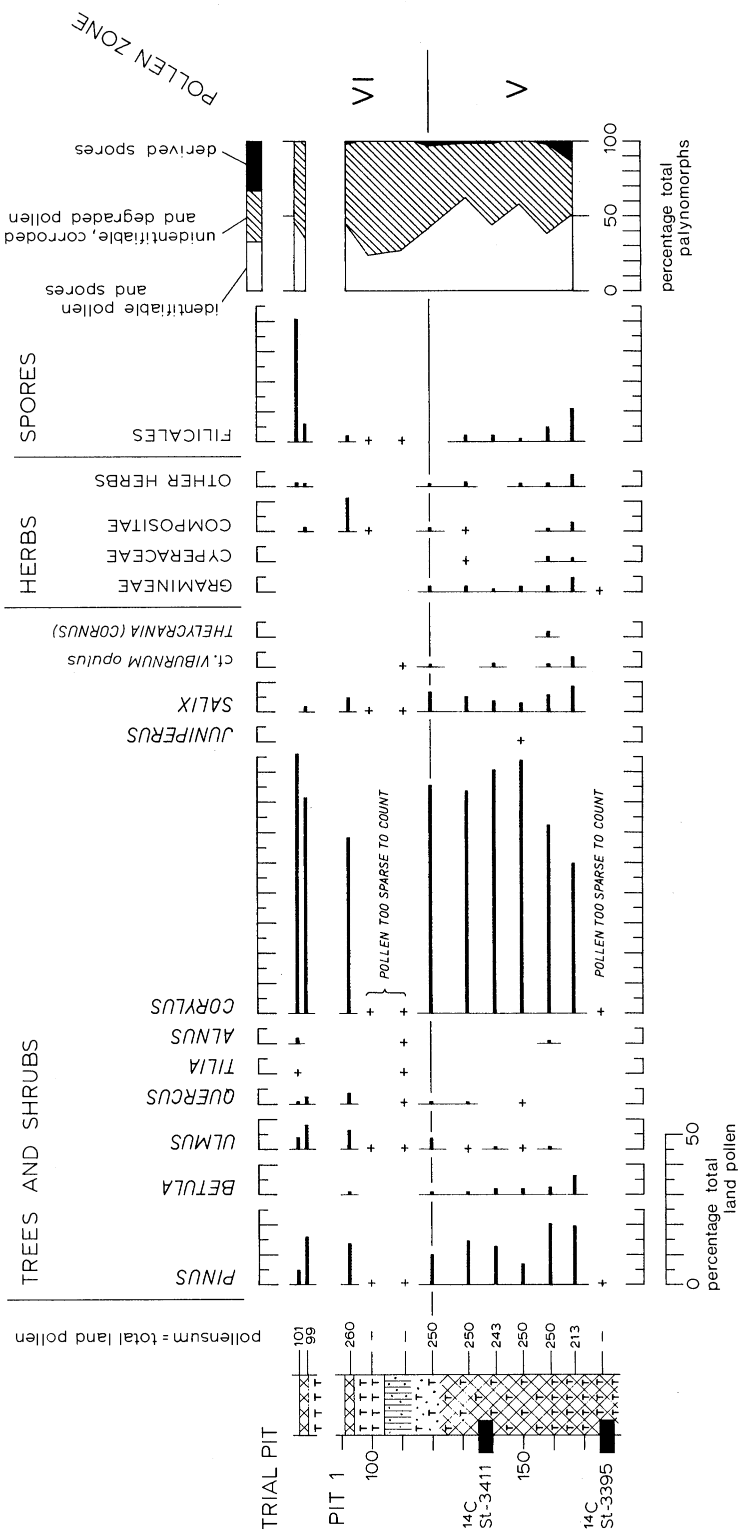

FIGURE 6. Pollen diagram, Folkestone.

TABLE 4. PLANT MACROFOSSILS FROM PIT 1, FOLKESTONE

		170–180	160–170	150–160	140–150	130–140	120–130	110–120	100–110	90–10
trees and shrubs										
Betula sp.	fr.	—	—	—	—	—	—	—	—	3
Corylus avellana L.	n.	+	3	31	17	15	24	2	—	—
	b., ct.	+	+	++	++	++	+	—	—	—
Crataegus monogyna Jacq.	fst.	—	4	5	7	2	3	—	—	—
Populus sp.	b.	—	—	—	—	—	1	—	—	—
Salix spp.	b.	—	—	—	+	+	—	—	—	—
Thelycrania (*Cornus*) *sanguinea* (L.) Fourr.	fst.	+	—	25	12	26	25	—	—	—
herbs										
Callitriche sp.	fr.	—	—	—	—	—	—	—	—	1
Carex riparia Curt.	nt. + u.	—	—	—	—	7	1	—	—	—
Carex spp.	nt.	—	—	—	1	6	—	—	—	—
Eupatorium cannabinum L.	fr.	—	—	1	—	1	6	*ca.* 50	+++	+++
Galium cf. *mollugo* L.	fr.	—	—	1	—	—	—	—	—	—
Labiatae indet.	nt.	—	—	1	—	—	—	—	—	—
Potentilla cf. *palustris* (L.) Scop.	a.	—	—	1	1	—	—	—	—	—
Potentilla sp.	a.	—	—	—	—	1	—	—	—	—
Silene vulgaris (Moench) Garcke	s.	—	—	1	—	—	—	—	—	—
Stachys cf. *sylvatica* L.	nt.	—	—	2	—	2	—	—	—	—
Urtica sp.	fr.	—	—	—	—	1	—	—	—	—
mosses										
Bryum spp.		—	—	—	+	—	+	—	—	—
Calliergon cuspidatum (Hedw.) Kindb.		—	—	—	—	—	+	—	—	—
Crataneuron commutatum (Hedw.) Roth		—	+	+	+	—	+	—	—	—
Eurhynchium sp.		—	—	+	—	—	—	—	—	—
Homalothecium (Hedw.) Robins.		—	—	+	—	—	+	—	—	—
cf. *Pohlia* sp.		—	—	—	—	—	+	—	—	—
Thamnobryum alopecurum (Hedw.) Nieuwl.		+	+	+	+	—	—	—	—	—
fungal fruiting bodies ('*Geococcum*')		—	+	+	+	+	+	—	—	—

Key: +, occasional; ++, common; +++, abundant; a., achene; b., bud; ct., catkin; fr., fruit; fst., fruitstone; n., nut; nt., nutlet; s., seed; u., urticle.

Pit 1, 180–120 cm

The pollen assemblages, like those of the molluscs, are rather uniform over this section of the deposits, which is believed to have accumulated rather rapidly, a conclusion supported by radiocarbon dating. The pollen diagram is dominated by *Corylus*, with values of up to 80% of total land pollen, though values for *Pinus* are significant, as to a lesser extent are those for *Salix*. Towards the base of the deposit there is a definite increase in the pollen values for *Betula*, Gramineae, Compositae and other herbaceous types such as Umbelliferae, Leguminosae, Chenopodiaceae, *Filipendula* and other Rosaceae. Only occasional grains of thermophilous trees, *Ulmus* and *Quercus*, were detected.

The dominance of *Corylus* in the pollen record is both explained and reinforced by the presence of large numbers of hazel nuts, catkins and bud scales. This shrub was clearly very abundant and growing virtually on the site of deposition. Likewise, *Thelycrania sanguinea*, dogwood, must have been present in quantity. The third shrub to be well represented is *Crataegus monogyna*, hawthorn. A few complete fruits permitted the species to be determined with certainty. Despite the abundant macrofossil evidence for the two latter taxa, only a very few pollen grains of *Thelycrania* and of appropriate Rosaceae type were recovered, although pollen grains believed to belong to *Viburnum opulus*, guelder rose, occurred regularly.

A few fruits of *Galium*, *Stachys* and *Urtica* and numerous moss fragments represent the ground flora of the woodland and the more open areas of marsh within it in which the tufa was forming. *Carex riparia* still surrounds springs emerging at the foot of the Chalk escarpment a few hundred metres from the site.

Pit 1, 120–94 cm

Above 120 cm the tufa and silt deposits were considerably less organic, and appear to have accumulated much less rapidly, in a more unstable environment and to have undergone a certain amount of oxidation either during or after deposition. This is reflected in the much poorer preservation of pollen. The only horizon from which it was possible to obtain a proper count was at 120 cm, where the assemblage is basically similar to those below except for the occurrence of 4% *Ulmus* and 1% *Quercus* pollen, the first consistent appearance of these thermophilous trees. At 110 cm too few pollen grains were recovered to permit a statistically meaningful count, but these included not only *Ulmus* and *Quercus* but also *Tilia*.

The macrofossil record is also very sparse, with the notable exception of the fruits, technically cypselas, of *Eupatorium cannabinum*, hemp agrimony, which occurs in abundance here, as, indeed, in many tufa deposits. The chemistry of the walls of these cypselas is uncertain, but their resistance to decay, particularly to oxidation, is quite unlike that of any other member of the British flora. Their characteristic fragments are even commonly recognizable in pollen preparations, having survived all the rigorous procedures intended to destroy most organic debris. Certainly in tufas they survive where all other plant material is destroyed, and fine dark lenses in tufa may contain thousands of these fruits. The plant itself is a tall perennial herb commonly occurring in marshes and along streamsides, often tolerating a certain amount of shade.

Pit 1, 94–91 cm

Several pollen samples were examined from this conspicuous organic seam found in the 1968 trial pit as well as in pits 1 and 2. All contained large amounts of *Corylus* pollen, and also 5–15 % *Pinus*. Low percentages of *Ulmus* and *Quercus* were found in all samples, as were occasional grains of *Tilia*. Significantly, some samples contained 1–2 % *Alnus* pollen, which is only represented by the occasional grain at lower horizons. One sample contained abundant fern spores, another 11 % Compositae pollen, which can almost certainly be attributed to *Eupatorium*, the fruits of which occurred in great abundance throughout the organic seam, together with a few battered fruits of *Betula* and a single fruit of the water weed *Callitriche*.

(*d*) *Radiocarbon dates*

Four samples were submitted through the Institute of Geological Sciences to the Stockholm laboratory (St) (Welin *et al.* 1972). An additional sample was measured at the Godwin Laboratory (Q) of the Subdepartment of Quaternary Research, Cambridge, in 1976. The samples are listed below in descending stratigraphical order.

St-3410 (I.G.S.-48)	highly organic silt in upper tufa, pit 2 (= 91–94 cm, pit 1)	7500 ± 100 B.P.
St-3411 (I.G.S.-46)	wood fragments (mainly *Corylus* nuts), 135–140 cm, pit 1	8980 ± 100 B.P.
St-3395 (I.G.S.-47)	wood fragments (mainly *Corylus* nuts), 175–180 cm, pit 1	9305 ± 115 B.P.
Q-1508	wood fragments (*Betula*), sample B, 1968 trial pit	9960 ± 170 B.P.
St-3409 (I.G.S.-49)	wood fragments, sample A, 1968 trial pit	8120 ± 420 B.P.

The 91–94 cm layer proved insufficiently organic for dating in the monolith sample from pit 1, and a sample from the adjacent pit 2 was used instead. The stratigraphy matched exactly and the Mollusca extracted from the assay sample itself (table 2) are in very good agreement with those from the corresponding layer in pit 1. The sample showed some penetration by modern roots and was very carefully picked to avoid contamination from this source.

St-3409 is less satisfactory than the other four dates, being anomalously young, and not compatible with the date from the layer immediately above (Q-1508). The sample was much smaller than the others (a few grams only) and dilution with inactive CO_2 was necessary before counting, giving a very large standard deviation. There is also a possibility that the sample may have been contaminated by roots infiltrating down from the more richly organic layers above.

(*e*) *Conclusions*

In general terms, the following sequence of environments may be inferred from the deposits at Holywell Coombe.

(*a*) Solifluxion and niveo-fluvial action resulting in the formation of the basal clastic gravels and chalky silts above the Gault Clay. Vegetation cover was treeless and of a discontinuous tundra type with dwarf shrubs.

(*b*) A period of vigorous spring activity, depositing a series of largely biogenic sediments (organic silts and tufas) in which clastic detritus is scanty or absent. Woodland cover developed in which first *Betula* and later *Corylus* played an important role.

(*c*) A period of slope mobilization, soil material and fine clastic detritus accumulating on the valley floor, probably as a result of vegetational clearance and cultivation by man.

The basal chalky gravels and silts are solifluxion deposits, containing a flora and a molluscan fauna representing an open environment of late-glacial character. For reasons given above, the radiocarbon date from this horizon is evidently untrustworthy. At two nearby sections (Castle Hill, TR 212375, and Dover Hill, TR 235376) a similar molluscan fauna can be related to a Late Devensian litho- and biostratigraphy (Kerney 1963). On the evidence of these sequences the basal deposits at Holywell Coombe are assigned to the Younger Dryas (Loch Lomond) stadial (pollen zone III). The beetles are in good agreement with this interpretation (appendix I). Similar deposits occur at Brook (TR 064445), overlying a radiocarbon-dated layer with a pollen flora of 'Allerød' (pollen zone II) character (Kerney *et al.* 1964).

The earliest Flandrian deposits, seen only in the 1968 trial pit, are strongly organic, reflecting the ending of periglacial slope processes. The flora and fauna reveal an environment of relatively open woodland and marsh. During much of the early Flandrian spring deposits accumulated. At first these consist of loose highly organic tufaceous silt with much macroscopic wood debris, and later, of purer soft tufa. The ovoidal or cylindrical form of many of the abundant tufa nodules and their symmetrical internal structure shows that the discharge of water was at times sufficiently powerful to produce rolling. The aquatic Mollusca suggest that the water is unlikely at any time to have been more than an inch or two deep and that there were no large bodies of standing water. The environment was that of a marsh crossed by a braided system of streams. The surrounding forest was at first rather open, and then denser, evidently impinging closely on the valley floor.

The more clayey organic horizons (pit 1, 104–113 cm and 91–94 cm) probably represent stillstands in deposition. The rapidity of the mollusc changes at these levels is a function of this, as is the poor pollen preservation. A consideration of the radiocarbon dates also reveals the condensed nature of this part of the succession. It is hard to decide whether these episodes of local drying-out have any regional significance. The reasons for such sedimentary changes within spring deposits, as between organic layers, inorganic silts, and various kinds of tufa, are not clear, and attempts to interpret them in climatic terms are probably premature.

Above the tufa there is an evident discontinuity, represented by weathering. The overlying hillwash cannot be precisely dated, although accumulation began within the period of prehistoric agriculture. Similar deposits are widespread on the Chalk of southern England, spanning the period from the Neolithic onwards.

4. WATERINGBURY

(*a*) *Location and stratigraphy*

There are numerous occurrences of tufa in the vicinity of Maidstone, all associated with the outcrop of the Kentish Rag limestones within the Hythe Beds (Lower Cretaceous), the source of the calcium carbonate. The known sites are mostly summarized by Worssam (1963). Hard tufa, presumably of local origin, was widely used in the early mediaeval period in this area as a building stone, notably in St Leonard's Tower, West Malling (TQ 675570; Newman 1969).

Only the deposit at Wateringbury has received serious scientific attention (Brown 1939). Its position is shown in figure 7. It rests on the Atherfield Clay, below the main escarpment of the overlying Hythe Beds to the north. Sections in soft tufa are visible to a height of about 2.5 m for about 80 m along the eastern side of a sunken unmetalled lane (Love Lane; figure 8). Augerings have confirmed Brown's conclusion that 'the material occupies a roughly elliptical area 110 yards (100 m) long by 80 yards (73 m) wide, is banked up against a clay slope to the west and thins out to the east' (Brown 1939). The springs that formed the deposit still flow from the base of the Hythe Beds about 500 m to the northwest, north of Wateringbury church. They are now largely confined to underground conduits, to re-emerge close to the margin of the tufa (figure 7), from which point the water runs partly in an artificial channel along the western side of Love Lane.

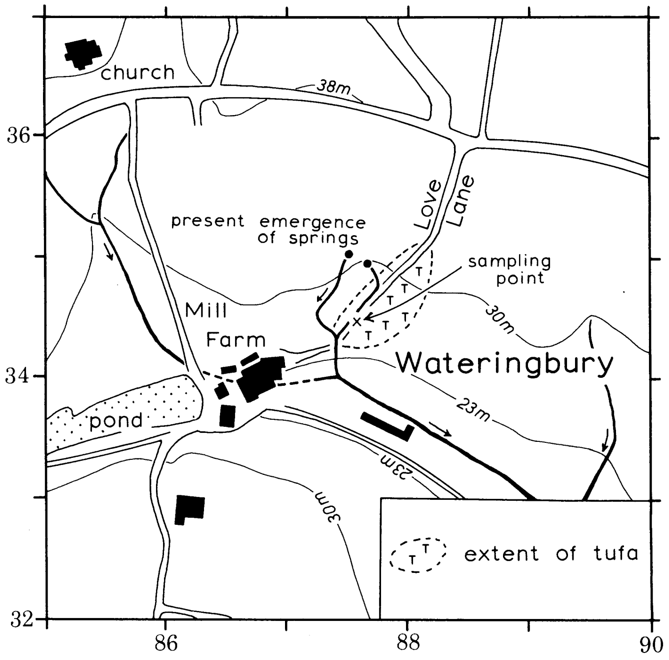

FIGURE 7. Location of Wateringbury tufa. National Grid 100 m coordinates are marked.

The tufa was examined in 1975 at or near its thickest point on the east side of the lane (figure 8; TQ 68765344). A clean vertical face was prepared and sampled in open section from the present soil surface to just beneath the level of the road, where the deposit became waterlogged. Augering showed that over a further metre of tufa existed beneath the water table; this was cored by means of a 10 cm diameter percussion corer.

The complete succession at this point is as follows.

depth/cm	
0–20	modern soil (10YR 4/2)
20–120	soft white (10YR 7/3, drying to 8/2) tufa, nodular in places; much disturbance by roots and animal burrows in upper part
120–124	grey (10YR 6/2) tufa
124–132	soft white tufa
132–138	grey (10YR 6/2) tufa

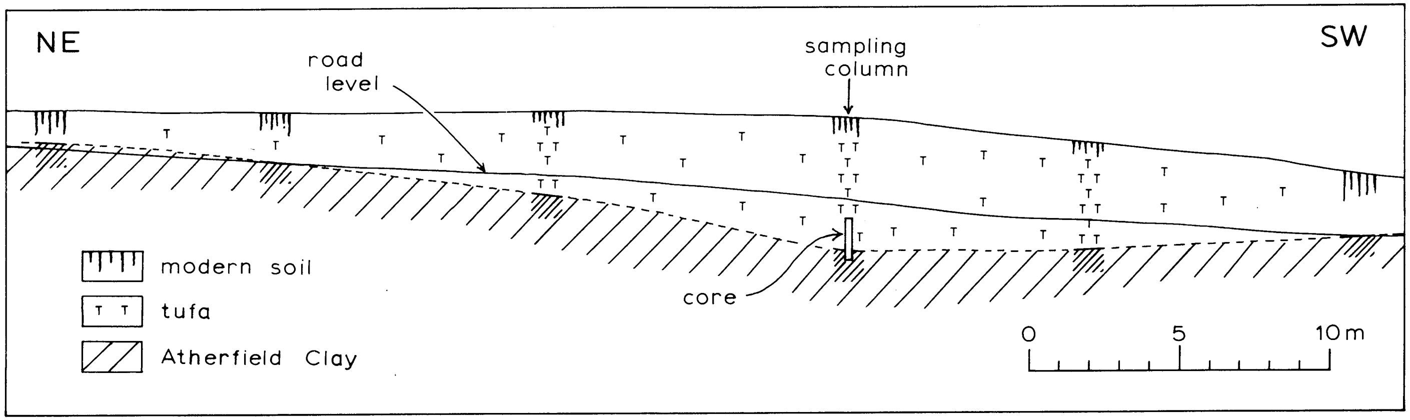

FIGURE 8. Profile of tufa, Love Lane, Wateringbury (TQ 687534).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

depth/cm	405–410	400–405	395–400	390–395	385–390	380–385	375–380	370–375	365–370	360–365	355–360	350–355
dry mass of sample/g	220	400	350	320	310	325	340	350	370	360	370	500
natias elegans (Müller)	—	—	—	—	—	—	—	—	—	—	—	—
hynia tentaculata (Linné)	—	—	—	—	—	—	—	—	—	—	1	—
icula fusca (Montagu)	—	—	—	—	—	—	—	—	—	—	—	—
rychium minimum Müller	8	9	15	33	39	61	38	23	32	7	23	20
rychium tridentatum (Risso)	1	1	—	—	1	5	3	9	18	15	44	195
mnaea truncatula (Müller)	—	—	2	1	5	6	6	7	5	1	3	5
Oxyloma pfeifferi (Rossmässler)	3	—	1	1	—	—	1	1	5	—	—	1
chlicopa lubrica (Müller)	—	1	—	2	4	11	10	9	5	2	8	25
chlicopa lubricella (Porro)	—	—	—	—	—	1	—	—	—	—	1	1
umella edentula (Draparnaud)	—	—	1	2	3	8	2	1	2	1	—	6
umella aspera Waldén	—	—	—	—	—	—	—	—	—	—	—	—
rtigo pusilla Müller	—	?1	—	2	4	10	9	8	6	3	4	6
rtigo antivertigo (Draparnaud)	—	—	1	—	?2	?2	?2	?5	2	—	—	1
rtigo substriata (Jeffreys)	—	—	—	—	3	6	9	2	3	2	2	1
rtigo pygmaea (Draparnaud)	—	—	—	1	—	—	—	—	—	—	—	—
rtigo moulinsiana (Dupuy)	—	—	—	—	—	—	—	—	—	—	—	—
rtigo alpestris Alder	—	—	—	—	—	—	—	—	—	—	—	—
rtigo angustior Jeffreys	—	—	3	3	8	17	25	17	18	13	12	34
pilla muscorum (Linné)	—	—	—	—	—	—	1	—	—	—	—	—
iostyla anglica (Wood)	—	—	—	—	—	—	—	—	—	—	—	—
uria cylindracea (da Costa)	—	—	—	—	—	—	—	—	—	—	—	—
llonia costata (Müller)	1	1	1	8	21	51	57	45	33	21	39	145
llonia pulchella (Müller)	8	4	3	3	3	6	4	—	5	—	1	—
llonia excentrica Sterki	1	3	1	—	—	1	—	—	—	—	—	—
llonia pulchella/excentrica	15	9	9	6	20	23	17	19	18	4	4	3
anthinula aculeata (Müller)	—	—	—	—	1	—	1	—	—	—	1	4
ermodea lamellata (Jeffreys)	—	—	—	—	—	—	—	—	—	—	—	—
a obscura (Müller)	—	—	—	—	—	—	—	—	—	—	1	—
nctum pygmaeum (Draparnaud)	9	9	10	18	6	27	11	9	9	4	10	19
scus ruderatus (Férussac)	—	—	—	—	—	—	—	—	—	—	—	2
scus rotundatus (Müller)	—	—	—	—	—	—	—	—	—	—	—	—
trina pellucida (Müller)	9	3	1	6	2	1	1	3	2	—	—	—
trea crystallina (Müller)	—	—	—	—	—	—	—	—	—	—	—	—
trea contracta (Westerlund)	—	—	—	1	9	22	12	14	19	8	32	96
sovitrea hammonis (Ström)	3	2	2	3	6	16	9	4	4	1	1	9
gopinella pura (Alder)	—	—	—	—	—	—	—	—	—	—	—	—
gopinella nitidula (Draparnaud)	—	2	3	1	4	8	11	6	6	4	12	41
ychilus cellarius (Müller)	—	—	—	—	—	—	—	—	—	—	—	—
ychilus alliarius (Miller)	—	—	—	—	—	—	—	—	—	—	—	—
nitoides nitidus (Müller)	2	2	5	4	6	8	1	1	5	—	3	5
roceras/Limax spp.	7	7	8	6	6	6	7	6	19	7	5	13
conulus fulvus (Müller) agg.	1	4	2	10	4	7	3	3	5	1	4	12
chlodina laminata (Montagu)	—	—	—	—	—	—	—	—	—	—	—	—
acrogastra rolphii (Turton)	—	—	—	—	—	—	—	—	—	—	—	—
ausilia bidentata (Ström)	—	—	—	—	—	—	—	—	—	—	—	—
lea perversa (Linné)	—	—	—	—	—	—	—	—	—	—	—	—
ichia hispida (Linné)	2	1	—	1	1	2	1	2	7	1	2	16
ichia striolata (Pfeiffer)	—	—	—	—	—	—	—	—	—	—	—	—
licigona lapicida (Linné)	—	—	—	—	—	—	—	—	—	—	—	—
ianta arbustorum (Linné)	—	×	—	×	×	×	×	×	×	×	×	×
ianta/Cepaea spp.	—	2	2	2	3	4	4	3	3	2	1	9
paea spp.	—	—	—	—	—	×	×	×	×	—	—	×
sidium casertanum (Poli)	3	7	7	13	5	7	7	3	7	2	2	16
sidium personatum Malm	6	—	—	—	1	9	6	3	5	2	6	16
sidium obtusale (Lamarck)	—	—	—	—	—	—	—	—	—	—	1	—
sidium milium Held	—	—	—	—	—	—	—	—	—	—	1	—

TABLE 5. MOLLUSCA, WATERINGBURY

345–350	340–345	335–340	330–335	325–330	320–325	315–320	310–315	305–310	290–300	275–285	260–270	250–260	240–250	230–240	210–220	200–210
420	420	370	370	380	330	400	300	400	500	500	500	800	500	500	500	700
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	3	16	12	24	2	30	2	6	51	29	48	82	85	28	13	13
24	2	11	118	292	14	95	24	45	414	354	421	359	623	499	85	194
—	—	—	1	3	—	1	—	3	14	7	37	40	3	1	—	—
—	—	—	—	—	—	—	—	—	—	—	18	33	1	1	4	7
3	1	3	25	38	2	24	5	6	24	21	33	31	37	30	16	18
—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
—	—	1	5	10	1	3	1	14	46	40	31	94	35	20	15	21
—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
1	1	—	6	14	1	3	1	3	20	13	16	10	23	8	6	6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	2	—	2	2	4	19	21	32	50	31	6	—	3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	2	1	65	77	3	—	3	—
—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—
1	—	—	—	1	1	4	7	33	125	105	86	350	59	47	22	30
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	4	28	35	16	43	55	25	2	14
18	3	1	20	65	1	5	4	11	55	40	61	50	6	2	4	21
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	4	3	—	—	—	1	5	1	2	1	19	19	2	6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
1	—	—	8	21	2	1	—	2	34	13	23	99	23	16	3	4
—	—	—	—	—	—	?1	—	—	1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	1	1	1	4	2	13	4	2	7
—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	2	1
—	—	—	—	—	—	—	—	—	7	12	12	22	59	48	7	18
6	1	3	36	58	2	7	2	4	11	9	16	13	18	27	2	13
2	—	4	21	19	3	16	2	3	20	17	25	17	11	5	6	3
—	—	2	6	19	1	2	2	3	17	13	21	19	88	65	7	34
4	1	2	29	41	1	18	6	32	66	53	67	54	54	26	10	8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	4	2	5	28	30	44	56	23	12	13	10
10	7	33	9	14	1	11	—	1	7	10	9	24	9	1	1	2
2	3	—	3	14	1	12	12	21	20	31	13	16	12	5	2	4
2	—	2	9	24	2	6	2	4	12	13	29	40	19	22	7	4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	3	1	1	1
?1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5	1	3	22	36	1	13	3	1	15	15	10	11	5	2	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	—
2	2	2	3	8	2	2	3	3	11	7	11	12	5	10	2	1
—	—	×	×	—	—	×	×	×	×	×	×	×	×	×	—	—
—	—	—	3	5	—	—	—	—	2	1	28	4	4	—	—	—
1	4	1	5	6	—	1	1	—	24	8	55	22	9	1	2	3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

195–200	190–195	180–185	170–175	160–165	150–155	140–145	130–135	120–125	110–115	100–105	90–95	80–85	70–75	60–65	50–55	45–50	40–45
500	500	500	500	500	500	500	500	500	500	500	500	500	500	500	500	500	500
—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
17	18	5	5	32	44	36	48	10	22	40	23	29	27	84	16	6	26
148	1289	524	609	568	514	362	1177	278	371	853	636	475	1274	1210	284	61	357
—	1	6	—	3	10	2	4	1	6	26	5	35	14	3	9	—	2
2	1	22	2	3	8	2	3	2	2	1	5	3	5	7	2	7	2
12	55	41	48	51	45	26	80	37	62	78	64	48	143	90	15	2	18
—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
11	28	42	21	34	32	17	48	21	48	52	63	41	64	64	43	15	20
—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	1	—
3	34	35	10	7	3	7	19	—	5	9	14	11	4	11	4	3	7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	2	33	24	18	20	7	16	34	25	23	22	15	59	74	32	23	15
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	2	3	2	1	—	—	—	1	1	23	2	14	38	36	20	12	4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
21	153	42	35	2	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	1	8	16	49	58	47	45	114	115	152	82	15	22
3	24	4	22	23	32	27	28	7	7	44	34	60	130	66	19	—	49
11	59	16	—	—	—	—	—	—	34	119	48	27	121	9	5	4	67
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7	65	37	19	34	41	23	89	7	10	38	32	6	52	19	11	2	15
—	—	—	—	—	—	—	—	—	—	13	37	16	228	311	52	9	23
—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—
8	51	34	26	55	39	16	69	16	17	82	50	26	63	42	14	6	24
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10	109	47	83	53	20	12	139	11	20	119	75	19	68	54	27	6	65
—	—	—	—	1	—	—	2	—	—	1	4	—	3	—	1	—	—
22	94	29	54	67	57	32	125	20	39	62	57	27	105	55	24	2	59
16	40	22	24	32	24	16	45	15	16	18	27	13	30	8	1	—	5
5	36	31	51	52	41	37	83	24	19	42	36	20	66	57	19	2	8
24	87	47	28	59	49	29	142	39	43	64	96	42	213	139	13	4	34
8	51	28	56	73	67	26	126	30	42	67	58	29	42	92	27	1	33
—	68	51	47	40	33	24	118	7	20	48	61	22	115	133	33	3	40
8	9	?1	2	1	2	?1	3	—	—	?1	1	—	—	—	2	—	?1
1	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	35	12	11	26	14	2	38	7	16	11	10	9	27	27	13	9	21
1	20	40	19	16	29	17	44	15	13	28	24	31	72	57	24	8	19
—	—	—	—	—	—	—	1	—	—	1	4	—	1	1	1	—	—
—	—	—	—	—	—	—	2	—	—	—	4	—	—	—	—	—	—
—	4	3	6	2	—	1	4	—	2	4	4	2	4	3	2	1	2
—	—	—	—	—	—	—	—	—	1	1	5	—	—	1	—	—	—
1	7	3	1	3	8	1	23	1	6	14	15	3	12	27	5	1	10
—	1	1	—	—	—	—	4	—	—	5	1	1	—	—	—	—	4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
—	—	—	—	×	—	—	—	—	—	×	×	—	—	—	—	—	×
1	8	9	10	11	4	4	13	6	4	10	10	8	23	23	10	2	9
—	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
—	—	—	—	—	2	3	—	—	—	—	—	—	—	—	—	—	—
—	—	13	—	—	2	—	8	12	2	34	8	3	—	—	30	4	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Kerney et al., pullout 1

35–40	30–35	25–30	20–25
500	500	500	500
3	3	2	3
—	—	—	—
62	102	84	149
22	39	22	41
596	686	571	805
21	6	33	71
5	6	6	20
45	38	33	48
—	—	—	1
32	30	16	23
—	—	—	—
19	11	5	19
—	—	—	—
6	4	—	—
—	—	—	—
4	—	—	—
—	—	1	—
—	—	—	—
—	—	—	—
11	7	3	4
59	26	21	24
76	54	9	17
—	—	—	—
—	—	—	—
—	—	—	—
31	44	24	38
31	9	9	34
—	—	—	—
18	8	15	23
—	—	—	—
346	198	102	140
5	—	—	2
100	62	59	83
11	19	7	19
9	6	13	12
89	106	89	93
45	49	49	102
92	67	61	45
2	1	1	1
—	—	—	—
29	13	14	29
39	18	30	26
3	—	4	—
—	—	—	1
7	3	2	6
2	2	2	1
9	6	6	17
6	3	—	3
—	—	1	1
×	—	×	×
18	15	11	11
×	×	×	×
—	—	11	28
6	2	11	94
—	—	—	—
—	—	—	—

(*Facing p.* 25)

depth/cm	
138–190	soft white tufa
190–194	grey (10YR 6/2) tufa
194–220	white tufa, lightly cemented and rather 'biscuity' in texture
220–230	iron-stained (7.5YR 5/6) layer of hard cellular tufa, containing occasional leaf impressions (*Salix*)
230–410	loose greyish brown (2.5YR 5/2) nodular tufa becoming coarser downwards; some macroscopic plant detritus towards base; waterlogged below 270 cm
410+	very dark grey (5Y 3/1) clay (Atherfield Clay)

(*b*) *Mollusca*

The results of the molluscan analyses are listed in table 5 and displayed in part in figure 9.

The tufa is rich in molluscs and their preservation is exceptionally good. Over 42000 shells were extracted from 51 analysed samples. The general nature of the fauna throughout is that of a calcareous swamp. Very few aquatic species, mainly *Lymnaea truncatula*, *Pisidium casertanum* and *P. personatum*, are represented. These are typical of swampy ground or small pools. Only at one level (355–360 cm) do single individuals of *Bithynia tentaculata* (an operculum fragment) and *Pisidium milium* suggest the presence of a larger, more permanent body of water.

Conditions were certainly much wetter in the lower portion of the sequence, where the terrestrial swamp element (*Carychium minimum*, *Oxyloma pfeifferi*, *Vertigo antivertigo*, *V. moulinsiana*, *Zonitoides nitidus*) sometimes accounts for over 50% of the total land fauna. The hygrophile *Vertigo angustior* (plotted separately in figure 9) is also common in these lower levels, but begins to decline at about 185 cm and disappears by 155 cm. It is interesting to note that the *V. angustior* maxima do not coincide with the peaks of aquatic and swamp species; indeed *V. angustior* is temporarily absent around 340 cm, where other hygrophiles are most common. Its behaviour throughout the Wateringbury sequence suggests a restriction to habitats intermediate in character between open swamp and drier, more deeply shaded situations. This is in keeping with its specialized liking at the present day for sunny wet meadows or dune slacks with a rich grassy vegetation (Norris & Colville 1974), a habitat type, of transient character, which appears to have been much commoner in the early Flandrian than it is today.

It is the changes in the composition of the dry ground Mollusca that are the most important, and these are described below.

410–365 cm

This division shows high values of terrestrial group 'A' (catholic snails of wide ecological tolerance, e.g. *Cochlicopa*, *Punctum*, *Vitrina*, *Vitrea*, *Nesovitrea*, *Euconulus*) together with very low values (less than 10%) for group 'B' (e.g. *Carychium tridentatum*). *Vallonia* is abundant. The environment was evidently quite open. The shade-intolerant grassland xerophile *Vallonia excentrica* occurs uniquely in this zone.

365–195 cm

In this division terrestrial group 'B' (especially *Carychium tridentatum*) increases rapidly to make up over 50% of the land fauna, remaining at this value for the rest of the succession. *Vallonia* declines from about 30% to less than 10%. These changes reflect the development of woodland at the expense of grassland. Above 345 cm the only *Vallonia* to survive is *V. costata*,

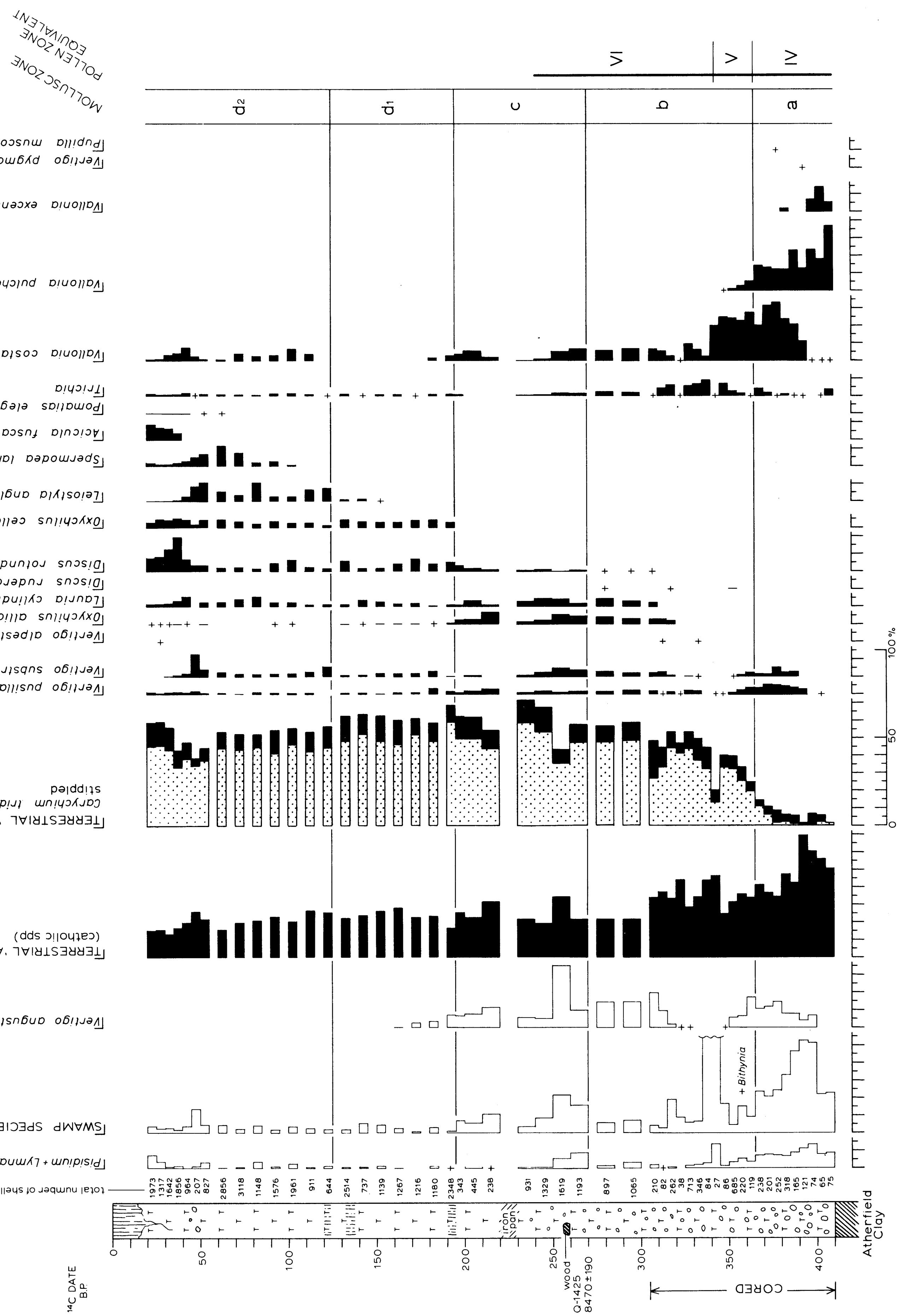

FIGURE 9. Molluscan diagram, Wateringbury. Strongly nodular tufa is shown by circles. Note that *Vertigo substriata* is plotted separately, not included in terrestrial group 'A' as in figures 5 and 9.

the most shade-tolerant of the three British species. The canopy was probably light and open, perhaps that of *Corylus* woodland. Relatively high values for *Trichia* are also indicative of an absence of deep shading.

Throughout this division the fauna becomes progressively enriched in species. Characteristic new elements are *Oxychilus alliarius* and *Lauria cylindracea*. *Discus ruderatus*, a species of boreal and montane woodland, extinct in Britain, occurs at Wateringbury only in the lower half of this division; it disappears above 270 cm, to be replaced by *Discus rotundatus*.

195–125 cm

Woodland elements remain dominant. *Vallonia* disappears, which suggests deep shade. The final disappearance of *Vertigo angustior* probably reflects the elimination of suitable open grassy areas within the tufa swamp as the forest impinged more closely around its margins. *Oxychilus cellarius* replaces *O. alliarius*; the ecological significance of this regionally important change remains unclear.

125–20 cm

Woodland elements continue dominant. *Vallonia costata* returns, at values of about 5 %, this perhaps indicating some slight opening of the vegetation. Two new arrivals, *Leiostyla anglica* and *Spermodea lamellata*, quickly become important and reach combined values of about 15% between 70 and 50 cm; they suggest humid, oceanic woodland.

Some further changes are apparent above 50 cm. *Leiostyla* and *Spermodea* decline, while the minute woodland prosobranch *Acicula fusca* appears in some numbers. *Pomatias elegans* also appears sparsely. The species is not common in shaded contexts and is therefore likely to be under-represented in the Wateringbury deposit. It is a calcicole, requiring broken ground in which it can burrow; no doubt it was here living on elevated dried-out patches of tufa during the final phase of tufa formation. It occurred much more commonly in a trial sample from the top of the tufa at a point about 40 m NE of the main sampling column. *P. elegans* lives on the site today, but it is noticeable that the mean size of adult shells is significantly smaller than that of the tufa fossils (Preece 1978). This change may be demonstrated at other sites in southern England (Burleigh & Kerney 1980); possibly it may be connected with the effect of the Flandrian thermal decline on this essentially southern species.

Some brief comments can now be made on the stratigraphical source of the previously published molluscan lists from Wateringbury (Kennard 1939; Kerney 1956). Kennard's sample lacked *Vertigo angustior* but came from a level below the expansion of *Spermodea* (i.e. *ca.* 165–105 cm). Kerney's sample also lacked *V. angustior*, but contained numbers of *Leiostyla* and *Spermodea*, together with five shells of *Acicula*; it must therefore have come from a higher stratigraphical level (*ca.* 100–20 cm).

(*c*) *Plant remains*

The tufa deposit at Wateringbury is considerably thicker than that at Folkestone, but again it is virtually only the lower levels, which have remained more or less continuously waterlogged, in which plant remains have been preserved. Originally the lower part of the deposit was sealed beneath a cemented iron-pan, formed of hard cellular tufa (220–230 cm). The sunken lane has now cut down through this horizon. The iron-pan layer itself contained occasional leaf impressions, which can be identified as those of sallows, either *Salix cinerea* or *S. caprea*. Nevertheless,

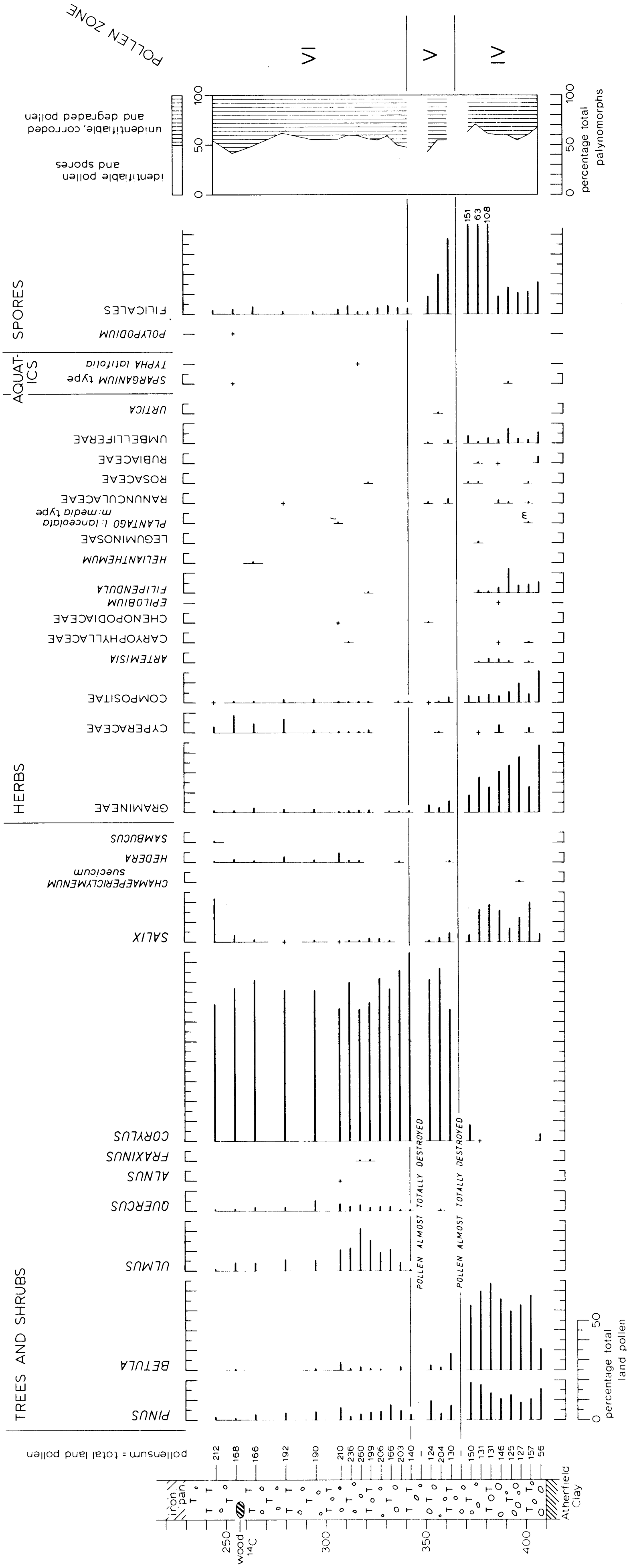

FIGURE 10. Pollen diagram, Wateringbury.

in the largely oxidized tufa deposits above, a few levels still preserve cypselas of *Eupatorium cannabinum*, whose remarkable resistance to decay has been discussed earlier.

The pollen diagram for the lower portion of the deposit, much more extensive than that for Folkestone, is presented in figure 10 and the accompanying list of plant macrofossils as table 6. The pollen diagram may conveniently be discussed in three sections that correspond to three distinct groups of pollen assemblages.

TABLE 6. PLANT MACROFOSSILS, WATERINGBURY

	Quercus sp.		*Salix* cf. *cinerea* L. or *caprea* L.	*Chelidonium majus* L.	*Chenopodium* cf. *album* L.	*Eupatorium cannabinum* L.	*Rumex* sp. (sg. *Rumex*)	*Solanum* sp.	*Viola odorata* L. or *hirta* L.	*Carex* sp.
type of remains depth/cm	l.f.	w.	l.i.	s.	s.	fr.	fr.	s.	s.	n.
20–25	—	—	—	—	—	2	—	—	—	—
35–40	—	—	—	—	—	3	—	—	—	—
40–45	—	—	—	—	—	4	—	—	—	—
45–50	—	—	—	—	—	2	—	—	—	—
60–65	—	—	—	—	—	*ca.* 15	—	—	—	—
80–85	—	—	—	—	—	4	—	—	—	—
220–230	—	—	+	—	—	—	—	—	—	—
255–260	—	+	—	—	—	—	—	—	—	—
260–270	—	—	—	—	—	*ca.* 80	1	—	—	—
270–280	—	—	—	—	—	13	—	—	—	23
290–300	—	—	—	—	—	14	—	—	—	19
305–310	+	—	—	—	—	3	—	—	—	—
310–315	—	—	—	—	—	2	—	—	—	—
315–320	—	—	—	—	1	—	—	—	—	—
320–325	—	—	—	—	—	1	—	—	—	—
345–350	—	—	—	1	—	—	—	—	—	—
350–355	—	—	—	*ca.* 15	—	3	—	—	—	—
355–360	—	—	—	2	—	2	—	—	—	—
360–365	—	—	—	1	—	1	—	—	—	—
365–370	—	—	—	2	—	6	—	—	—	—
370–375	—	—	—	—	—	15	—	—	—	—
375–380	—	—	—	1	—	*ca.* 25	—	—	—	—
380–385	—	—	—	1	—	*ca.* 20	—	—	—	—
385–390	—	—	—	—	—	10	—	—	—	—
390–395	—	—	—	—	—	—	—	—	1	—
400–405	—	—	—	—	—	—	—	1	1	—
405–410	—	—	—	—	*ca.* 38	—	—	—	7	—

Key: fr., fruit; l.f., leaf fragments; l.i., leaf impressions; n., nutlet; s., seed; w., wood.

410–365 cm

The dominant tree pollen type of the lowest section of the diagram is *Betula* (30–45 %), though *Pinus* (up to 18 %) and *Salix* (up to 20 %) are also important. Herbaceous pollen types, principally Gramineae (9–34 %), together with Compositae, *Filipendula* and Umbelliferae, are, however, comparatively abundant, as too are fern spores. This suggests a vegetation of open birch woodland. *Chamaepericlymenum suecicum*, dwarf cornel, is present in the pollen record and occurs in just such habitats in northern Britain today. Stands of pine occurred somewhere in the region, probably on the more acid soils of the sandy beds within the Lower Greensand. At the top of this section *Corylus* appears and begins to expand rapidly.

The plant macrofossil record is sparse but records open-ground and marsh species. The basal sample contains an unusual conjunction of *Viola* and *Chenopodium* seeds, probably reflecting bare ground conditions as the tufa began to form. *Eupatorium* fruits are abundant from 390 cm upwards and indicate that this plant was an early colonizer of the marsh. The most unexpected record is that of seeds of *Chelidonium majus*, greater celandine, which probably colonized the calcareous surface of the tufa itself. Its significance is discussed shortly.

365–345 cm

Between 370–365 cm occurs a horizon in which pollen has largely been destroyed, presumably because of temporary drying out of the tufa surface. Above this, *Corylus* increases rapidly to over 85 % of the total land pollen, and this corresponds with an immediate and drastic decline of *Betula*. *Pinus* values are below 10 % and those for *Salix* are greatly reduced too. Herbaceous pollen also declines, with Gramineae falling to below 5 %. A second horizon in which virtually all pollen has been destroyed occurs between 350 and 345 cm. It seems possible that there is some relationship between these horizons, where pollen is lacking, and horizons immediately overlying them in which numbers of molluscs recorded are reduced to distinct minima.

The macrofossil record is restricted to two species, *Eupatorium* and *Chelidonium*, the latter being particularly abundant between 355 and 350 cm.

Chelidonium majus, greater celandine, is today widespread in the British Isles, except for northern Scotland. It almost always occurs in the vicinity of human habitations and tends to grow in moist waste places and roadsides, particularly at the foot of limestone walls or as a garden weed. The plant has a well documented history as a medicinal herb since Roman times, and, indeed, the seeds have been recovered from Roman and mediaeval archaeological sites. There are two further records of fossil seeds, from interglacial deposits of Ipswichian age at West Wittering, Sussex, and at Wretton, Norfolk, but the opinion of most botanical authorities has been that it is at present an introduced member of the British flora, largely on the grounds that it has no obvious natural habitat. Godwin (1975) nevertheless speculated that it could well have been native to Britain in the Flandrian, and this is confirmed by the present investigations. Under the circumstances it seems likely that the plant has persisted and that at least part of the present population is derived from this indigenous stock. The pollen of *Chelidonium* is finely reticulate. A few poorly preserved grains of this nature were encountered at the same levels as the seeds, but no certain identification could be made.

345–240 cm

The upper section of the Wateringbury pollen diagram is characterized by the occurrence of pollen of the thermophilous trees *Ulmus* and *Quercus*. Nevertheless *Corylus* is still overwhelmingly the most abundant pollen type, sometimes reaching values of over 80 % of the total land pollen. Between 350 and 315 cm *Ulmus* rises to 17 %. *Quercus*, though constantly present, was never found in abundance and seldom reached 5 %. This matter has already been discussed in § 2*b* of this paper. Above 300 cm a slight change is detectable: *Ulmus* values drop to 5 %, and *Betula* almost disappears. With the exception of Cyperaceae, herbaceous pollen contributions are very low. Occasional Compositae pollen can be attributed to *Eupatorium*.

The uppermost pollen sample, 15 cm below the base of the iron-pan, yields particularly conspicuous values for *Salix*. Sallows were certainly growing on the site, as impressions of their leaves are preserved in the hard tufa of the iron-pan.

Other plant macrofossils are recorded sporadically from this part of the deposit, but include leaf fragments and wood of *Quercus*, cypselas of *Eupatorium*, of course, and abundant *Carex* seeds between 300 and 270 cm, approximately at levels where an increase in Cyperaceae pollen occurs.

Interpretation of the vegetation of this period depends on understanding the effects of differential destruction of pollen grains in this environment. However, it seems that this tufa was forming in restricted areas of marsh, with sallow scrub and sedge beds with *Eupatorium* within a mixed-oak forest in which *Ulmus*, *Quercus* and *Corylus* were all abundant.

(*d*) *Vertebrates*

The following mammalian remains were recovered from the mollusc samples, and identified by A. J. Stuart:

Talpa europaea L. (mole), 160–165 cm (m^3); *Clethrionomys glareolus* (Schreber) (bank vole), 350–355 cm (m^1), 90–95 cm (3 m^1), 20–25 cm (m^3); *Microtus agrestis* (L.) (field vole), 120–125 cm (m_1, mandible).

A fragmentary right mandibular ramus without teeth of *Neomys* cf. *fodiens* (Schreber) (water shrew) is also known from the tufa (Kerney 1956). This is likely to have come from above 100 cm (see §4(*b*)).

(*e*) *Radiocarbon date*

The following sample was measured at the Godwin Laboratory, Cambridge, in 1976:

Q-1425 Wood (*Quercus*), 255–260 cm 8470 ± 190 B.P.

The sample was taken from a large (50 cm) fragment of waterlogged wood lying horizontally in the tufa at the location of the sampling column. The identification was made by J. F. Levy. There was some minor rootlet penetration at this level but the material selected for assay appeared quite clean and uncontaminated.

(*f*) *Conclusions*

The Wateringbury tufa formed in a calcareous swamp fed by springs. There were no large bodies of standing water, but only small pools and shallow films trickling across wet ground. Both the molluscs and the ostracods demonstrate this. The more nodular lithology of the lower part of the deposit suggests that at first there was a more vigorous discharge of water, causing rolling, and this is supported by the higher percentages of aquatic molluscs at these levels. The ostracods (appendix II) give some evidence also of a recurrence of strong spring flow in the upper part of the deposit, especially above 100 cm. Conversely, very quiet conditions are indicated in the middle parts of the deposit; several grey horizons within this zone (190, 132, 120 cm) probably reflect pauses in the deposition of carbonate, though these intervals were probably short.

The top of the underlying Atherfield Clay is fresh and unoxidized. Evidently this is not a land surface but an erosional surface, possibly cut by periglacial slope processes during the late Devensian.

The molluscan sequence is valuable for its length and completeness, and also for its relative uniformity of facies. Furthermore, the area of deposition was small, allowing large numbers of dry-ground snails to be washed in; these are of much greater value for the interpretation of regional changes than are the autochthonous freshwater and swamp elements.

The dry-ground molluscs reflect a change from open ground with grassy herbaceous vegetation to shaded forest. Pollen analysis suggests a transition from a rather open birch woodland, through hazel scrub, to a fairly dense temperate forest with elm, oak and hazel. This covers Godwin's pollen zones IV to VI, and the radiocarbon date on oak wood falls within the latter.

It is not known when the tufa ceased to form. No clear synanthropic effects are detectable at the uppermost levels. The reason why accumulation stopped is similarly unclear. A purely climatic cause is unlikely. Possibly a connection may exist with the destruction of the natural vegetational cover of the area, which, by increasing runoff, accentuated erosion. The waters from the springs now enter a channel cut down through the deposit (occupied by the present road), whereas formerly they ran as a braided system of distributaries across its surface, taking the form of a prograding delta. A similar change appears to be a common feature of tufa bodies in many parts of Britain.

5. Discussion and general conclusions

The deposits at Folkestone and Wateringbury have provided an uncommon opportunity to study successive Late Devensian and Flandrian mollusc faunas. A series of terrestrial mollusc assemblages is recognizable, and may usefully be characterized in terms of formal biostratigraphical *assemblage zones* (Kerney 1977). The definition of these zones, as established at Holywell Coombe, Folkestone (figure 5), is as follows.

zone z	open ground fauna; restricted periglacial assemblage with *Pupilla*, *Abida*, *Vallonia*, *Trichia*, *Columella columella*
zone a	as zone z, but with decline of bare soil species (notably *Pupilla*) and corresponding expansion of catholic species (terrestrial group 'A'); appearance of *Carychium*, *Vitrea*, *Aegopinella*
zone b	woodland fauna; expansion of *Carychium tridentatum* and *Aegopinella* (terrestrial group 'B'); *Discus ruderatus* characteristic
zone c	woodland fauna; replacement of *Discus ruderatus* by *Discus rotundatus*
zone d	woodland fauna; expansion of *Oxychilus cellarius* (subzone d1) and of *Spermodea*, *Leiostyla*, *Acicula* (subzone d2)
zone e	open ground fauna; decline of shade-demanding species; re-expansion of *Vallonia*
zone f	open ground fauna; as zone e, but with appearance of *Helix aspersa*

At Wateringbury zones a to d are clearly recognizable (figure 9), excellently developed within a thick sequence and usefully amplifying the information available at Folkestone.

At other sites in Kent an additional *zone y* may be recognized below zone z, representing the first appearance of a terrestrial molluscan fauna following the period of maximum cold of the Late Devensian. Assemblage y may be defined as having a very simple, restricted character, dominated by *Pupilla*, *Vallonia* and *Vitrina*, and lacking *Abida*, *Helicella* and *Trichia*. It occurs stratigraphically below zone z at, for example, Dover Hill, Folkestone (Kerney 1963, fig. 3), Holborough, Kent (fig. 10) and Oxted, Surrey (fig. 12).

These assemblages are defined in terms both of the stratigraphical ranges of certain species, and of their changing dominance. In the earlier part of the sequence (zones y to d inclusive) the controlling process is clearly one of migration in response to climatic change, acting either indirectly through the vegetation (e.g. causing the replacement of open-ground species by shade-demanding species) or more directly providing suitable conditions for molluscs with particular thermal requirements. Thus, *a priori*, it might reasonably have been predicted that *Discus rotundatus*, *Oxychilus cellarius* or *Acicula fusca* would appear relatively late, since their present-day northern ranges in Europe suggest thermal limitation. Conversely one can draw attention to the decline and disappearance of the high alpine and arctic species *Columella columella*, *Catinella arenaria* and *Vertigo genesii*, now extinct or relict only in Britain (maps in Kerney & Cameron (1979)).

The late-glacial zones (y and z) contain a fauna of peculiar and diagnostic character (Kerney 1963; Kerney *et al.* 1964). As with the flowering plants (Godwin 1975), the mixture of biogeographical elements encountered has no modern analogy. Similar 'incompatible' mixtures occur also in the early Flandrian, e.g. in the unexpected association in zone b of *Discus ruderatus* (a boreal and alpine species of coniferous forest) with *Lauria cylindracea* (a mediterranean and atlantic species with a European distribution like that of *Ilex*).

The overwhelming impression conveyed by the mid-Flandrian assemblages (zones b, c and d) is their richness in marsh and woodland species, a diversity certainly greater than that to be found at any surviving site in the British Isles today. A number of these species are now only relict in Britain, e.g. *Vertigo pusilla* or *Vertigo angustior*. No doubt this effect is very largely due to the destruction by man of nearly all primary habitats on calcareous soils, but some climatic factors may also be involved.

Zones e and f owe their character to anthropogenic effects. Much detail is given by Evans (1972). Zone f is defined by the appearance of *Helix aspersa*, an introduced mediterranean species which seems to have spread rapidly across lowland Britain during the Roman period. Other non-native helicids unknown before zone f are *Candidula intersecta*, *C. gigaxii*, *Cernuella virgata*, *Cochlicella acuta* and *Monacha cantiana*.

It remains to be considered to what extent these assemblages can be recognized elsewhere. At Brook, 16 km NW of Folkestone, comparable deposits lie within a scarp-face coombe (TR 076451) and show a similar lithostratigraphic sequence: periglacial detritus, tufa, and lastly hillwash (Kerney *et al.* 1964). The molluscan data are here replotted (figure 11). No radiocarbon dates are available from the main Flandrian sequence but the pattern of molluscan change is similar to that at Folkestone, and a parallel zonation (z to f) is shown on the diagram. At a nearby section in the same valley the base of zone e, a Neolithic clearance level, is dated at 4540 ± 105 B.P. (Burleigh & Kerney 1980). The molluscan sequence within the hillwash (zones e and f) at Brook and Folkestone shows detailed similarities, notably in the upward replacement of *Monacha cartusiana* by *Monacha cantiana*, the decline of *Helicella itala*, and the appearance of *Succinea oblonga* and *Vallonia pulchella*. Increasing dampness is indicated. The cause is uncertain, though local anthropogenic changes (e.g. in agricultural practice) should be considered before regional, climatic causes are invoked.

The zonation of the pollen diagrams from Folkestone and Wateringbury must now be considered. Because of the probability of significant differential destruction of pollen within the tufa deposits, it was thought to be fruitless to define local assemblage zones on the basis of these data. It does, however, seem to be possible to correlate both diagrams with the standard pollen zonation scheme of Godwin (1975). This correlation is supported quite independently by the evidence of radiocarbon dating.

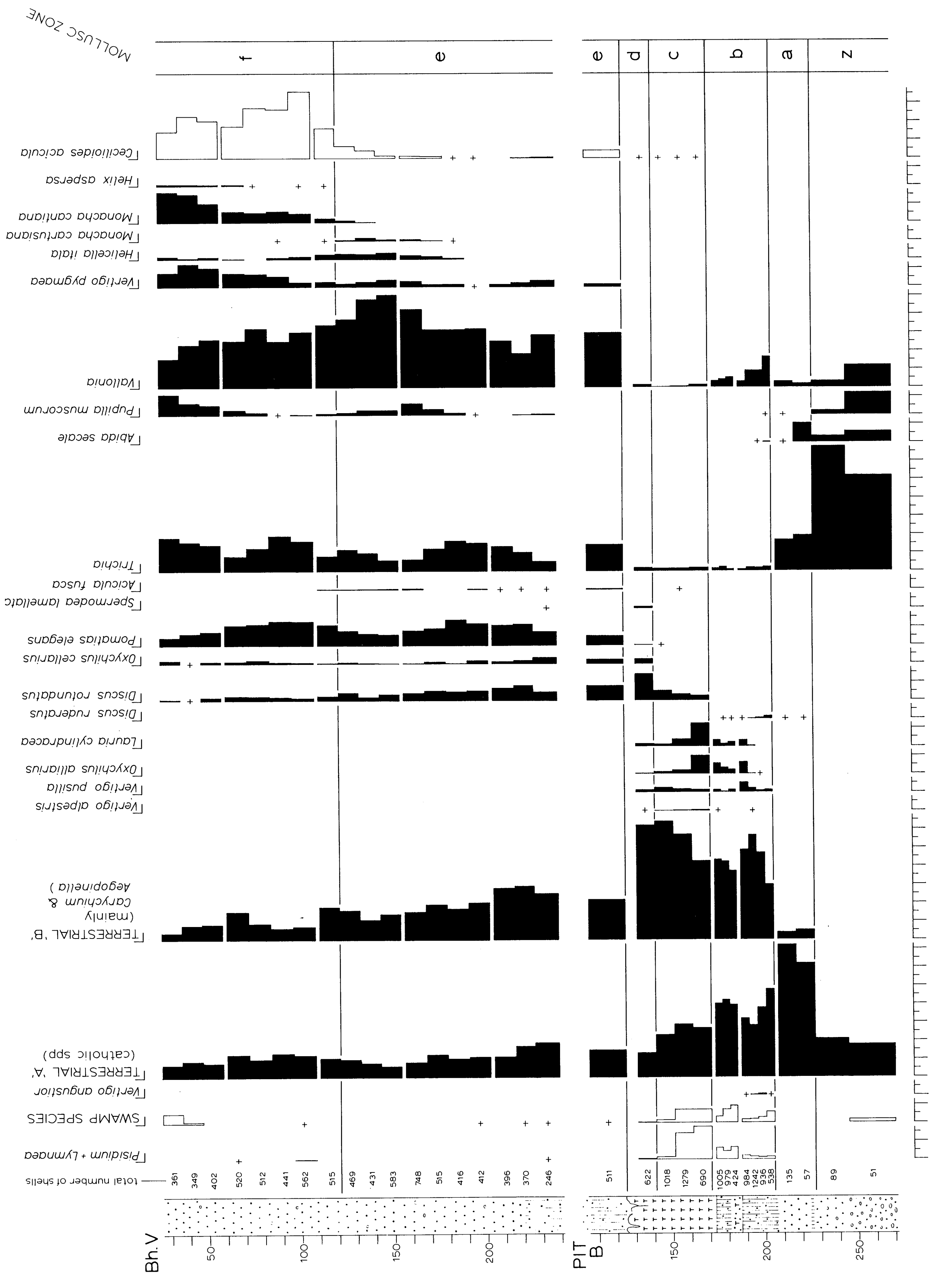

FIGURE 11. Molluscan diagram, Devil's Kneadingtrough, Brook, Kent. Data replotted from Kerney *et al.* (1964). Lithological symbols as in figure 5.

At Wateringbury the pollen assemblages in the lowest section of the deposit between 410–365 cm contain *Betula* as the dominant tree component, and *Corylus* is virtually absent. It is suggested that these assemblages fall without doubt within Godwin's pollen zone IV. The rise of *Corylus* at approximately 365 cm is taken to mark the onset of zone V. Zone VI begins at approximately 345 cm, where the first continuous curves for *Ulmus* and *Quercus* commence. The evidence does not seem adequate for any further subdivision of zone VI to be attempted, though the virtual absence of *Alnus* must mean that zone VIc is not represented in that part of the deposit covered by the pollen diagram (i.e. below 240 cm). The radiocarbon date of 8470 ± 190 B.P. for oak wood from 260–255 cm is fully in accordance with a zone VI age.

No pollen evidence is available from the oldest samples from Folkestone, but it has already been suggested on biostratigraphical and other grounds that sample A belongs to the Younger Dryas stadial (pollen zone III) and sample B to the time of pollen zone IV. The lower part of the pollen diagram from Folkestone, between 180 and 120 cm, shows pollen assemblages dominated by *Corylus* with very little trace of pollen from other thermophilous trees, and is, therefore, ascribed to pollen zone V. This is fully supported by the independent evidence of two radiocarbon dates. Between 120 and 94 cm pollen is poorly preserved and the sequence of deposits is apparently somewhat condensed. However, the appearance of countable quantities of both *Ulmus* and *Quercus* together in the sample at 120 cm is taken tentatively as evidence for the commencement of pollen zone VI close to this horizon. The organic layer between 94 and 91 cm represents a particularly condensed sequence. Some but not all samples from within this horizon contain *Alnus* pollen. This can be interpreted as suggesting either early pollen zone VIc or late pollen zone VIb, which again matches the evidence of the radiocarbon date from this level.

Early Flandrian pollen diagrams are few and far between in southern, particularly south-eastern, England. Pollen records covering this period are available from Dorset (Seagrief 1959), the New Forest, Hampshire (Seagrief 1959, 1960; Barber 1975), Berkshire (Clapham & Clapham 1939) and, nearest to the area under consideration, Elstead, Surrey (Seagrief & Godwin 1960). All these pollen diagrams represent areas with a predominantly acid soil cover in contrast to the areas of Kent here discussed. With allowances for the different pollen base on which these above mentioned diagrams are calculated, the principal differences are the much higher values for *Corylus* recorded from the Kentish sites and the low values for *Quercus* there in comparison with values of *Ulmus*. At present it cannot be decided with confidence whether these differences relate entirely to differential pollen preservation, or to local over- or under-representation of individual taxa or to major vegetational differences.

It is now possible to make a comparison between the mollusc zones just described and the pollen assemblage zones of the Godwin scheme for southern Britain, at least for the early Flandrian. A provisional correlation is presented below, based on the evidence presently available, together with the radiocarbon dates from these same sites in Kent.

A little further evidence from two further sites in south-east England may be presented here. Rich mollusc faunas of 'forest optimum' (zone d) type have been published from many Flandrian deposits in Essex. Recently it has been possible to obtain pollen spectra from shell samples from two of these sites: Copford (TL 9224; Brown 1853; Kennard & Woodward 1897) and Tilekiln Green, Takeley (TL 520213; Kennard 1945). Neither deposit is now accessible for examination. It should be noted that at Copford Hoxnian interglacial strata are also present

^{14}C dates B.P. for mollusc zones (Kent)	mollusc zones	approximate pollen zone equivalents
	f	VIIb–VIII
	e	
4540 ± 105 (BM-254)	d2	VIIa
7500 ± 100 (St-3410)	d1	VI
	c	
8470 ± 190 (Q-1425) 8980 ± 100 (St-3411) 9305 ± 115 (St-3395)	b	V
9960 ± 170 (Q-1508)	a	IV
11900 ± 160 (Q-618) 11934 ± 210 (Q-463)	z	II–III
13180 ± 230 (Q-473)	y	I

(Turner 1970) but these contain only a sparse freshwater mollusc fauna of very different character from that of the Flandrian deposits above.

The Copford sample consists of a washed shelly residue, with abundant *Discus rotundatus*, *Oxychilus cellarius*, *Spermodea*, *Leiostyla* and *Acicula* (i.e. zone d2). The label reads 'Copford, ex Jn Brown & Wm Whitaker'. It was probably collected in the 1840s. The pollen spectrum given below was obtained from organic silt extracted by crushing some of the larger shells. The pollen was highly corroded. Figures are for percentages of total identifiable land pollen based on a count of 203 grains; corroded, degraded and crumpled grains account additionally for more than 34 %.

TABLE 7. POLLEN SPECTRUM, COPFORD

Pinus	2.0	Caryophyllaceae	0.5
Ulmus	1.0	Umbelliferae	+
Quercus	4.5	—	
Tilia cordata	15.5	*Botrychium*	0.5
Alnus	56.5	*Equisetum*	0.5
Corylus	13.5	*Pteridium*	9.0
Hedera	2.0	*Polypodium*	1.5
Gramineae	1.5	Filicales	38.0
Cyperaceae	2.0	*Sphagnum*	1.0
Compositae	1.5		

The very high value of *Alnus* clearly indicates that this sample belongs to zone VII, probably but not definitely to zone VIIa. It is uncertain whether the low values of both *Ulmus* and *Quercus* can be accounted for by differential pollen destruction.

The material from Takeley was collected by one of the present writers about 1955. The mollusc fauna is of well developed zone d2 type (Kennard 1945). Organic silt extracted from within snail shells yielded the spectrum given below. The pollen was very heavily corroded. Figures are for percentages of total identifiable land pollen based on a count of 50 grains only; corroded, degraded and crumpled grains account additionally for over 52 %. The sample also contained derived Tertiary pollen and spores.

TABLE 8. POLLEN SPECTRUM, TAKELEY

Ulmus	8	Gramineae	2
Quercus	12	—	
Tilia cordata	54	*Polypodium*	+
Corylus	22	Filicales	18
Hedera	2		

The high values for resistant palynomorphs of *Tilia* and Filicales are accounted for by the high degree of corrosion of the sample. However, there is a notable absence of *Alnus*. The sample must therefore pre-date pollen zone VIIa, and probably belongs to the later part of zone VI.

Only much further work can show to what extent the mollusc zones are applicable over large areas. A radiocarbon date of 6730 ± 150 B.P. (Q-1343) has been published for a zone d2 assemblage associated with a pollen zone VIIa spectrum at Blue Anchor Bay, Somerset (Kerney 1976*b*). Unpublished results from elsewhere in Britain (e.g. from Lincolnshire, Dorset and north Wales (Preece 1978)) are encouraging, though differences certainly exist. In particular the subdivision of zone d (zone of *Oxychilus cellarius*) appears to be of local value only: the oceanic elements that characterize zone d2 may be absent, or in western areas of Britain and Ireland may appear at considerably earlier stratigraphical levels.

The base of zone e/f raises a special difficulty. Assemblage e, as defined by the re-expansion of the grassland genus *Vallonia*, results from human clearance, an effect that is unlikely to be at all time-parallel. Its base is likely to correspond only in a very general way with palynological criteria for zone VIIb (the Sub-boreal) at least some of which probably reflect regional changes taking place close to 5000 B.P. (Smith 1961; Hibbert *et al.* 1971). As yet it is not possible to isolate in any clear way molluscan changes subsequent to the forest optimum (zone d) that might be independent of anthropogenic effects, though the widespread extinction of certain species, coupled with their geographical retreat within the British Isles (Kerney 1968, 1976*a* maps 7, 67, 73, 78, 86, 87) is suggestive of climatic change and difficult to explain solely in terms of human interference.

We should like to thank Mr A. Weeks (formerly of Kent County Council Highways Department) and Mr E. R. Shephard-Thorn (Institute of Geological Sciences) for drawing our attention to the Folkestone site and for arranging further excavations. The radiocarbon dates were made possible by courtesy of the Director, Institute of Geological Sciences, and by Dr V. R. Switsur and Professor R. G. West, F.R.S., Subdepartment of Quaternary Research, Cambridge. We are grateful to Dr G. R. Coope and Dr J. E. Robinson for reporting separately on the beetles and ostracods. Other identifications were provided by Dr J. H. Dickson, Dr B. M. Huntley (mosses), Mr J. F. Levy (wood), Dr C. R. C. Paul (*Columella*) and Dr A. J. Stuart (vertebrates).

Appendix I. Coleoptera from late-glacial and early Flandrian deposits at Folkestone

By G. R. Coope

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Sample A, 1968 *trial pit*

†*Bembidion dauricum* Mtsch.
†*Bembidion difficile* Mtsch.
†*Helophorus glacialis* Villa
†*Olophrum boreale* Payk.
†*Arpedium quadrum* Gr.
Hypnoidus riparius F.
†*Hypnoidus rivularis* Gyll.
Otiorrhynchus clavipes Bon. ssp. *fuscipes* Ol.
Otiorrhynchus dubius Ström (= *nodosus* Muell.)

† Species no longer found living in Britain.

One of the striking features about this small fauna is the high proportion of species that are now extinct in Britain. However, they are all members of the present-day boreal or boreomontane fauna of Europe. Of these, the following species are usually found above the treeline, though all have ranges that extend down into the northern parts of the boreal forest: *Bembidion dauricum*, *B. difficile*, *Helophorus glacialis* and *Olophrum boreale*. The distribution of *Otiorrhynchus clavipes* subsp. *fuscipes* is curious in the light of its companions. It is not found today in Fennoscandia or elsewhere in the high north of Europe, but it is common in the Alps and other mountain chains of central Europe, where it reaches an elevation of 2500 m (Hoffmann 1950). It is, however, a nocturnal species and thus its absence from the high north of Europe is probably due to prolonged daylight at those latitudes rather than to any intolerance of low temperatures.

The assemblage indicates cold conditions with summer temperatures similar to those near to the tree line today in northern Europe. Even though the sample of the local fauna was seemingly very small, the dominance of obligate arctic–alpine species would be highly unlikely if this local fauna had not itself been dominated by such species. It seems inescapable that average July temperatures must have been close to 10 °C.

The picture of the local environment derived from the present-day requirements of the fossil species in this assemblage is entirely in keeping with the thermal environment inferred above. All are species of open habitats, unshaded by any trees. The environmental implications of *Helophorus glacialis* are of particular interest. This species is represented by at least five individuals and is in fact the only species in this assemblage represented by more than one individual. It was thus the commonest species present. Typically, this species inhabits the small pools at the margins of melting snow patches, where the dead vegetation of the previous year is still black (Angus 1973). There is little evidence from the Coleoptera of the nature of the vegetation. The two species of *Hypnoidus* are grass-root feeders and the two *Otiorrhynchus* species are polyphagous whose larvae feed on roots of numerous plants and whose adults feed at night time on their leaves.

All the species in this assemblage have been found in late-glacial deposits elsewhere in Britain. So far *Arpedium quadrum* has only been found in 'pollen zone III' deposits at Orleton near Ludlow (unpublished record). *Helophorus glacialis* is typically very abundant in deposits of the same age and conspicuously rare in deposits that date from the full-glacial. The most probable age for these Folkestone deposits thus appears, on the evidence of the fossil Coleoptera, to be pollen zone III (= Loch Lomond stadial, = Younger Dryas times).

The existence of arctic climatic conditions in the south of England is further supported by a fossil assemblage of Coleoptera from a site of similar age near Croydon (Osborne 1971) and by the recent discovery of arctic–alpine Coleoptera in pollen zone III deposits at Hawks Tor on Bodmin Moor (Coope 1977).

Sample B, 1968 *trial pit*

Pterostichus strenuus Panz.
Anthobium unicolor Marsh.
Phosphuga atrata L.
Quedius sp.
Brachysomus echinatus Bon.

All the species in this assemblage are still living in the British Isles. In Fennoscandia they are widespread in southern and central regions but are absent from the far north. From this meagre faunal list it may be safe to infer that the summer temperatures were considerably warmer than during the deposition of the sediment from which the sample A fauna was obtained. No further precision in estimating summer warmth is possible on the basis of this small assemblage.

The local environment seems to have been more shaded than that indicated by the previous sample. *Pterostichus strenuus* is typically found in damp places in moss and leaves in deciduous woodland (Lindroth 1945). Similarly, *Anthobium unicolor* is also a woodland floor species though it can also be found in damp meadowland (Horion 1963). Both the larvae and the adults of *Phosphuga atrata* predate snails and the species is also found in woodland situations. *Brachysomus echinatus* is found in moss and plant debris and is probably polyphagous.

Appendix II. Ostracoda from Wateringbury

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The ostracods picked from the mollusc sievings above B.S. 30 mesh (0.5 mm) are plotted as absolute numbers (figure 12). Totals were recalculated where necessary to give numbers per 0.5 kg. United carapaces are scored as two individual valves. Sub-30-mesh residues from the core were kept but have not been analysed quantitatively; as expected, they contain much greater numbers of the smaller forms, together with early instars of the larger species. However, no additional species is present and the general conclusions remain unaffected.

The following five species were recovered: *Ilyodromus olivaceus* (Brady & Norman), *Eucypris pigra* (Fischer), *Candona compressa* (Koch), *Potamocypris wolfi* Brehm and *Ilyocypris bradyi* Sars. All are extant, so that environmental interpretation can be made from present-day ecology. The assemblage is essentially a cool-spring fauna and includes elements suggesting flowing water.

The fauna of springs comprises a relatively limited number of species, perhaps no more than five or six, compared with the twenty or thirty characterizing ponds or small lakes. Recently, in reviewing the fauna of the Postglacial, Absolon (1973) distinguished six assemblages comprising those of subterranean streams, springs, streams, small ponds, lakes, and temporary or intermittent pools. Each association is distinct in species make-up, or shares only a few species in common. *Ilyodromus olivaceus* and *Eucypris pigra*, the dominant species from the Wateringbury samples, belong to his spring (Quellkalkablagerung) and stream (Bachkalke) assemblages respectively, although other authors would bracket both as indicating cool springs.

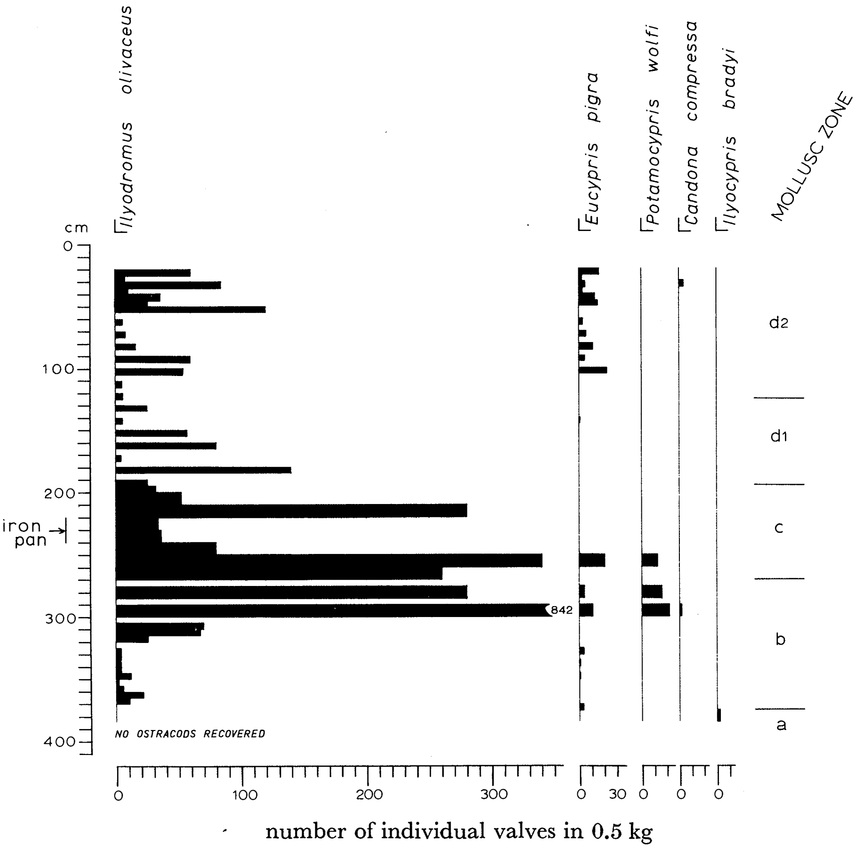

FIGURE 12. Ostracod diagram, Wateringbury.

Ilyodromus olivaceus was described originally by Brady & Norman (1889) from 'amongst weeds in the River Lathkill, Derbyshire', and subsequently by Sars (1928) from a ditch near Oslo. To Klie (1938), it was 'the most characteristic inhabitant of cold springs and associated streams'. In more recent years, it has been similarly cited by Diebel & Pietrzeniuk (1975, 1977) and by Diebel & Wolfschläger (1975) as a krenophile, common in most of the calcareous tufas of southern Germany and Brandenburg. It is a crawling form rather than a swimmer and indicates cold springs and shallow flowing waters; it commonly makes up over 70% of the total ostracod faunas in such situations.

Eucypris pigra has a similar record, but according to G. W. Müller it has a particular preference for areas flooded to a depth of only a few millimetres by permanently flowing water (quoted by Absolon 1973). It has been frequently listed as a cool-spring species by Diebel & Pietrzeniuk (1975, 1977) and by Diebel & Wolfschläger (1975). From the literature it emerges as a cool-water, stenothermal species, which, like the genus as a whole, lives in shallow films, pools and waterlogged ground.

In the Wateringbury succession there is a marked dominance of *Ilyodromus olivaceus* between 180 and 300 cm. The other species listed above occur principally above and below this *Ilyodromus* peak. These are, by and large, active ostracods. Accurate ecological interpretation is somewhat premature, but from the foregoing comments it would seem that flowing water conditions were present in the basal and upper parts of the succession while quieter water conditions prevailed in the intervening levels. The following additional points may be made on the basis of the ostracod record.

Temperature. All comparisons with European sites suggest cool to cold conditions, with the qualification that it is a spring-water temperature that is being assessed and not necessarily the prevailing climate.

Substrate. This was continuously of a soft silty nature and well vegetated.

Water movement. Except for *Ilyocypris*, all the species are delicate-valved. To find that for the *Ilyodromus* peak more than 10% of the specimens are two-valved carapaces, in spite of the weak valve articulation, suggests very quiet, undisturbed conditions of sedimentation. Conversely, the fact that the upper and lower assemblages consist almost entirely of separated valves confirms the interpretation, offered above, of early and late flooding periods, when current flow was sufficient to produce some measure of transportation and valve separation.

References

Absolon, A. 1973 Ostracoden aus einigen Profilen spät- und postglazialer Karbonatablagerungen in Mitteleuropa. *Mitt. bayer. Staatssamml. Paläont. hist. Geol.* **13**, 47–94.

Andersen, S. T. 1970 The relative pollen productivity and pollen representation of north European trees, and correction factors for tree pollen spectra. *Danm. geol. Unders.* R II, **96**, 1–99.

Angus, R. B. 1973 Pleistocene *Helophorus* (Coleoptera, Hydrophilidae) from Borislav and Starunia in the western Ukraine, with a reinterpretation of M. Lomnicki's species, description of a new Siberian species and comparison with British Weichselian faunas. *Phil. Trans. R. Soc. Lond.* B **265**, 299–326.

Barber, K. E. 1975 Vegetational history of the New Forest: a preliminary note. *Proc. Hants. Field Club Archaeol. Soc.* **30**, 5–8.

Bates, C. D., Coxon, P. & Gibbard, P. L. 1978 A new method for the preparation of clay-rich sediment samples for palynological investigation. *New Phytol.* **81**, 459–463.

Bell, F. G. 1968 *Weichselian glacial floras in Britain.* Ph.D. thesis, University of Cambridge.

Bell, F. G. & Dickson, C. A. 1971 The Barnwell station arctic flora: a reappraisal of some plant identifications. *New Phytol.* **70**, 627.

Brady, G. S. & Norman, A. M. 1889 A monograph of the marine and freshwater Ostracoda of the north Atlantic and of northwestern Europe. Section I. Podocopa. *Trans. R. Soc. Dublin II*, **4**, 63–270.

Brown, C. A. 1960 *Palynological techniques.* Louisiana: Baton Rouge.

Brown, E. E. S. 1939 A tufaceous deposit near Wateringbury, Kent. *Proc. Geol. Ass.* **50**, 77–80.

Brown, J. 1852 On the Upper Tertiaries at Copford, Essex. *Q. Jl geol. Soc. Lond.* **8**, 184–193.

Burleigh, R. & Kerney, M. P. 1980 Some chronological implications of a fossil molluscan assemblage from a Neolithic site at Brook, Kent, England. *J. archaeol. Sci.* **7**, in press.

Clapham, A. R. & Clapham, B. N. 1939 The valley fen at Cothill, Berkshire. Data for the study of Post-glacial history. II. *New Phytol.* **38**, 167–174.

Conolly, A. P. 1957 The occurrence of seeds of *Papaver* sect. Scapiflora in a Scottish Late-glacial site. *Veröff geobot. Inst., Zürich* **34**, 27–29.

Coope, G. R. 1977 Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. *Phil. Trans. R. Soc. Lond.* B **280**, 313–340.

Dickson, C. A. 1970 The study of plant macrofossils in British Quaternary deposits. In *Studies in the vegetational history of the British Isles*. (ed. D. Walker & R. G. West), pp. 233–254. Cambridge University Press.

Diebel, K. & Pietrzeniuk, E. 1975 Ostracoden aus dem holozänen Travertin von Bad Langensalza. *Quartärpaläontologie* **1**, 27–55.

Diebel, K. & Pietrzeniuk, E. 1977 Ostracoden aus dem Travertin von Taubach bei Weimar. *Quartärpaläontologie* **2**, 119–137.

Diebel, K. & Wolfschläger, H. 1975 Ostracoden aus dem jungpleistozänen Travertin von Ehringsdorf bei Weimar. *Abh. zentral. geol. Inst. Paläont.* **23**, 91–136.

Dimbleby, G. W. & Evans, J. G. 1974 Pollen and land-snail analysis of calcareous soils. *J. archaeol. Sci.* **1**, 117–133.

Evans, J. G. 1972 *Land snails in archaeology*. London and New York: Seminar Press.

Faegri, K. & Iversen, J. 1974 *Textbook of pollen analysis* (3rd edn). Oxford: Blackwell.

Godwin, H. 1975 *The History of the British flora* (2nd edn). Cambridge University Press.

Havinga, A. J. 1964 Investigation into the differential corrosion susceptibility of pollen and spores. *Pollen Spores* **6**, 621–637.

Havinga, A. J. 1967 Palynology and pollen preservation. *Rev. Palaeobot. Palynol.* **2**, 81–98.

Hibbert, F. A., Switsur, V. R. & West, R. G. 1971 Radiocarbon dating of Flandrian pollen zones at Red Moss, Lancashire. *Proc. R. Soc. Lond.* B **177**, 161–176.

Hoffmann, A. 1950 *Faune Fr.* **52**, 1–486.

Horion, A. D. 1963 *Faunistik der mitteleuropaischen Kafer* **9**, 1–412.

Iversen, J. 1954 The late-glacial flora of Denmark and its relation to climate and soil. *Danm. geol. Unders.* R II, **80**, 87–118.

Kennard, A. S. 1939 Report on the non-marine Mollusca from deposits of tufa at Wateringbury, Kent. *Proc. Geol. Ass.* **50**, 80–82.

Kennard, A. S. 1945 Mr Kennard's report. *Essex Nat.* **27**, 279–280.

Kennard, A. S. & Woodward, B. B. 1897 The Post-Pliocene non-marine Mollusca of Essex. *Essex Nat.* **10**, 87–109.

Kerney, M. P. 1956 Note on the fauna of an early Holocene tufa at Wateringbury, Kent. *Proc. Geol. Ass.* **66**, 293–296.

Kerney, M. P. 1963 Late-glacial deposits on the Chalk of south-east England. *Phil. Trans. R. Soc. Lond.* B **246**, 203–254.

Kerney, M. P. 1968 Britain's fauna of land Mollusca and its relation to the Post-glacial thermal optimum. *Symp. zool. Soc. Lond.* no. 22, 273–291.

Kerney, M. P. 1976*a* *Atlas of the non-marine Mollusca of the British Isles*. Cambridge: Institute of Terrestrial Ecology.

Kerney, M. P. 1976*b* Two Postglacial molluscan faunas from south-west England. *J. Conch., Lond.* **29**, 71–73.

Kerney, M. P. 1977 A proposed zonation scheme for Late-glacial and Postglacial deposits using land Mollusca. *J. archaeol. Sci.* **4**, 387–390.

Kerney, M. P., Brown, E. H. & Chandler, T. J. 1964 The Late-glacial and Post-glacial history of the Chalk escarpment near Brook, Kent. *Phil. Trans. R. Soc. Lond.* B **248**, 135–204.

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, Muschelkrebse. In *Tierwelt Dtl.* **34**, 1–230.

Lindroth, C. H. 1945 Die Fennoskandischen Carabidae, ein tiergeographische Studie. 1. *Göteborgs K. Vitensk.-O. VitterhSamh. Handl.* B **4**, 1–709.

Morgan, A. 1969 A Pleistocene fauna and flora from Great Billing, Northamptonshire, England. *Opuscula ent.* **34**, 109–129.

Newman, J. 1969 *The Buildings of England. West Kent and the Weald*. London: Penguin Books.

Norris, A. & Colville, B. 1974 Notes on the occurrence of *Vertigo angustior* Jeffreys in Great Britain. *J. Conch., Lond.* **28**, 141–154.

Osborne, P. J. 1971 The insect fauna of the organic deposits within the Wandle gravels. *Proc. Trans. Croydon nat. Hist. scient. Soc.* **14**, 162–175.

Preece, R. C. 1978 *The biostratigraphy of Flandrian tufas in southern Britain*. Ph.D. thesis, University of London.

Preece, R. C. 1979 The molluscan fauna of an early Postglacial tufa at Totland, Isle of Wight. *J. Conch., Lond.* **30**, 35–42.

Sars, G. O. 1928 Ostracoda. *An account of the crustacea of Norway*, vol. 9, pp. 1–227. Bergen Museum.

Seagrief, S. C. 1959 Pollen diagrams from southern England: Wareham, Dorset and Nursling, Hampshire. *New Phytol.* **58**, 316–325.

Seagrief, S. C. 1960 Pollen diagrams from southern England: Cranes Moor, Hampshire. *New Phytol.* **59**, 73–83.

Seagrief, S. C. & Godwin, H. 1960 Pollen diagrams from southern England: Elstead, Surrey. *New Phytol.* **59**, 84–91.

Smith, A. G. 1961 The Atlantic–Sub-boreal transition. *Proc. Linn. Soc. Lond.* **172**, 38–49.

Turner, C. 1970 The Middle Pleistocene deposits at Marks Tey, Essex. *Phil. Trans. R. Soc. Lond.* B **257**, 373–437.

Waldén, H. W. 1976 A nomenclatural list of the land Mollusca of the British Isles. *J. Conch., Lond.* **29**, 21–25.

Welin, E., Engstrand, L. & Vaczy, S. 1972 Institute of Geological Sciences radiocarbon dates. III. *Radiocarbon* **14**, 331–335.

Worssam, B. C. 1963 Geology of the country around Maidstone. (One-inch sheet 288.) *Mem. geol. Surv. U.K.* London: H.M.S.O.

TABLE 3. MOLLUSCA, WATERINGBURY

depth/cm	405–410	400–405	395–400	390–395	385–390	380–385	375–380	370–375	365–370	360–365	355–360	350–355	345–350	340–345	335–340	330–335	325–330
dry mass of sample/g	330	400	350	320	310	325	340	350	370	360	350	500	450	420	370	370	380
matias elegans (Müller)	—	—	—	—	—		—	—	—	—	—	—	—	—	—	—	—
thynia tentaculata (Linné)	—	—	—	—	—	—	—	—	—	—	1		—	—	—	—	—
icula fusca (Montagu)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
rychium minimum Müller	8	9	13	33	30	61	33	23	32	7	23	30	2	3	10	12	21
rychium tridentatum (Risso)	1	1	—	—	1	5	3	9	13	15	44	105	24	2	11	118	202
mnaea truncatula (Müller)			2	1	5	6	6	7	5	1	3	5	—	—	—	1	3
Oxyloma pfeifferi (Rossmässler)	8	—	1	1	—	—	1	1	5	—	—	1					
chlicopa lubrica (Müller)	—	1	—	2	4	11	10	8	5	2	6	25	3	1	3	25	39
chlicopa lubricella (Porro)	—	—	—	—	—	1	—	—	—	—	1	1	—	—	—	—	1
lumella edentula (Draparnaud)	—	—	1	2	3	8	2	1	2	1	—	6	—	—	1	6	10
lumella aspera Waldén		—				—				—			—	—	—	—	—
rtigo pusilla Müller	—	21	—	3	4	10	9	5	6	8	4	6	1	1	—	6	14
rtigo antivertigo (Draparnaud)	—		1	—	22	22	22	26	5		—	1	—	—	—	—	—
rtigo substriata (Jeffreys)	—	—	—	—	3	6	9	2	3	3	2	1				1	2
rtigo pygmaea (Draparnaud)				6	—		—	—	—	—	—	—	—	—	—	—	—
rtigo moulinsiana (Dupuy)	—	—	—	—	—	—	—	—	—	—	—		—	—	—	—	—
rtigo alpestris Alder	—	—	—	—	—	—	—	—	—	—	—	—		—	—	1	—
rtigo angustior Jeffreys	—	—	3	3	8	15	25	17	18	13	12	34	1	—	—	—	1
pilla muscorum (Linné)	—	—	—	—	—	—	1	—	—	—	—	—		—		—	—
iostyla anglica (Wood)										—	—	—	—	—	—	—	—
uria cylindracea (da Costa)	—	—	—	—	—	—	—	—	—	—	—		—	—			—
llonia costata (Müller)	1	1	1	8	21	51	57	45	33	21	39	145	19	3	1	20	66
llonia pulchella (Müller)	6	4	3	3	3	4	4	—	3	—	1		—	—	—	—	—
llonia excentrica Sterki	1	3	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—
llonia pulchella/excentrica	16	9	9	8	20	23	17	19	18	4	4	3	1	—	—	—	—
canthinula aculeata (Müller)	—	—	—	—	1	—	1	—	—	—	1	4	—		—	4	3
ermodea lamellata (Jeffreys)				—	—						—	—	—	—	—	—	—
na obscura (Müller)	—	—	—	—	—	—	—	—	—	—	1		—	—	—	2	—
nctum pygmaeum (Draparnaud)	9	9	10	18	8	27	11	9	9	4	20	19	1	—	—	8	21
scus ruderatus (Férussac)	—	—	—	—	—	—	—	—	—	—		2	—	—	—	—	—
scus rotundatus (Müller)	—	—	—	—	—	—	—	—	—	—	—	—				—	—
trina pellucida (Müller)	9	3	1	6	2	1	1	3	2		—	—	—	—	—	—	—
trea crystallina (Müller)	—	—	—	—	—	—	—	—	—	—	—		—			—	
trea contracta (Westerlund)				1	9	22	12	14	19	8	32	86	6	1	3	36	58
sovitrea hammonis (Ström)	3	3	3	3	6	16	9	4	4	1	1	8	2	—	4	21	19
egopinella pura (Alder)	—	—	—	—	—		—	—	—	—	—	—	—	—	2	6	10
egopinella nitidula (Draparnaud)	—	2	3	1	4	6	11	6	6	4	12	41	4	1	2	28	46
xychilus cellarius (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
xychilus alliarius (Miller)	—	—	—	—	—	—	—	—	—	—		—	—	—	—	—	—
nitoides nitidus (Müller)	2	2	3	4	6	8	1	1	5	—	3	6	10	7	33	9	14
roceras/Limax spp.	7	7	8	6	6	6	7	6	19	7	5	13	3	3	—	3	14
uconulus fulvus (Müller) agg.	1	4	2	10	4	7	3	3	5	1	4	12	3	—	2	9	24
chlodina laminata (Montagu)						—	—			—	—	—	—	—	—	—	—
acrogastra rolphii (Turton)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
ausilia bidentata (Ström)					—				—	—	—	—	—	—	—	—	—
[illegible] (Linné)	—	—	—	—	—	—	—	—	—	—	—	—	21	—	—	—	—
richia hispida (Linné)	2	1		1	1	3	1	2	7	1	2	10	6	1	3	23	36
ichia striolata (Pfeiffer)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
licigona lapicida (Linné)	—		—	—	—	—	—	—	—	—	—	—		—	—	—	
rianta arbustorum (Linné)	—	×	—	×	×	×	×	×	×	×	×	×	×	×	×	×	×
rianta/Cepaea spp.	—	2	2	2	3	4	1	3	3	2	4	9	2	2	2	3	8
paea spp.	—	—	—	—	—	×	×	×	×	—	—	×	—	—	×	×	—
sidium casertanum (Poli)	3	7	7	13	5	7	7	3	7	2	2	10	—	—	—	3	5
sidium personatum Malm	6	—		—	1	9	6	3	5	2	6	16	1	4	1	5	6
sidium obtusale (Lamarck)	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
sidium milium Held	—			—	—	—	—	—	—	—	1	—		—		—	—

depth/cm	320–325	315–320	310–315	305–310	290–300	275–285	260–270	250–260	240–250	230–240	210–220	200–210	195–200	190–195	180–185	170–175	160–165
dry mass of sample/g	330	400	300	400	600	500	500	600	500	600	500	700	500	500	600	500	500
matias elegans (Müller)	—	—		—	—	—	—	—	—	—	—	—		—	—	—	—
thynia tentaculata (Linné)	—	—	—	—	—	—			—	—	—	—	—	—	—	—	—
icula fusca (Montagu)	—		—	—	—	—	—	—	—	—	—	—			—	—	—
rychium minimum Müller	2	30	3	6	51	20	13	92	35	28	13	13	17	18	5	5	32
rychium tridentatum (Risso)	14	96	24	45	474	304	421	359	623	490	85	194	148	1259	824	809	504
mnaea truncatula (Müller)	—	1		3	11	7	37	40	3	6	—		—	1	6	—	3
Oxyloma pfeifferi (Rossmässler)	—	—	—	—	—	—	18	33	1	1	4	7	2	1	22	2	3
chlicopa lubrica (Müller)	2	24	6	6	24	21	33	31	37	30	16	18	12	45	41	48	61
chlicopa lubricella (Porro)	—	—	—	—	—				—	—	—	—	—	—	1	—	—
lumella edentula (Draparnaud)	1	3	1	14	45	40	31	94	35	20	15	21	11	23	42	24	34
lumella aspera Waldén	—	—	—		—	—	—	1					—	—	—	1	—
rtigo pusilla Müller	1	3	1	3	20	13	16	10	28	8	6	6	3	31	36	10	7
rtigo antivertigo (Draparnaud)	—	—		—	—	—	—	—	—	—	—		—	—	—	—	—
rtigo substriata (Jeffreys)		2	2	4	10	21	32	60	31	6	—	3	—	2	35	34	18
rtigo pygmaea (Draparnaud)	—	—	—	—	—	—	—	—	—	—	—		—	—	—	—	—
rtigo moulinsiana (Dupuy)	—	—	—	—	2	1	66	77	3	—	3	—	1	2	3	2	1
rtigo alpestris Alder	—		1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
rtigo angustior Jeffreys	1	4	5	33	128	106	88	306	69	47	33	30	21	133	12	35	9
pilla muscorum (Linné)	—		—	—	—	—	—	—	—	—	—	—	—		—	—	—
iostyla anglica (Wood)	—	—	—				—	—	—			—	—	—	—	—	—
uria cylindracea (da Costa)		—	—	4	28	36	16	43	55	25	2	14	3	21	1	22	23
llonia costata (Müller)	1	3	4	11	55	40	61	50	6	2	4	21	11	69	16	—	—
llonia pulchella (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
llonia excentrica Sterki	—		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
llonia pulchella/excentrica	—	—	—	—	—				—	—	—	—	—	—	—	—	—
canthinula aculeata (Müller)		—	—	1	5	1	2	1	19	19	2	9	7	66	37	19	34
ermodea lamellata (Jeffreys)	—	—			—	—	—	—	—			—	—	—	—	—	—
na obscura (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—
nctum pygmaeum (Draparnaud)	2	1		3	34	13	23	99	23	18	3	4	8	61	34	26	55
scus ruderatus (Férussac)	—	21	—	—	1	—	—	—	—	—	—	—	—	—	—		
scus rotundatus (Müller)	—		—	1	1	1	1	2	13	4	2	7	10	100	47	83	53
trina pellucida (Müller)	—	1	—	—		—	1	—	—	—	2	1	—	—	—	—	1
trea crystallina (Müller)			—	—	7	12	12	22	59	18	7	18	22	64	29	64	67
trea contracta (Westerlund)	2	7	2	4	11	9	16	13	19	27	2	13	18	40	22	24	32
sovitrea hammonis (Ström)	3	10	2	3	20	15	30	17	11	5	6	3	5	38	31	61	83
egopinella pura (Alder)	1	3	2	3	17	13	21	19	88	65	7	34	24	87	47	23	59
egopinella nitidula (Draparnaud)	1	16	6	32	66	58	67	64	54	26	10	3	6	51	28	66	73
xychilus cellarius (Müller)	—	—		—	—	—	—	—	—	—	—		—	66	51	47	40
xychilus alliarius (Miller)	—	4	2	3	34	30	44	36	23	12	13	10	6	9	24	2	1
nitoides nitidus (Müller)	1	11	—	1	7	10	9	24	8	1	1	2	1	—	6	—	—
roceras/Limax spp.	1	12	12	31	20	31	15	16	12	6	3	4	2	35	13	11	26
uconulus fulvus (Müller) agg.	2	8	2	4	12	13	20	40	19	22	7	4	1	20	40	19	16
chlodina laminata (Montagu)	—	—	—	—	—						—		—	—	—	—	—
acrogastra rolphii (Turton)	—	—	—	—	—	—	—	—	—	—	—	—	—			—	—
ausilia bidentata (Ström)	—	—		—	—	—	—	—	3	1	1	1	—	4	3	6	2
[illegible] (Linné)	—	—	—	—	—	—	—	—	—	—	—	—	—		—		—
richia hispida (Linné)	1	13	3	1	15	15	10	11	5	2	—	—	1	7	3	1	3
ichia striolata (Pfeiffer)	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—
licigona lapicida (Linné)			—	—	—	—	—	—	—	—	—	—		—	—	—	—
rianta arbustorum (Linné)	×	×	×	×	×	×	×	×	×	×	×	—	—	—	—	—	×
rianta/Cepaea spp.	2	2	3	3	11	7	11	12	5	10	2	1	1	8	9	10	11
paea spp.	—	×	×	×	×	×	×	×	×	×	—		—	×	×	×	×
sidium casertanum (Poli)	—	—	—	—	2	1	28	4	4	—	—	—	—		—	—	—
sidium personatum Malm	—	1	1	—	24	8	56	22	9	1	2	3	—	—	13	—	—
sidium obtusale (Lamarck)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
sidium milium Held	—	—		—	—	—	—	—				—	—	—	—	—	—

depth/cm	150–155	140–145	130–135	120–125	110–115	100–105	90–95	80–85	70–75	60–65	50–55	45–50	40–45	35–40	30–35	25–30	20–25
dry mass of sample/g	600	500	500	600	600	500	600	600	500	500	500	600	600	600	600	500	500
matias elegans (Müller)	—	—	—	—	—	—	—		—	1	1	—	2	3	3	2	3
thynia tentaculata (Linné)	—			—		—	—	—	—	—	—			—	—	—	—
icula fusca (Montagu)	—	—	—	—	—	—	—	—	—		—	—	—	62	102	64	140
rychium minimum Müller	14	38	48	10	22	40	33	20	27	84	10	8	26	22	30	32	41
rychium tridentatum (Risso)	514	302	1177	278	371	853	486	175	1274	1240	284	61	367	596	686	571	805
mnaea truncatula (Müller)	10	2	4	1	8	26	5	35	14	3	9	—	2	21	6	33	71
Oxyloma pfeifferi (Rossmässler)	8	2	3	2	2	1	5	3	5	7	2	7	2	5	6	6	20
chlicopa lubrica (Müller)	45	26	80	37	82	78	64	48	140	90	15	2	18	15	38	33	48
chlicopa lubricella (Porro)			1		—	—	—	—	—	—	—		—	—	—	—	1
lumella edentula (Draparnaud)	32	17	48	24	48	52	63	41	64	64	43	15	20	32	30	18	23
lumella aspera Waldén	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—
rtigo pusilla Müller	3	7	19	—	5	9	14	11	4	11	4	3	7	19	11	5	19
rtigo antivertigo (Draparnaud)	—	—	—	—	—	—	—		—	—	—	—	—	—	—	—	—
rtigo substriata (Jeffreys)	20	7	16	34	25	28	22	15	59	74	32	23	16	6	4	—	—
rtigo pygmaea (Draparnaud)	—	—	—	—	—	—	—	—		—	—	—	—	—	—	—	
rtigo moulinsiana (Dupuy)	—		—	1	1	23	2	14	38	36	20	12	4	4	—	—	—
rtigo alpestris Alder	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
rtigo angustior Jeffreys	—	—	—		—	—	—	—	—	—	—	—	—	—	—	—	—
pilla muscorum (Linné)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
iostyla anglica (Wood)	1	8	16	40	68	47	46	114	115	153	62	15	22	11	7	3	4
uria cylindracea (da Costa)	32	25	25	7	7	44	34	60	130	68	10	—	49	59	20	21	24
llonia costata (Müller)	—	—	—	—	34	110	46	27	121	9	5	4	67	76	64	8	17
llonia pulchella (Müller)	—					—	—	—	—	—	—	—		—	—	—	—
llonia excentrica Sterki	—	—	—	—	—	—	—	—	—	—		—	—	—	—	—	—
llonia pulchella/excentrica	—	—	—	—	—		—	—	—	—	—	—	—	—	—	—	—
canthinula aculeata (Müller)	41	23	89	7	10	38	32	6	52	19	11	2	13	31	44	24	33
ermodea lamellata (Jeffreys)	—	—	—	—	—	13	37	18	223	311	52	9	25	31	8	9	34
na obscura (Müller)	—	—	1	—	1	—	—	—	—	—	—		—	—	—	—	—
nctum pygmaeum (Draparnaud)	39	16	69	16	17	52	50	28	63	42	14	6	24	13	8	13	23
scus ruderatus (Férussac)	—	—				—	—	—	—	—	—	—		—	—	—	—
scus rotundatus (Müller)	20	12	139	11	20	119	75	19	88	54	27	6	65	346	198	102	140
trina pellucida (Müller)	—	—	2	—	—	1	4	—	3	—	1	—	—	5	—		2
trea crystallina (Müller)	57	32	135	20	30	62	57	27	105	55	24	2	59	100	62	59	63
trea contracta (Westerlund)	21	10	45	15	10	18	27	13	30	8	1	—	5	11	19	7	19
sovitrea hammonis (Ström)	41	37	83	34	10	42	36	20	66	57	19	2	8	9	6	13	13
egopinella pura (Alder)	19	29	142	39	43	64	90	42	213	130	17	4	34	89	106	89	93
egopinella nitidula (Draparnaud)	67	20	128	30	42	67	79	20	42	92	27	1	33	45	49	49	102
xychilus cellarius (Müller)	33	24	119	7	20	18	61	22	115	133	33	3	40	92	67	61	45
xychilus alliarius (Miller)	2	21	3	—	—	21	1	—	—	—	2	—	21	2	1	1	1
nitoides nitidus (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
roceras/Limax spp.	14	2	38	7	10	11	10	9	27	27	13	9	21	29	13	14	29
uconulus fulvus (Müller) agg.	20	17	44	15	13	28	24	31	72	57	24	8	10	30	18	30	26
chlodina laminata (Montagu)	—	—	1	—	—	1	4	—	1	1	1	—	—	3	—	4	—
acrogastra rolphii (Turton)	—		2	—	—	—	4	—	—	—	—	—	—	—	—		1
ausilia bidentata (Ström)	—	1	4	—	2	4	4	2	4	3	2	1	2	7	3	2	6
[illegible] (Linné)	—		—	—	1	1	5	—	—	1	—	—	—	3	2	2	1
richia hispida (Linné)	8	1	23	1	6	14	15	3	12	27	5	1	10	9	6	6	17
ichia striolata (Pfeiffer)	—	—	4	—	—	5	1	1		—		—	4	6	3	—	3
licigona lapicida (Linné)	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
rianta arbustorum (Linné)	—	—	—	—	—	×	×	—	—			—	×	×	—	×	×
rianta/Cepaea spp.	4	4	13	6	4	10	10	8	28	23	10	2	9	18	15	11	11
paea spp.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
sidium casertanum (Poli)	2	3	—			—	—	—	—	—	—	—	—	—	—	11	28
sidium personatum Malm	2	—	8	12	2	34	6	3	—	—	30	4		6	2	11	94
sidium obtusale (Lamarck)	—	—	—	—	—			—	—	—	—	—	—	—	—	—	—
sidium milium Held	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

(facing p. 93)