PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Late Pleistocene Floras from Earith, Huntingdonshire

Frances G. Bell

Phil. Trans. R. Soc. Lond. B 1970 **258**, 347-378
doi: 10.1098/rstb.1970.0039

LATE PLEISTOCENE FLORAS FROM EARITH, HUNTINGDONSHIRE

By FRANCES G. BELL

Department of Geology, University of Birmingham

(*Communicated by R. G. West, F.R.S.—Received* 28 *November* 1969)

[Plates 71 and 72]

CONTENTS

A pit in fluviatile gravel of the River Ouse at the western edge of the East Anglian fenland has exposed several richly organic beds of Last-glacial age. A radiocarbon date of 42000 years from one bed confirms the terrace stratigraphy in placing the beds in a fairly early part of the Weichselian. The organic beds are succeeded by cryoturbation phenomena and ice wedge casts, indicating a severely cold climate with permafrost.

The beds represent former pools on the flood-plain into which plant detritus was washed from the surroundings, chiefly by melt water in the spring. Pollen is sparse, but the macroscopic plant remains indicate a vegetation dominated by dwarf willows, accompanied by many herbs of base-rich, open habitats. Identification of the macrofossils is discussed and comments are made on the ecology and taxonomy of important species. The flora contains a mixture of northern and southern distributional types, the southern including species requiring a July mean temperature approaching 16 °C. Halophytes are frequent, and four species are considered to be obligate halophytes and to demonstrate the presence of salt in the substrate.

The plant mixtures are explained as a result of the peculiarly open habitats of the glacial landscape and of the climate, which appears to have had warm summers and very cold winters, with a mean annual temperature slightly below 0 °C, resulting in discontinuous permafrost.

Vol. 258. B. 826. (Price £1; U.S. $2.60) 35 [Published 23 July 1970

1. Introduction

The gravel pit known as Earith lies on the south-west margin of the East Anglian Fens (figure 1), just to the north of the junction of the River Ouse and the Old West River, and between the villages of Colne and Earith. The pit (National Grid Reference TL 388764) is still being worked at present, but the plant beds described here were exposed between 1962 and 1967 and are now destroyed or obscured. Their position and the former boundaries of the pit are shown on figure 2.

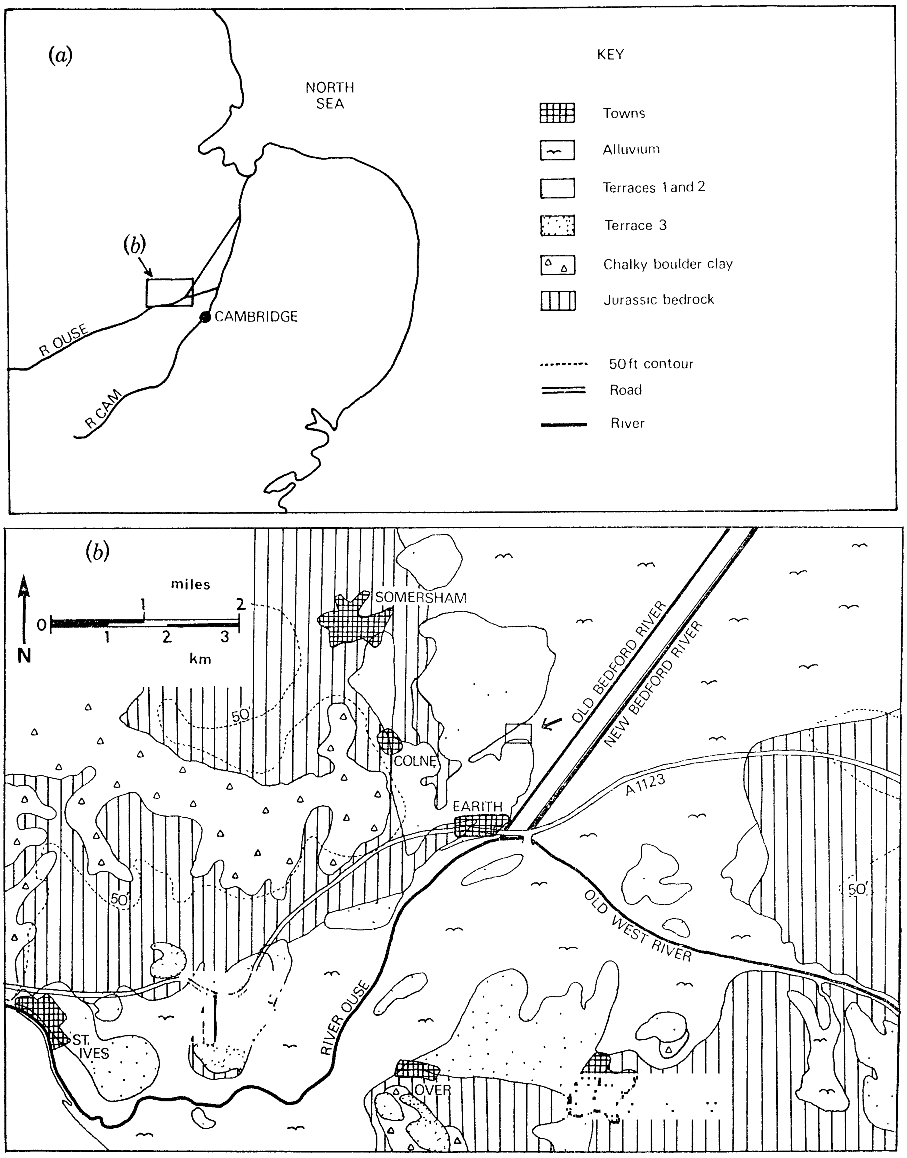


Figure 1. The location of the Earith site.

The gravels of the pit are fluviatile, and were deposited by the former, enlarged, River Ouse. Today, this river flows north-eastwards along a well-defined valley from St Ives to Earith, where part of it continues eastwards as the Old West River and part is diverted into the Old and New Bedford Rivers, which are seventeenth-century drainage cuts. There is evidence from several sources (Fowler 1933) that the Old West River, too, is artificial in its present form, and that the Ouse formerly followed a course northward (which is shown on seventeenth-century maps), to join the River Nene south of March.

There are gravels of the type found at Earith and with similar terrace heights underlying both the former northerly course of the Ouse and the present Old West River, suggesting that during the Weichselian the Ouse followed both these courses, perhaps shifting from one to the other as aggradation and erosion changed the local topography.

2. STRATIGRAPHY

(*a*) *Succession*

The major features are illustrated by figure 2, a sketch of the east face of the pit.

The gravels lie on an unweathered erosion surface of Ampthill Clay at −5 ft (1.5 m) O.D. The top of the gravel succession appears to be a sloping planation surface at +11 to +15 ft (+3.5 to 5 m) O.D., and there is evidence (discussed below) that this surface was cut in Weichselian times. The coarsest gravels occur just above the solid clay, with pockets of large boulders; otherwise the gravels are regularly cross-bedded, with few pockets of coarser stones, and vary from medium gravel to coarse sand. At intervals there are beds of finer sediment, chiefly fine sand and silt. Generally these are discrete lenticular beds with more or less horizontal bedding, but the example E 4 (figure 5*c*, plate 71) was markedly cross-bedded.

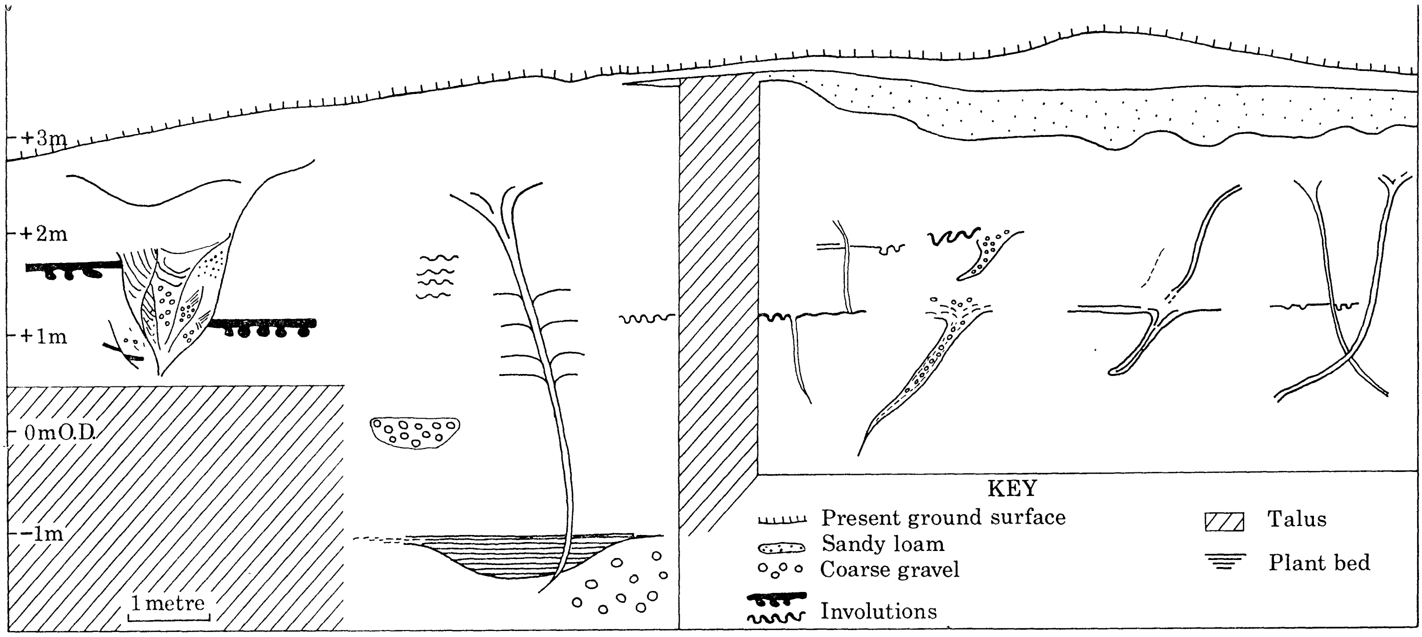


FIGURE 2. A diagrammatic section of the east face of the pit. The plant bed E 9 is shown cut by an ice wedge cast. The wide wedge on the left is no. 18.

The beds of this nature which contain organic detritus are known as plant beds; these all occur in the lower part of the succession. The fine-grained beds in the upper part proved to be sterile. Although the plant beds are *in situ*, their contents are sedimentary, having been brought in by water transport (§3(*b*)). Their plant content is therefore of allochthonous origin.

Besides the plant beds, the succession of gravels contains a number of ice wedge casts, which are considered under the section on frost structures below.

(*b*) *Stratigraphical correlations and radiocarbon dating*

The gravels revealed in the pit are mapped by the Geological Survey (Sheet 187) as belonging to terraces 1 and 2, which are not separated on this sheet. These terraces are the youngest preceding the recent (Post-glacial) alluvium, and are generally considered equivalent to the Barnwell Station and Intermediate Terraces of the Cam. They are both younger than terrace 3, the Barnwell Terrace, which yielded a late Ipswichian flora at Histon Road (Walker 1953). At the Sidgwick Avenue site at Cambridge (Lambert, Pearson & Sparks 1963) gravels of the Intermediate Terrace yielded a Weichselian flora, unfortunately unsuitable for radiocarbon dating, of great similarity to the floras of the present site at Earith. The Barnwell Station Terrace gravels at Cambridge (Chandler 1921) yielded a Weichselian flora with less similarity to the Earith ones but still of an aspect which may be called Full-glacial in the sense explained below. The flora was dated to 19500 ± 650 years B.P. (Q-590, Godwin & Willis 1964).

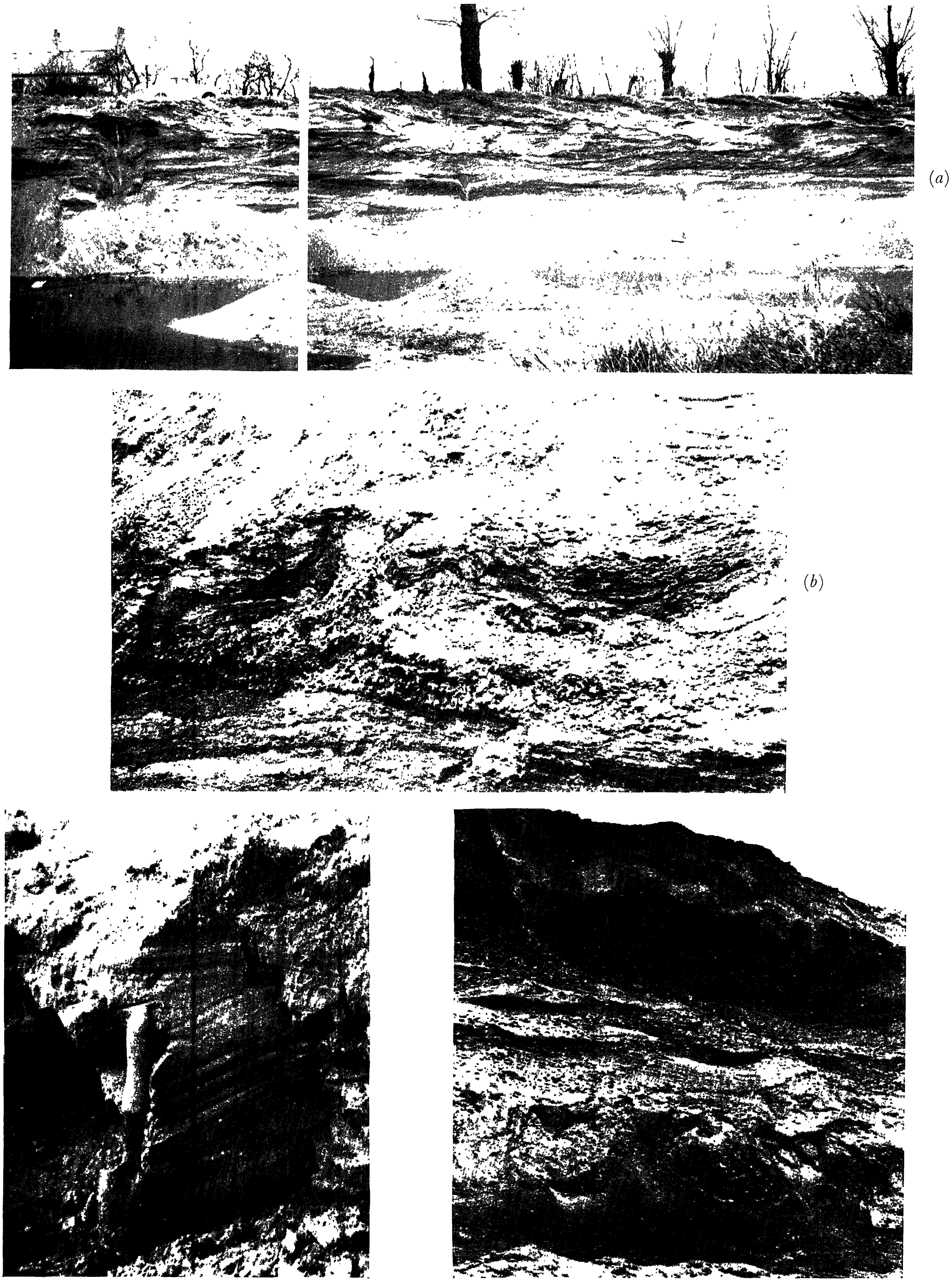
The terrace stratigraphy thus indicates a post-Ipswichian age for the Earith deposits. Fortunately a more precise dating of the Earith beds has been possible with the help of two radiocarbon dates. The dates were obtained from the University of Birmingham and are as follows:

Birm. 86 Plant bed E 9 > 45000 years B.P.
Birm. 88 Plant bed E 7 42140^{+1890}_{-1530} years B.P.

The single date cannot place the flora in time more precisely than within a range of several thousand years. The large standard deviations of dates of this magnitude mean that a span of 5000 years is the nearest to the fixing of a date that can be taken as statistically fairly probable.

A single date is always less satisfactory than a number of dates, because of the numerous potential errors of radiocarbon dating in addition to the statistical errors in the counting. However, in the present case some confirmation of the E 7 date is provided by the infinite date of E 9, which at least indicates that the true date of E 7 is not likely to be younger than the 42000 years obtained. The difference between the two Earith dates has a fair probability of being a real one, although more dates are needed before an improved probability for this can be obtained. It will be noticed that the date of 42000 is the same as that of Upton Warren (Coope, Shotton & Strachan 1961). This is a satisfactory correlation in view of the similarities of the floras discussed below.

The Earith dates can be considered reliable compared with Weichselian dates in general, as the plant material was fully identified and the history of the organic detritus was known. This is important in the Full-glacial where the amount of organic matter is small and the age rather old, a situation which increases the effect of any contamination by younger material. The present samples were obtained from the central portions of bulk 'monoliths' from fresh exposures on the pit face. There was no indication of secondary penetration by recent rootlets. The material was washed in HCl, followed by distilled water. In the case of the E 7 sample *Salix* twigs were picked out. In the E 9 sample there was insufficient twiggy material and the total organic residue was collected from a coarse sieve. In each case the samples were



(*c*) (*d*)

FIGURE 5. Stratigraphical features of the site. (*a*) The east face of the pit showing two horizons of ice wedge casts. (*b*) Injection of gravel through the plant bed E 5. (*c*) The plant bed E 4. (*d*) Flame type of involutions.

Figure 6. The plant bed E 2 and its context. (*a*) The bed in relation to an ice wedge cast and to a silt bed above it. (*b*) Detail of E 2

quickly dried in glass dishes and stored in Polythene bags. They were further pretreated at Birmingham.

The date of 42000 years places the plant bed E 7 within the Full-glacial, in the sense used by Godwin (1956) for that portion of the last glaciation between the Chelford Interstadial at 60800 years B.P. (Vogel & Zagwijn 1967) and the Late-glacial *sensu stricto*. As seen above, this is consistent with the terrace stratigraphy.

(*c*) *Frost structures*

Two categories of frost structures are present; involutions and ice wedge casts.

(i) *Involutions*

Some of these are of the drip type (West 1968), where the appearance is of lobes of finer sediment hanging down into the gravel beneath. These sometimes have a very regular interval of repetition, giving a regular polygonal pattern in the surface views seen in horizontally cut sections. Other involutions are of the tongue or flame type, where tapering injections of finer sediment are thrust upwards, as shown in figure 5*d*, plate 71. In addition there are various features such as the injection of gravel upwards through the silt bed E 5 (figure 5*b*, plate 71).

These structures are all believed to be cryoturbation phenomena, the result of differential freeze–thaw in sediments of different grain size and water content. Involutions are most commonly produced in the active layer above permafrost (Sharp 1942), but they also occur outside permafrost regions, as for example on the coastal ground of the island of Öland, off the coast of southern Sweden (Sterner 1922). However, in this latter instance there is a hard bedrock beneath the soil, providing the same impermeable susbtrate, above which freeze–thaw processes may act, that permafrost provides in northerly latitudes. Wayne (1967) states that involutions are only produced where there is an impermeable substrate within 1 to 2 m of the surface. It is thus considered that the involutions at Earith, occurring in beds underlain by unconsolidated gravel, must have been formed in the presence of permafrost.

Only one of the plant beds is affected by involutions. This is the bed E 5, illustrated, with an injection of gravel, in figure 5*b*, plate 71. This is the lowest horizon at which involutions were observed, but it is also the lowest occurrence of a fine-grained bed. From this level upwards most fine-grained beds show involutions, suggesting that freeze–thaw conditions were continuously present but left no trace in the intervening coarser grained gravels. The plant bed E 2 is an interesting case, itself being unaffected while a fine-grained lens just above it (figure 6*a*, plate 72) is involuted and is, moreover, shortly followed by an ice wedge cast. Figure 2, a diagrammatic sketch of the east face of the pit in 1965, includes a succession of minor fine-grained horizons, each one of them involuted.

(ii) *Ice wedge casts*

The casts occur in at least two horizons, which are clearly seen on the east face (figure 5*a*, plate 71). The lower horizon here consists of neat, small wedges, shown on the photograph, and the upper of a variety of forms. The left-hand wedge on figure 5*a*, known as wedge 18, is a good example of the wide form, here also subsequently disturbed. Others, such as that which cuts the plant bed E 9 (figure 2), are narrow. As is shown on figure 2, some of the upper wedge casts are formed over the same positions as the lower and may be a renewal of their growth, or merely the expression of weak spots in the ground.

The tops of the upper wedge casts in some exposures appeared to flare out to meet the surface of the gravel planation slope, thus suggesting that they originated after the cutting of this slope (Dr R. B. G. Williams, personal communication). This would place the date of cutting of this slope into Weichselian times.

Some of the upper casts, such as wedge 18, can be followed through the various positions of the pit face to produce a line which links up with the polygonal pattern, apparent from aerial photographs, on the ground around the pit. This pattern is an irregular network with polygon diameters of the order of tens of metres. This large scale is characteristic of ice wedge networks in the Arctic today. The network seen from the air is illustrated superimposed on the plan of the pit in figure 3.

The great breadth of casts such as number 18 is notable. Some of this is obviously due to faulting and slumping on melting, and some is related to the plane of the section which happens to be exposed by the direction of the pit face. Nevertheless, it can be observed today in the Arctic that wedge growth takes place by annual increments of only a few millimetres; thus it appears that some wedges at Earith must have grown over an extended period of time.

Ice wedges today can be classified with two formation types: syngenetic and epigenetic. Syngenetic wedges grow upwards, keeping pace with sediment accumulation, while epigenetic wedges grow downwards from a stable surface.

Some of the casts at Earith may be assigned to the epigenetic type from their pointed shape, the occurrence of crossed wedge-casts and the minimal disturbance of the plant bed E 9, where it is cut by a cast (figure 2). These characters, together with an origin from the same horizon at least in the small, lower casts of figure 5*a*, plate 71, suggest that the wedges extended downwards from a single surface. Syngenetic wedges tend to be parallel-sided and might be expected to have their bases at the same horizon rather than their tops; no cast at Earith suggests this type of formation.

The deduction of palaeotemperatures from ice wedge casts has been discussed by Péwé (1966) on the basis of the temperatures correlated with ice wedge formation in Alaska today. A mean annual temperature of −6 to −8 °C is found to be necessary for actual wedge growth, which only occurs in the continuous permafrost region. The grain size of the substrate affects the temperature needed for wedge initiation: the coarser the sediment the lower must be the temperature. At Earith, where the wedge casts are all in gravel, a relatively low mean annual temperature is indicated, probably −8 °C or lower. The long period of this low temperature indicated by the wide wedge casts at Earith in the upper horizon may represent the total period of such low temperature. Alternatively this wedge growth may have occupied only parts of a low temperature period, with wedges growing at horizons of standstill in sedimentation and thawing upon the return of river water.

3. THE PLANT BEDS

(*a*) *General*

The plant beds were numbered in order of their discovery, from E 1 to E 9. E 6 was eliminated by combining it with E 5, and M 4 was retained as a name for an additional bed, near E 4, containing many molluscs. The beds E 1, E 2 and E 3 were exposed and examined by members of the Botany School before I started this work: I have re-examined the macrofossils picked out but not the pollen slides. This early work is chiefly that of Mrs C. A. Dickson, and is included in the tables of plant fossils below.

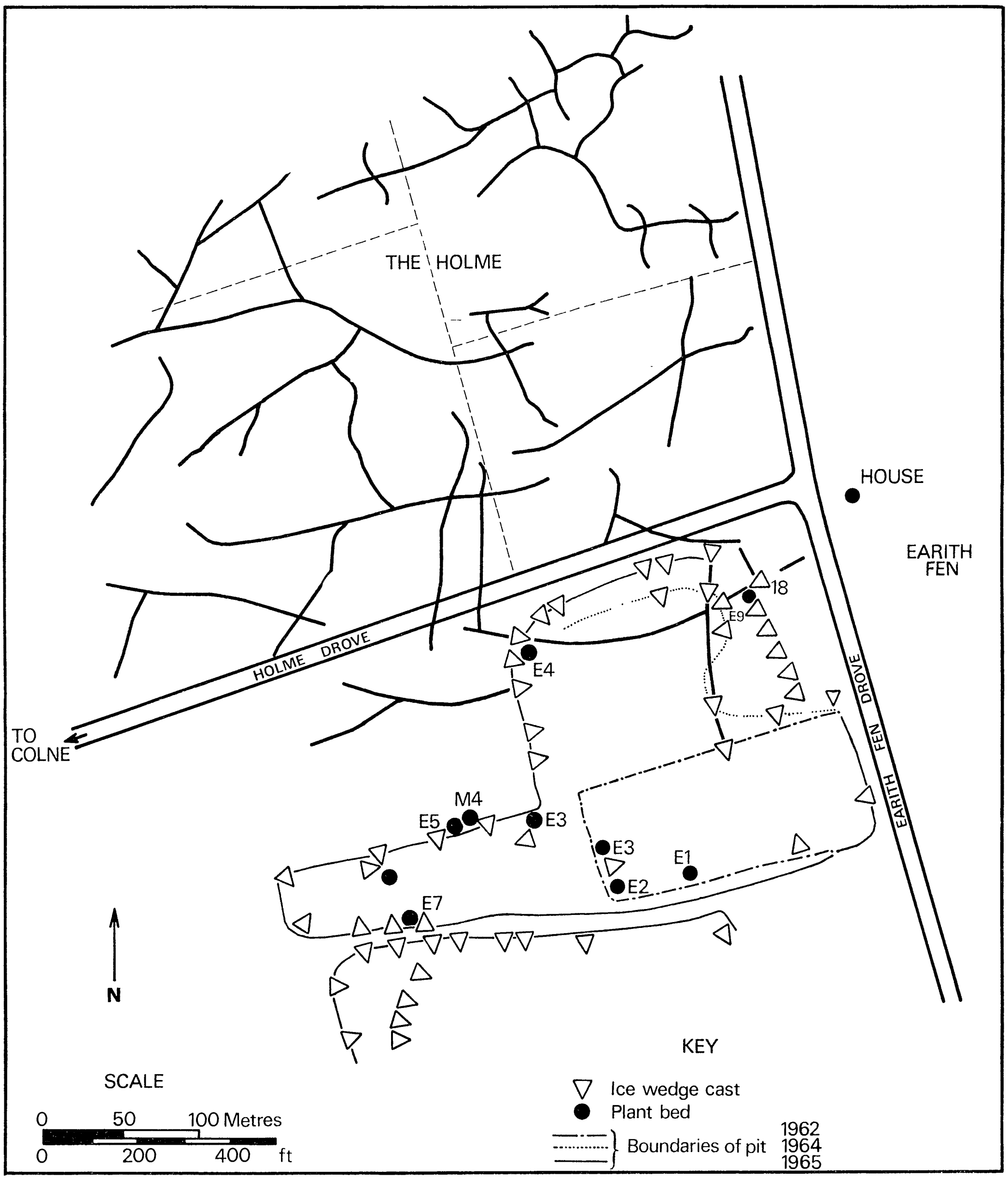


FIGURE 3. A plan of the pit, showing the positions of the ice wedge casts and of the plant beds. The patterned ground as seen on aerial photographs has been superimposed.

The plant beds range from a few to 20 or more feet (6 m) in lateral extent, and from 2 or 3 ft (0.7 to 1 m) in thickness at their centres, to nothing as they gradually thin out laterally. The central portions contain the most plant and animal matter, which, because of reducing conditions, is dark in colour and well preserved. Towards the edges the sediment becomes lighter in colour, more oxidized and less organic. The central organic part is usually laminated, in the same way as at Barnwell Station (Chandler 1921). The laminae are about 0.5 to 2 cm in thickness and number up to 40 in one bed, but the individual laminae may be discontinuous, thinning out within the bed or being truncated (figure 6*b*, plate 71). The beds E 4, E 7 and E 9 were referred to in the field as 'willow leaf layers' on account of the dense matted detritus of *Salix* species lying along the bedding planes, which thus appeared densely organic and black. This can be seen on figure 5*c*, plate 71. Other beds and other parts of the leafy beds had fewer leaves but often many seeds. Figure 6, plate 72, is included as a large-scale illustration of a laminated plant bed (E 2) of this less leafy type.

(*b*) *Formation*

These plant beds are considered to represent former shallow backwater channels or ponds on the flood plain of the River Ouse in which finer-grained sedimentation, both inorganic and organic, occurred. As the plant detritus contains a greater bulk of terrestrial material than of aquatic, it is believed that the detritus was washed into the pools from the dry ground of the surroundings, both from the flood plain and possibly from the slopes of the hillsides to the west and south.

The possible agents of this transport are river water, run-off and snow melt-water. The regularity of the sedimentation and lack of violent erosion seems to rule out river water as the major agent. It seems possible that the laminae, or at least the most regular of them, represent repeated, and thus perhaps annual, events. The run-off water from the spring thaw in high altitudes and latitudes today can be observed to carry away vegetable debris, and also pollen (Terasmae 1968), and this would be consistent with the seasonal heterogeneity of the fossil assemblage—a mixture of mature leaves, fruits and seeds (previous autumn) with budscales and catkins (succeeding spring). Flood water in spring may then be a major agent in assembling and transporting both pollen and macrofossils. At other times run-off or river water may have been the agent. It is also possible that organic macroscopic material was blown overland before entering the pools and could include a long-distance component. Similarly pollen could have arrived as 'pollen rain', thus including a long-distance element.

(*c*) *Derived material*

In a fluviatile environment where material from the load of a river was settling out, any derived organic material in the load would be expected to become incorporated into the beds along with contemporary material of similar sedimentary characteristic. At Earith the finding of nuts of *Carpinus* and *Corylus* gave a clue to the presence of derived material, but only these and of *Thelycrania sanguinea* are considered to be secondary (Bell 1969): they are believed to be derived from Ipswichian deposits upstream. The positions of the present remnants of Ipswichian terraces can be seen (as terrace 3) on figure 1.

The pollen preparations contain large numbers of pre-Pleistocene microfossils; for example, *Classopollis*, *Pinus haploxylon* and *Caytonanthus*. There are also occasional Mesozoic megaspores in the macrofossil assemblage. The quantity of derived microfossils is due to the method of preparation of the samples: the material had a high sand and silt content, and HF was used to remove this. The resulting breakdown of solid rock produced microfossil assemblages for the Mesozoic sediment as much as for the Pleistocene. Thus the presence and quantity of these derived microfossils is related principally to the inorganic content of the pollen sample, and is not an indication of the presence of derived Pleistocene fossils.

4. The plant fossils

(a) *Methods*

Bulk samples and pollen samples were collected in the field. In the laboratory, plant macrofossils were recovered by washing the material, small quantities at a time, in sieves of 100 mesh to the inch. As deposits were impregnated with carbonate, dilute (7 %) HCl was used to separate fossils from the matrix and from each other. This procedure also facilitated identification of the fossils by its mild bleaching action.

(b) *Nomenclature*

The names follow *Flora Europaea*, volumes 1 and 2 of which are currently available, and Clapham, Tutin & Warburg (1962). The name of the one non-British species which does not occur in *Flora Europaea*, *Pedicularis lanata*, is taken from the latest flora of its region (Böcher, Holmen & Jakobsen 1968, *Flora of Greenland*).

'cf.' used before a name or part of a name denotes uncertainty about the whole or part respectively of the determination. These uncertainties concern the morphology of the fossil and the reference material.

Alternatives mean either that two species are inseparable morphologically or that the particular fossil cannot be referred to one rather than the other.

'Agg.' refers to an aggregate of species corresponding to a recognized taxonomic group, e.g. *Rumex acetosella* agg.

'Type' refers to a special classification group erected for a particular case; it allows a further narrowing down of the determination but the groups do not necessarily correspond between pollen and macrofossils, nor between one author and another.

Table 1. List of micro- and macrofossils from the Earith beds

Abbreviations: f, fruit, including nuts and caryopses; a, achene; s, seed; l, leaf; b, bulbil; m, megaspore; p, pollen or spore. * denotes cf. and † denotes a non-British taxon

	plant bed						
taxon	E 1	E 2	E 4	M 4	E 5	E 7	E 9
Achillea millefolium L.	.	.	f	.	.	f	f
Alisma plantago-aquatica L.	.	.	f	.	.	f	.
Allium schoenoprasum L.	.	.	s	s	s	s	s
Alyssum sp.†	f	f	f	.	.	f	f*
Arabis sp.	.	.	.	.	.	s	.
'*Arabis* Type A'	.	.	.	.	.	s	.
Arenaria ciliata L.	.	.	.	.	.	s	s
Armeria maritima (Mill.) Willd.	f, p	f, p	p	.	f, p	f	f, p
Artemisia sp.	p	p	p	.	p	.	.
Atriplex hastata-Type	.	.	.	.	.	s	.
Atriplex sp.	.	.	.	.	s	.	.
Barbarea sp.	.	s	.	.	.	.	.
Batrachium spp.	.	a	a	a	a	a	a
Betula nana L.	.	.	.	.	.	l	.
Betula sp.	.	.	.	l*	p	.	.
Carduus sp.	.	.	.	.	.	f	.
Campanula rotundifolia L.	s	s	s	s	.	s	s
Campanula sp.	p*	.	.	.	s	.	.
Carex bigelowii-Type	.	.	.	.	.	.	f
Carex spp.	.	f	f	f	f	f	f

TABLE 1 (*cont.*)

	plant bed						
taxon	E 1	E 2	E 4	M 4	E 5	E 7	E 9
Carpinus betulus L.	.	.	.	.	.	f	.
Caryophyllaceae	p	p	.	.	p	.	p
Cerastium arvense L.	s	.	s	s	s	s	.
Cerastium sp.	.	.	.	.	.	.	s
Chenopodiaceae	p	.	.	.	.	.	.
Compositae liguliflorae	.	p	p	.	p	.	p
C. tubuliflorae	.	p	.	.	p	.	p
Corispermum sp.†	.	.	.	.	.	f	.
Corylus avellana L.	f	.	.	.	.	.	.
Cruciferae	.	p	.	.	p	.	.
Cyperaceae	.	p	.	.	p	.	p
Damasonium alisma Mill.	.	.	.	.	.	s	.
Dianthus cf. *gratianopolitanus* Vill.	.	.	.	.	.	s	s
Diplotaxis tenuifolia (L.) DC.	s	s	s	s	s	s	s
Draba incana L.	.	s	s	s*	s	s	s
D. incana-Type	.	s	s	.	.	.	s
Eleocharis palustris (L.) Roem. & Schult.	.	.	f	.	f	f	f
E. uniglumis (Link) Schult.	.	.	f	.	.	f	.
Eleocharis sp.	.	.	.	.	.	.	f
cf. *Erophila spathulata* Lang	.	f	f	.	.	f	f
Euphorbia cyparissias L.	.	.	.	.	f, s	f, s	f, s
Euphorbia sp.	.	.	.	.	f	.	.
Festuca rubra L.	f	.	.	.	.	f	.
Filicales	.	p	.	.	.	.	.
Filipendula sp.	.	.	.	.	p	.	.
Glaux maritima L.	.	.	s	s	.	s	s
Gramineae	f, p	f, p	f, p	f	f, p	f	f, p
Groenlandia densa (L.) Fourr.	.	.	f	f	.	f	.
Helianthemum canum (L.) Baumg.	.	.	.	.	.	f, s	f, s
Herniaria sp.	.	.	.	.	.	s	.
Hippuris vulgaris L.	.	.	f	.	f	f	f
Juncus gerardii Lois.	.	.	.	.	s	s	.
Juncus sp.	.	.	.	s	s	.	s
Juniperus communis L.	.	.	p*	.	p*	.	.
Lapsana communis L.	.	.	.	.	.	f	.
Leontodon autumnalis L.	.	.	.	.	f	f	f
Linaria vulgaris Mill.	.	.	.	.	.	f	.
Linum perenne agg.	s	s	s	.	s, p	s, f	s
Lychnis alpina L.	.	.	s*	.	.	s	.
Lycopus europeus L.	.	.	.	.	.	f	.
Matricaria-Type	.	.	.	.	p	.	.
Mentha arvensis/aquatica	.	.	.	f	.	f	f
Minuartia rubella (Wahlenb.) Hiern	.	.	s	.	.	.	.
Myriophyllum spicatum L.	.	.	.	f	.	.	.
Naias flexilis (Willd.) Rostk. & Schmidt	.	.	.	.	.	f	.
Onobrychis viciifolia Scop.	.	.	.	.	f	f	.
Papilionaceae	.	.	.	.	.	f	.
Pastinaca sativa L.	.	.	.	.	.	.	f
Pedicularis lanata Cham. & Schlecht†	.	.	s	.	.	.	.
P. palustris	.	.	.	.	.	.	s
Picea†	.	p	.	.	p	.	.
Pinus	.	p	p	.	p	.	p
Plantago maritima L.	s, f	.	p	.	f, s, p	f, s	.
P. media/major	.	.	.	.	p	.	p

TABLE 1 (*cont.*)

taxon	plant bed						
	E 1	E 2	E 4	M 4	E 5	E 7	E 9
Poa cf. *trivialis* L.	.	.	.	.	.	.	f
Polygonum aviculare L.	.	.	.	.	.	f	.
P. aviculare agg.	.	.	f	.	f	.	.
P. viviparum L.	.	.	.	b	b	b	b
Potamogeton acutifolius Link.	f	.	.	.	.	f	.
P. filiformis Pers.	f*	.	.	f	.	f	.
P. obtusifolius Mert. & Koch	.	.	.	.	f*	.	.
Potamogeton spp.	.	.	.	.	f	.	f
Potentilla anserina L.	.	.	.	a	a	a	a
P. crantzii-Type	.	.	.	a	a	a	a
P. erecta-Type	.	.	.	a	.	.	.
Potentilla spp.	a	a	a	a	.	.	.
Ranunculus section *Ranunculus*	.	.	.	.	a	a	.
R. aconitifolius L.†	.	.	a	.	.	a	a
R. hyperboreus Rottb.†	.	a	.	.	.	a	.
R. sardous Crantz	.	.	.	.	.	a	.
R. sceleratus L.	.	.	.	.	.	a	.
Rhinanthus sp.	s	.	.	.	s	.	s
Rubiaceae	.	.	.	.	p	.	p
Rumex acetosa L.	f	.	.	.	.	f	f
R. maritimus L.	.	.	.	.	f	.	.
Rumex sp.	.	p	.	.	f, p	.	f
Sagittaria sagittifolia L.	.	.	.	.	f	.	f
Salix herbacea L.	.	.	l	l	l	l	l
S. herbacea/polaris	.	l	.	.	.	.	.
S. polaris Wahl†	.	.	l	l	.	l	l
S. phylicifolia L.	.	.	l	.	.	l	.
S. viminalis L.	.	.	.	.	.	l	l
Salix sp.	l, p	l, p	l	.	l, p	l	l, p
Saxifraga oppositifolia L.	l	l	s	.	.	l	l
Saxifraga sp.	.	s	s	.	.	.	.
Scabiosa columbaria L.	.	.	.	.	.	f	.
Scirpus lacustris L.	f	.	.	.	f*	.	f
Selaginella selaginoides (L.) Link	.	.	.	.	m*	.	.
Silene vulgaris agg.	s	.	.	.	.	s	s
Sonchus sp.	f*	.	.	.	.	.	.
Stellaria media (L.) Vill.	.	.	.	s	.	.	s
S. graminea L.	.	.	.	.	.	.	s
Suaeda maritima (L.) Dum.	.	.	.	.	.	s	.
Taraxacum section *Alpina*	.	.	.	.	.	f	.
T. sect. *Erythraea*	.	.	.	.	.	f	.
T. sect. *Palustria*	.	f	.	.	.	.	.
T. sect. *Spectabilia*	.	.	f	.	.	.	.
T. sect. *Vulgaria*	.	f	f	.	.	f	.
Taraxacum sp.	f	.	.	.	.	.	.
Thalictrum alpinum L.	.	.	.	.	.	a	a
T. minus agg.	.	.	.	a	a	a	a
Thalictrum sp.	.	.	.	.	p	.	p
cf. *Thelycrania sanguinea* (L.) Fourr.	s	.	.	.	.	.	.
Triglochin maritima L.	.	.	.	.	f	f	.
Tripleurospermum maritimum (L.) Koch ssp. *inodorum* (L.) Hyl. ex Vaarama	.	.	a	.	.	a	.
Umbelliferae	.	.	.	f	f, p	f	f
Urtica dioica L.	.	.	.	.	f	f	.
Viola sp.	s	s	s	.	s	s	s
Zannichellia palustris L.	.	.	.	.	s	s	.

TABLE 2. POLLEN ANALYSES

The percentages are calculated on the basis of total pollen plus spores.

	plant bed									
	E 1		E 2		E 4		E 5		E 9	
taxon	no.	%	no.	%	no.	%	no.	%	no.	%
Pinus	.	.	.	.	5	.	16	10	7	5
Picea	.	.	1	2	.	.	4	2	.	.
Betula	.	.	.	.	.	.	3	2	.	.
Salix	2	14	3	5	.	.	1	1	1	1
cf. *Juniperus*	.	.	.	.	1	.	.	.	.	.
Gramineae	1	7	17	27	2	.	13	8	83	60
Cyperaceae	.	.	10	16	.	.	3	2	.	.
Armeria maritima	3	21	1	2	1	.	.	.	33	24
Artemisia	2	14	1	2	1	.	24	15	.	.
Campanula	1	7	.	.	.	.	.	.	.	.
Caryophyllaceae	4	29	3	5	.	.	4	2	3	2
Compositae										
Liguliflorae	.	.	2	3	1	.	7	4	4	3
Tubuliflorae	.	.	19	30	.	.	16	10	2	1
Chenopodiaceae	1	7	.	.	.	.	1	1	.	.
Cruciferae	.	.	1	2	.	.	1	1	.	.
Filipendula	.	.	.	.	.	.	2	1	.	.
Linum perenne agg.	.	.	.	.	.	.	1	1	.	.
Matricaria-type	.	.	.	.	.	.	2	1	.	.
Plantago maritima	.	.	.	.	1	.	1	1	.	.
P. media/major	.	.	1	2	.	.	25	15	1	1
Rubiaceae	.	.	1	2	.	.	5	3	2	1
Rumex	1	7	.	.	.	.	.	.	.	.
Thalictrum	.	.	1	2	.	.	30	2	3	2
Umbellifereae	.	.	.	.	.	.	4	2	.	.
Filicales	.	.	1	2	.	.	.	.	.	.
Pollen and spore total	15		64		12		163		139	

5. NOTES ON SOME OF THE MACROFOSSILS

Allium schoenoprasum *L.*

The seeds are distinguished from other *Allium* seeds of triangular shape and flattened faces by the cell pattern of polygonal, angular cells which have a raised surface and are separated by narrow grooves. The fossils retain the black colour of the outer coat, and the texture is reminiscent of derived Mezozoic megaspores. The cell surface is either unornamented or has additional ridges or grooves parallel to those of the cell margins. This differs from the regularly tuberculate ornament of the cell surfaces of *A. sphaerocephalum* L., which is the nearest relative. A fossil seed is illustrated in figure 4 (*a*).

'Arabis Type A'

In E 7 several prominently winged, large crucifer seeds were found which appear to be, from general morphological considerations, a species of *Arabis*. One is illustrated in figure 4 (*b*). They are crucifers, with the double-pointed apex of radical and cotyledonary protrusions; the cells are squarish, and the seed is parallel-sided with rounded top and bottom in just the same way as *Arabis*. It is difficult to separate crucifer seeds into genera on a natural basis and there are other genera such as *Cardamine* which are very similar. All available *Arabis* species were examined, this including nearly all the European ones except for local Mediterranean species, and nothing remotely resembling the fossils was found. Other genera were examined, again with no success. The fossils have very definite characteristics and should be readily identifiable if the corresponding reference material can be found. At present it is left as a completely unidentified species.

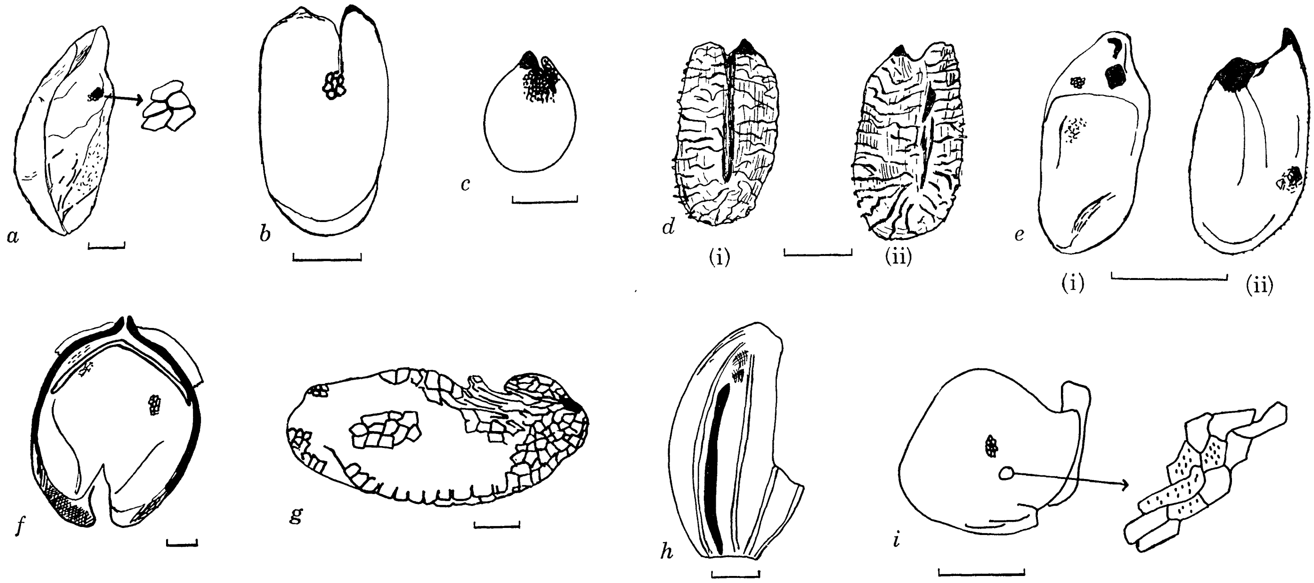


FIGURE 4. Drawings of macroscopic plant fossils from Earith. All scales are 0.5 mm. *a*, *Allium schoenoprasum* seed and detail of the testa cells. *b*, *Arabis* Type A seed. *c*, *Draba incana*-Type seed. *d* (i, ii), Two sides of the small *Damasonium alisma* seed (see §5). *e* (i, ii), Different aspects of *Diplotaxis tenuifolia* seeds. *f*, *Corispermum* sp. fruit. *g*, *Pedicularis lanata* seed. *h*, *Pastinaca sativa*, portion of fruit. *i*, *Suaeda maritima*, seed and detail of testa cells.

Arenaria ciliata *L.*

A special study was made of the seeds of the *A. ciliata* group: *A. ciliata*, *A. norvegica* Gunn. and *A. gothica* Fr., a full account of which is in preparation. It was found that seeds of *A. ciliata* L. *sensu stricto* can be distinguished from the rather similar seeds of *norvegica* and *gothica* using characters of the testa cells. In *A. ciliata* protuberances occur towards the margins of these cells; these are the 'grits' described and illustrated by Jessen & Farrington (1938). In *A. norvegica* and *A. gothica* the cell margins are without such distinct protuberances, although they may be broadly inflated into spurs.

While examining seeds of *A. ciliata* from a great variety of populations it was noticed that the seeds found at Earith bore a close resemblance to those of the present Irish population, and differed in several respects from seeds belonging to other European and Greenland populations.

Corispermum *sp.*

The genus *Corispermum* is found today in central Europe, extending northwards to Germany, and also in Asia including arctic Siberia. Fruit characters, especially wing breadth and thickness, are of taxomomic importance in recent European species, and therefore with well-preserved fossil fruits it should be possible to determine the species. However, in the Earith fossils it is difficult to judge the degree of erosion of the wing, and hence its original nature.

Assuming that some of the best fossils are nearly unchanged from the fresh state, the wing was originally thin. In this case, and with the maximum size of 4.5 mm, three European species resemble the fossils. These are *C. intermedium* Schweigger, *C. marshallii* Steven and *C. hyssopifolium* L. The Asiatic species have not been considered because of this close enough fit existing with the above European species. It is not considered worth while, in such cases where a fossil is morphologically similar to species nearer Britain, to investigate Asiatic species, as the general relationship of the British Weichselian is with the present European flora.

The three species mentioned above grow in sandy places, and especially on loess, from Hungary to Germany. This distribution is thus the most extreme case of southern and continental affinity in the Earith flora and also in the British Full-glacial so far found, although approached by *Androsace septentrionalis* L., found at Upton Warren and at Brandon (Kelly 1968). A fossil *Corispermum* fruit is illustrated in figure 4 (*f*).

Damasonium alisma *Mill.*

Four seeds of this species were found, three being of normal size, 2 mm long, and one only 1.4 mm long though fully mature and with a sculpture identical with that of the normal seeds. This small seed is illustrated in figure 4 (*d*). Being the first seed to be found, it suggested that the species involved might not be *alisma*. However, an examination of European herbarium material of several species showed that there is no other species with similar seed sculpture. Additionally, no seed of *D. alisma* was found that was substantially below 2 mm. Whether the size of this one fossil seed was due to chance, or whether it indicates that in glacial times there was more variation in the species, is a question which cannot be answered with the present data. It is interesting that this is not an isolated phenomenon; exceptionally small seeds of *Suaeda maritima* were also found (see below).

Dianthus *cf.* gratianopolitanus *Vill.*

Two seeds of *Dianthus* were found: one in E 7 and one in E 9. They resemble each other in their ovate shape, size (lengths including beak 2.7 and 2.6 mm), and cell pattern. They probably are of the same species and were treated together. They were compared with material of all species of *Dianthus* native in Britain and Scandinavia. As a reasonable match was found within this area, it was thought unnecessary to consider the vast range of other European species.

In the reference material examined, seeds of *D. deltoides* L. were around 1.5 mm long and thus too small for the fossils. However, Clapham *et al.* (1962) give the length of these seeds as 2–2.5 mm. More herbarium material failed to produce any larger seeds and no reason could be found for the statement of seed size given in the flora. *D. armeria* L. can similarly be ruled out by its small seeds, and both these species have cells of different type from the fossil. *D. arenarius* L. is nearer to the fossil in size but a little smaller, and suborbicular in shape as opposed to ovate. *D. gallicus* Pers. can be excluded by its shape being less tapering, and it has a longer beak.

Two species fall within the general size and cell pattern of the fossils. These are *D. gratianopolitanus* and *D. carthusianorum* L. The latter is rather small but the cells are similar. Coope *et al.* (1961) use size as a distinction in identifying as *D. carthusianorum*, a fossil 2.2 mm in length. The Earith fossils fall within the range of *D. gratianopolitanus*, and have cells similar in every respect to this species, but they differ from the present British Cheddar population in being narrower and tapering more to the beak. Until the use of size as a distinguishing factor is confirmed, the determination is tentative. However, the presence of this species would fit in with the floristic and ecological character of the Full-glacial flora.

Diplotaxis tenuifolia (*L.*) *DC.*

Seeds of this species were abundant in all the samples from Earith. Their presence is usually immediately noticeable by their habit of floating to the top of the water in which fossil material is being washed or sorted. This buoyancy is due to their retention of a three-dimensional form, with inflation by air in the hollow centre. When dry, the seeds have a silvery, rough coat and the genus is further distinguished from other crucifers by the shallowness of the groove between the two apical protuberances of the seed. This can be seen in figure 4(*f*), which shows two typical aspects assumed by the fossils: compare the deep grooves in *Arabis* and *Draba*-Type seeds on the same figure.

The distinction between *D. tenuifolia* and *D. muralis* DC. is in the size of the cells of the outer testa layer (immediately underlying a papery external layer which may be rubbed off in recent seeds and has disappeared in the fossils). These cells in *D. tenuifolia* are half the size of those of *D. muralis* (Dickson 1970).

D. tenuifolia has not yet been found in the Late-glacial, and is one of the few species which is easily recognizable and which occurs in the Full- but not the Late-glacial. However, it may have been overlooked in the past, as it was at Barnwell Station, where Mrs Dickson has shown that *Geranium* sp. 'x' is really *Diplotaxis tenuifolia* (F. G. Bell & C. A. Dickson, in preparation). I have looked for it in the material from the Late-glacial Nazeing site (Allison, Godwin & Warren 1952), which would seem a suitable context, but without success.

Draba incana *L.*

Draba incana may be recognized by its capsule valves, which are long, with a twist that is sometimes preserved, and a prominent median vein. The longest may be determined by their size alone, no other species having valves reaching 9 to 10 mm. At Earith there are many valves reaching these dimensions, but an unbroken series links these with valves down to 3 mm. These shorter valves are likely to belong to *D. incana*, especially if they are twisted, but it is possible that these twisted ones belong to the Scandinavian species, *D. fladnizensis* Wulf., which has twisted valves. This species would certainly be missed in a mixed fossil assemblage containing *D. incana*. The other species which might be expected to occur is *D. norvegica* Gunn. This has untwisted valves, and it cannot be separated from smaller *D. incana* when the character of twist is not preserved, and so again would be missed in a mixed assemblage. The seeds of all three species are small, and have not been separated. Fossil seeds of this kind have been referred to as *Draba incana*-Type. A few were found in E 7 and E 9 and one is illustrated in figure 4(*c*).

Eleocharis palustris (*L.*) *Roem. & Schult.*

The nuts are recognized by their obovate, biconvex shape with a prominent style base (or the base outline together with a remaining central strand) marked off from the nut by a constriction (cf. *E. austriaca* Hayek). The surface of the nut is shiny and bears cell outlines which can be seen when damp-dry. The cells differentiate *E. palustris* from *E. uniglumis*; in the latter the cells are large and have sunken centres: hence the 'punctate' character given in floras (for example, Clapham *et al.* 1962) compared with 'smooth' in *E. palustris*.

Of the two subspecies of *E. palustris* in Britain, ssp. *vulgaris* S. M. Walters has nuts 1.45 to 1.8 mm long and ssp. *palustis* has nuts 1.2 to 1.4 mm. The fossils fall into both size categories, but it has been suggested (S. M. Walters, personal communication) that the small ones have shrunk and should really be referred to ssp. *vulgaris*. Alternatively the size ranges of the two subspecies may have overlapped in the glacial populations. This would be a further instance of greater variability in glacial times.

E. palustris is a member of the low reed swamp of shallow water, and it also grows in meadows where there is surface water during the spring. In summer it tolerates either submerged or dry habitats, providing that the water table is not more than 50 cm below ground level. It has a number of ecotypes, some of which are salt-tolerant, but all of which are competition-sensitive (Walters 1949).

Eleocharis uniglumis (*Link*) *Schult.*

This species occurs with *E. palustris* although it is less common. Coastal populations have been shown by cultivation experiments to be salt-tolerant, as are to a lesser extent the inland populations. It is characteristic of estuarine flats, dune slacks and inland fens; it has been suggested that the freshwater ecotypes are a recent evolution in this species, related to the spread in glacial times and subsequent survival in relict habitats in the Post-glacial (Walters 1949).

Cf. Erophila spathulata *Lang.*

Capsule valves resembling those of *E. spathulata* in every detail of shape, venation and cell pattern were found in great abundance in E 7 and E 9 and in lesser quantities in E 2 and E 4. They were originally determined as *E. spathulata*, but then the skeleton of a crucifer fruit was found which consisted of peduncle, the walls surrounding the capsule valves and a long style. The size and shape were such that the valves, previously identified as *E. spathulata*, fitted on to it perfectly. The skeleton, however, is not an *Erophila* because it has long styles: the genus *Erophila* has short styles. It is probably an *Alyssum*, of which several species are similar. This leaves the separate fossil valves, which have the venation of *Erophila* and not the 'criss-crossed' venation of *Alyssum*, as not belonging to the skeleton, which is unsatisfactory. Moreover, *Alyssum* capsule valves have been found in the same assemblage showing perfectly preserved 'criss-crossed' cells. These valves are rounded and not obovate as is the skeleton. They resemble the crucifer valve identified as *Cochlearia officinalis* L. at Barnwell Station (Chandler 1921), now reinterpreted as an *Alyssum* (F. G. Bell & C. A. Dickson, in preparation).

Thus there appear to be three unlinked fossils: *Alyssum* capsule valves, a second *Alyssum* represented by a pod skeleton, and *Erophila spathulata* capsule valves. Alternatively there could be one true *Alyssum* species (the capsule valves) plus an unknown plant with *Alyssum*-like shape but *Erophila*-like cells on the capsule valves.

Euphorbia cyparissias *L.*

Both seeds and capsules of *Euphorbia* were recovered from three beds at Earith. The capsules are 3 mm long and not covered with warts but with a few veins. The seeds are punctate with regular, isodiametric polygonal cells. The identification was made on the size and form of these cells, those of *E. cyparissias* being distinct from other north-western European species. The capsules agree with this identification although they themselves are not diagnostic.

Festuca rubra *L.*

The caryopses of this species were identified with the aid of the keys and illustrations in Körber-Grohne (1966) and the identifications were subsequently confirmed by Mrs Körber-Grohne. The diagnostic features of the species are the long hilum, ceasing some distance below the apex, and the arrangement of the cells in radiating lines from the hilum.

The species is a very variable one and no precise ecological role can be assigned to the fossils. Present-day habitats include salt-marshes and several grassland types. If the numbers of caryopses corresponds approximately to the number of plants, *F. rubra* may have been the most abundant grass both at Earith and in the British Full-glacial as a whole (Bell 1968).

Glaux maritima *L.*

Seeds were found in four plant beds. The seeds are around 1.6 mm in diameter, with an inconspicuous hilum on one of the three faces and bear a coarse network of cell walls. They differ from seeds of *Trientalis* in their smaller size and larger cells of the network, which measure 50 to 100 μm in diameter. *Androsace* is distinguished by a broader seed and a conspicuous decrease in cell size and increase in cell number on the opposite side of the seed from the hilum.

Glaux maritima is a member of saline communities in a variety of habitats. It almost certainly requires some salt, and its presence is consistent with that of other halophytes with which it grows today.

Helianthemum canum (*L.*) *Baumg.*

H. canum can be identified from its capsule, seeds or leaves. At E 7 whole capsules were found, one still containing seeds, and some *Helianthemum* leaves which although rather small could be referred to *canum* by their wide petioles.

The capsule valves of *H. canum* are smaller, ovate and acutely pointed compared with the larger obtuse valves of *H. chamaecystis* Mill. The seeds of *canum* are smoother and larger than those of *chamaecystis*. *H. appeninum* Mill. capsule valves have a distinct cell pattern different from that in other species. *H. oelandicum* DC. is not separated from *canum* here as the macrofossils are not distinguishable; the taxon is regarded here as included within *H. canum*.

H. canum is a southern plant of very open habitats whose distribution in Britain is related to the past and present lack of competition, to which it is more sensitive than *H. chamaecystis* (Proctor 1956). Its southern range may not be indicative of a high temperature requirement (Bell 1969).

Herniaria *sp.*

A well-preserved seed was found which unfortunately cannot be identified beyond the genus. The seeds of the three most likely species—*H. glabra* L., *H. ciliolata* Meld. and *H. hirsuta* L.—are remarkably similar. Kelly (1968) has used size to separate seeds of different species, but I have not obtained sufficient reference material to do this.

The seed from E 7 appears identical with the seed from Colney Heath (Godwin 1964), identified as *Herniaria* sp., which was considered to be a remarkably southern record for a Late-glacial deposit. However, one species, *H. glabra*, extends northwards just beyond the Arctic Circle in Scandinavia and the genus is thus not one of the most southern of glacial taxa.

Juncus gerardii *Lois.*

Five seeds were recovered, and identified by their cell pattern (Körber-Grohne 1966). The cells are in distinct rows with strong longitudinal walls and single weaker cross-walls.

J. gerardii is one of the group of obligate halophytes which is to be found in saline habitats inland and around coasts over a considerable area from southern Europe to the Arctic.

Lapsana communis *L.*

A fruit of Compositae type, 4.3 × 1.2 mm, and bearing 30 ribs was found in E 7. It can be distinguished from other composites by the straight shape, number of ribs and the lack of spines near the apex (cf. *Crepis*).

The species tolerates closed vegetation and stable soil conditions, and is another not very northern species, just reaching the Arctic Circle in Scandinavia.

Linum perenne *agg.*

This taxon includes various continental diploids and the British tetraploid *Linum perenne* ssp. *anglicum* Ockendon. The seeds of the two ploidy levels cannot be distinguished, so the records are left as the aggregate. The pollen can be distinguished (Ockendon 1968), that of the diploid having furrows and that of the tetraploid having pores. The one pollen grain found at Earith was not well-enough preserved for the presence of pores or furrows to be detected.

The seeds at Earith are of a great many different sizes, as is usual in fossil *Linum perenne* seeds from Full-glacial sites, including those from Barnwell Station which were identified as *Linum praecursor* Reid, a supposedly small-seeded extinct species.

The measurements of the lengths of the seeds from one part of E 7 are as follows (mm): 4.0, 4.0, 4.2, 3.7, 3.5, 3.0, 3.1, 3.7, 4.3, 4.8, 4.1, 3.6, 3.8, 3.8, 3.6, 4.4, 4.7 (mean 3.8 mm).

Besides seeds, capsules and segments of capsules were found. Like the seeds, these varied in size and showed greater variation than that in British populations today.

L. perenne agg. in all its forms is a colonizer of open habitats and requires high light intensity. In shade the shoot apex becomes deformed and flowering often fails to occur (Ockendon 1967). It favours soils with a high pH, including immature soils. The frequent finds of large numbers of seeds in Weichselian deposits indicate that the plant must have been very common then, which is quite consistent with these requirements.

Lychnis alpina *L.*

The seeds of this species are small, 0.4 to 0.6 mm in diameter (in recent European material) and are of the general form of those of *Silene*. They can be distinguished by the distinctly reniform shape.

The hilum is surrounded by a low collar-like projection which distinguishes *Silene* and *Lychnis* from other Caryophyllaceae.

On each face of the seeds of *L. alpina* are around 9 to 14 transverse rows of cells, the cells near the hilum being up to five times as long as they are broad. Long cells may be found in the middle of the seed face. Seeds with such long cells are found in recent British populations, but seeds entirely composed of short cells, little or no longer than they are broad, are found in Scandinavian populations. As with *Silene*, in which cell shape was investigated in prospect of possible interspecific differentiation, it was found that cell shape was nearly constant within a given collection from one locality, but that it was variable within the whole range of the species. The Weichselian fossils of *Lychnis alpina* are nearly all of the Scandinavian cell shape type (Bell 1968). This could indicate that the present British populations are derived from only a small number of glacial ones. This might throw light on the apparent anomaly of the species' rarity in Britain today compared with its abundance in glacial assemblages—in Earith, Lea Valley (Reid 1949); Upton Warren (Coope *et al.* 1961); Four Ashes (Bell 1968) and Syston (Bell 1968) from the Full-glacial and additionally from Late-glacial sites.

Lycopus europaeus *L.*

The one nutlet found in E 7 was well preserved, 1.5 × 1.0 mm, and exactly similar to modern material. There are no closely related species which it could be and its presence in three Late-glacial sites (Godwin 1956) makes the Full-glacial record less surprising.

Lycopus is a plant which has a southern and low-altitude distribution today, but the abundant fossil record shows that it extended to higher latitudes and altitudes in former Post-glacial times. It seems to require high temperatures in order to fruit, and may be regarded as truly thermophilous as well as merely of southern distribution (Bell 1969).

Minuartia rubella (*Wahlenb.*) *Hiern*

One seed was found in E 4. It is 0.75 × 0.7 mm, and subquadrate by slight compression of the originally rounded seed. Of the three related *Minuartia* species with seeds of this size and with prominently inflated cells—*M. verna* Hiern, *M. stricta* Hiern and *M. rubella*—*M. stricta* is rather distinct in its delicate tubercles (protrusions of the cell centres). Of the remaining two species, *M. rubella* appears to be separable from *M. verna* in a fair proportion of seeds by its more obtuse cell tubercles and by its having some cells which are not inflated, neatly round in outline and having the appearance of a double bounding wall. Some specimens among recent *M. rubella* were found where these cells graded into those typical of *M. verna*, and there may be an overlap between the two species making it impossible to identify every seed. In the present case no *M. verna* was found exactly like the fossil and some *M. rubella* seeds exactly matched it; thus the identification was considered possible.

The species is a further example from the glacial flora of a plant today confined to mountain refuge situations, on basic rocks with an incomplete vegetation cover.

Naias flexilis (*Willd.*) *Rostk. & Schmidt*

One definite fruit and a possible second one were found in E 7. The first one measured 2.3 mm in length, and it has the short, bordered cells characteristic of *N. flexilis*. The second was of similar size but very worn.

N. flexilis may be considered to be in the same ecological category as *Lycopus*, that of true thermophiles. It differs, however, in its annual habit. It has a continental distribution, southern to the extent of not reaching the Arctic Circle in Scandinavia but extending eastwards to the Mongolian highlands, where the climate is continental with high summer temperatures but winter temperatures around −20 °C (Backman 1948).

Onobrychis viciifolia *Scop.*

The fruit pods, or their skeletons, occur in some quantity in E 5 and E 7. A photograph of a fossil pod from E 7 is given in Bell (1966). This southern species is an example of a plant which was of doubtful status in the British flora until it was found in a Weichselian site of either Full- or Late-glacial age at Hartford, Hunts (Godwin 1959*b*). I have since discovered it in the collection of macroscopic remains from Nazeing: a pod skeleton, recovered from the level 'Upper MA', which belongs to zone III of the Late-glacial.

O. viciifolia is thus now a well-established member of the glacial flora in Britain. On the continent its pollen had been found in zone I of the Late-glacial in Central Germany (Beug 1957).

Pastinaca sativa *L.*

Rather more than half a carpel of this species was found, which was sufficient to identify it as enough of the necessary characters were preserved. The specimen is 4.2 mm long and would be approximately 5 mm if complete. It is illustrated in figure 4 (*h*). There is one shorter, thick vitta, on the originally inner side of the carpel, which extends for five-sixths of its length. On the other side are four equally spaced thinner vittae extending the whole length. Traces of ribs can be seen between them. This combination of thickness, length and position of the vittae is diagnostic of *Pastinaca*. The closest resemblances to it are in *Heracleum*, which has short vittae on its inner side, and *Peucedanum*, which has either inconspicuous or very long vittae on the inner side of the carpel. *Pastinaca sativa* is characteristic of open places, especially on chalk or limestone.

Pedicularis lanata *Cham. & Schlect*

One fossil seed was found in E 4 and referred to this species. It measures 3 × 1.4 mm, and bears a rectangular network of cells which are arranged in regular rows. A drawing of the seed is given in figure 4. The shape of the cells is quite different from that of all other European species examined, and exactly matches material of *P. lanata* from Greenland, which also agrees in all other respects with the fossil.

In Greenland the plant grows on dry ground on heaths, fell-field and sometimes in marshes (Böcher *et al.* 1968).

Polygonum aviculare *L.* (*sensu stricto*)

This identification was made on two specimens which had a whole and part of a perianth preserved. The characters used to distinguish the species of the aggregate have been very clearly set out by Styles (1962) and agree with reference material used in this work.

The seed from E 7 was totally enclosed in a closely fitting perianth. This perianth was removed and an oval, three-angled nut with the characteristic ornament of *P. aviculare* was revealed. The nut was 3.2 mm long and equally three-angled. The combination of the size and the complete enclosure of the nut by the perianth is diagnostic of *P. aviculare sensu stricto*.

Potentilla anserina *L.*

The achenes and half-achenes of *P. anserina* are quite distinctive and may be identified immediately on their shape and texture. The only possible confusion is with the arctic and boreal taxon, *P. egedii* Wormsk. This taxon is very closely related to *anserina*, with which it hybridizes where their distributions overlap in the Gulf of Bothnia: it may be better treated as a subspecies of *P. anserina* (Rousi 1965). The achenes of *P. anserina* ssp. *egedii* are sometimes smaller than those of ssp. *anserina*, and in Greenland they lack the dorsal groove. In Scandinavia this distinction is not so clear, possibly due to genetic mixing.

The fossils vary in size but none of them lacks the dorsal groove. There is no evidence for ssp. *egedii* being present among the fossils but the definitive statement that the fossils belong to the ssp. *anserina* equivalent to the present British population cannot be made.

The species is tolerant of saline conditions and is a regular member of sand dune, dune slacks and estuarine habitats.

Potentilla crantzii-Type

The type includes *P. crantzii* (Crantz) G. Beck, *tabernaemontani* Aschers., *arenaria* Borkh., *heptaphylla* L., and other non-British species with similar achenes. The seeds are neatly rounded in shape as opposed to the proximally elongated achenes of the *P. erecta*-Type. They have an ornament of curved ribs, with few or no spots, and the ribs all follow the outline of the achene in direction (cf. the characters of *P. erecta*-Type below).

Only some of the achenes of *P. crantzii* can be identified completely because they overlap with the seeds of other species listed above. Those which can be identified are at the upper half of the size range from 1.3 to 1.7 mm long. *P. arenaria* ranges from 1.3 to 1.5 mm and *heptaphylla* from 1.4 to 1.5 mm (although this was measured on a smaller sample than the others). Of the large achenes, *P. tabernaemontani* comes very near the shape and rib-pattern of *crantzii* in some populations.

In both *crantzii* and *tabernaemontani* each recent population examined was distinctive and could be recognized from the others. In the Weichselian, when there must have been many more populations, there must have been more variation in both these species with consequent difficulties of separation on seed characters.

Potentilla erecta-*Type*

The achenes of *P. erecta* (L.) Räusch are recognized by their size, over 1.3 mm long, and by the distinctive rib pattern. The ribs normally consist of two groups, from the top and bottom edges of the achene, which converge towards the pointed proximal end of the achene. There are also frequently spots in addition to ribs.

On the fossil, the rib pattern is not very clear and therefore the determination is left as *P. erecta*-Type, including *P. erecta*, *anglica* Laicharding and *reptans* L.

Potentilla *spp.*

Recent *Potentilla* plants produce a large proportion of abortive fruit, which is small, unexpanded and without external sculpture. There are fossil achenes found which look like this and are not believed to be further identifiable.

The Scandinavian species *P. nivea* L. and *P. nivalis* Lapeyr are fairly smooth on the outside and resemble immature achenes of other species. Care must therefore be taken that only full-sized achenes are identified to these species. The tendency to equate non-ornamented achenes with non-British ones has unfortunately been exaggerated by the reference material of these non-British species sometimes being collected from plants with only immature fruit, because of the relative scarcity of herbarium specimens.

Ranunculus aconitifolius *L.*

Several half-achenes were found with a venation pattern similar to recent *aconitifolius*. They are a little smaller than the recent reference material but exactly the same size as the fossil achenes from Barnwell Station. They are fully mature.

Ranunculus hyperboreus *Rottb.*

The achenes are identified by their size, 1 to 1.3 mm, rounded shape and rounded, air-filled inflated testa cells. The species is becoming recognized as a frequent Full- and Late-glacial one.

Ranunculus *Sect.* Ranunculus

Many achenes of this type could be further identified on a limited range of reference material to *R. acris* L., *repens* L. or *bulbosus* L. When a wide range of reference material is examined the species grade into each other, and *acris* especially is very variable. E. M. Reid (1949) identified R. *acris* on the size of the cells and their uniformity of size across the achene. *R. repens* was said to have larger cells in the centre of the achene. This distinction appears not to hold for European material as a whole, and no characters of cell type or general shape could be found which would consistently separate the three species. Moreover there are Scandinavian and British mountain related taxa of which achenes have not been seen by me.

Ranunculus sardous *Crantz*

Only a piece of an achene was found, but it included the margin and ornament on the outer portion of one half of the achene. The cells were 30 to 40 μm in diameter, decreasing to 10 μm at the margin, which was striated. Groups of cells were raised into low circular mounds on the seed surface, and these mounds were arranged in three rows parallel to the margin. The regularity of the arrangement of the ornament is characteristic of *R. sardous*. This species does not always have the ornament of mounds, and the number varies, but three is the number often found in present British populations.

It is a southern species, often occurring in coastal or open habitats inland. It was found at the Full-glacial site of Sidgwick Avenue (Lambert *et al.* 1963).

Rumex maritimus *L.*

One dissected perianth characteristic of this species was found. The species has a fairly southern distribution over its natural range, but is a casual much farther north in Scandinavia and reaches high latitudes in Russia. The seeds germinate better if they are dried out and sun-baked after initial submergence under water; conditions that were probably widespread on the flood plains of rivers in a glacial environment.

Salix polaris *Wahl.*

Many leaves of this species were found in the 'willow leaf layers' E 4, E 7 and especially E 9, while a small number were found in E 4. The leaves are distinguished from those of *S. herbacea* L., which were abundant in the Earith beds, by several characters. The shape of the leaf in *S. polaris* is orbicular, sometimes emarginate at the apex, and with its widest point some way from the base. The margin is entire, but more important is the way in which the veins do not reach the margin, but either turn back or join to form a marginal vein, leaving a clear area around the edge (Tralau 1963). The long petiole is characteristic, compared with a short one in *S. herbacea*. It was noticed that the fossil leaves of *S. polaris* were thinner and more delicate than the black, woody ones of *S. herbacea* in the present assemblages.

Salix viminalis *L.*

Leaves referred to this species were found in the beds E 7 and E 9. They are linear, up to 3.5 cm long, and with a revolute margin. They have a large number of strong, widely diverging lateral veins which are linked by a weak secondary network. The base is cuneate and the tip tapers to an acute point.

The leaves resemble closely the illustrations both of *S. viminalis* from the Late-glacial of Mapastown, identified by Jessen in Mitchell (1953), and of *S. incana* Schrank (= *S. elaeagnos* Scop.) from the Dryas flora of Wierden in Holland (Florschütz 1958). They are small compared with recent leaves of *S. viminalis* but their linear shape, cuneate base and revolute margins rule out most other species. The two European species with this combination of characters are *S. viminalis* and *S. elaeagnos*. There is also the more eastern *S. rossica* Nasarov, which also has linear revolute leaves, but this has a rounded base. Mitchell (1953) ruled out *S. elaeagnos* on geographical grounds: 'the leaves resemble those of *S. incana* Schrank to a certain extent but on account of the more southern distribution of this plant the leaves are unlikely to belong to it'. This argument can no longer be used, as southern plants are now recognized components of the glacial flora (Bell 1969). Florschütz does not comment on his means of identification for the Wierden leaves.

A difference between the two species can be found in the leaf margin. *S. viminalis* has an entire margin while *S. elaeagnos* has a glandular-toothed one. This character is not an easy one to use as fossil leaves tend to collapse if they are unrolled, but two fossil leaves were successfully unrolled after soaking in Eau de Javelle and the resulting fragments of margin could be seen to be entire. This is the basis of the present identification.

S. viminalis is a southern plant, being perhaps native in south Scandinavia (Clapham *et al.* 1962) and extending through southern and central Europe. Its presence as a glacial plant is surprising, and it is tempting to suggest that it was due to the occurrence of a distinct race of the species which is now extinct.

Scabiosa columbaria *L.*

Two fruits were found, in E 1 and E 7. It is another southern plant, just reaching the Arctic Circle in Scandinavia, and was found at Hartford (Godwin 1959*b*). It is known to be a strict calcicole (Rorison 1960), as opposed to merely basicole.

Silene vulgaris *agg.*

This species is recognized by its rather large seed, 1–1.3 × 1.2–1.8 mm; with a prominent hilar zone made up of several rows of cells and projecting beyond the proximal end of the seed. The shape of the seed tends to be somewhat triangular with the distal end narrowed. The cells are throughout in regular concentric rows, quadrate, with serrate margins. The number of rows of cells is difficult to estimate as those near the hilum are squashed together closely, but it is around 9 to 15 on a single face. Within the aggregate species *S. vulgaris* Garcke, the two subspecies involved are *maritima* A. and D. Love and *vulgaris* Garcke. In Britain, these two subspecies are ecologically separated and may be regarded as two distinct species as in Clapham *et al.* (1962). However, in Scandinavia the separation is incomplete and intermediates occur in the wild. Whether this is a recent phenomenon, due perhaps to an increase in open habitats made by man's activities, or whether it represents the original condition from which the British populations have progressed is not known. It cannot be assumed that the two ecospecies were separate in glacial Britain. Therefore the aggregate taxon has been retained for the fossils.

Suaeda maritima (*L.*) *Dum.*

Seeds from British populations, belonging to the various varieties of the species, can be distinguished from other related chenopodiaceous seeds by the cell pattern. The cells are polygonal, and irregularly arranged in the middle of the seed, but are in regular rows over the radicle where they are elongated along its long axis. At the distal margin, i.e. the edge away from the hilum, they are quadrate and in rows parallel to the margin. The cell boundaries are marked by sunken lines, the cell surface thus being raised. The cell surface is marked by many puncta, a feature which distinguishes *S. maritima* from *S. fruticosa* Forsk. Seeds of the latter have very faint puncta and less well-defined cell outlines, being glossier in general appearance. Recent seeds of *S. maritima* are from 1.5 to 2 mm in length and have a roughly equal breadth.

Two fossils were recovered from E 7 and one is illustrated in figure 4. They resemble each other closely, and are approximately 1 mm in both dimensions. They are both incomplete and somewhat squashed, but enough remains to distinguish the shape of the seed, and the shiny surface with well-marked punctate cells. The cells are the same size as in recent *S. maritima*, there being a smaller number of them in these smaller seeds. This is another example of a fossil seed being smaller than its recent equivalent, and as there are no other species which it might be, it must be concluded that either the Weichselian populations had seeds smaller than any of the recent material which has been examined, or that the seeds have shrunk.

Suaeda maritima has been recorded at Sidgwick Avenue in a similar context (Lambert *et al.* 1963) and is here considered to have grown on saline soil in these sites.

Taraxacum *sect.* Alpina

The fruits of this section are nearly smooth and lacking in spines, spindle-shaped and from 3.0 to 4.5 mm long. One fruit with these characters was found in E 4 and identified by Richards, who has recently discovered plants of this section growing in Scotland. This is then another case of a lowland glacial species with a present-day refuge habitat in the northern mountains.

Vicia *sp.*

Incomplete central portions of large pods were found. They agree best with the genus *Vicia* and appear to be the same as the Lea Valley *Vicia sylvatica* (Reid 1949), but it was not possible to identify the Earith fossils further than to *Vicia*.

6. THE VEGETATION AND FLORA

(*a*) *Vegetation*

The fossil assemblages contain in their richest form a great bulk of leaves and twigs from several dwarf willow species, and a smaller bulk of fruits and seeds representing a great number of plant species. The macrofossils are considered to be primary and local, except for *Corylus*, *Carpinus* and of *Thelycrania sanguinea* (§3).

The vegetation of the surroundings may thus be reconstructed as having areas where willow scrub was dominant, with (in descending order of frequency) the species *Salix herbacea*, *S. viminalis*, *S. phylicifolia*, *S. polaris* and possibly other unidentified species. *S. viminalis* today may grow to tree height, but it is believed, both because of the absence of stout twigs and the small size of the leaves, and also because of the scarcity of woodland undergrowth species from the assemblage, that the glacial plants of this species were no more than shrubs. The other shrub present was *Betula nana*, but in very small quantity; one fruit was recovered from E 7 and in addition a fruit in M 4 and three pollen grains in E 5 were referable to the genus *Betula*.

Although the pollen of *Pinus* and *Picea* were found, there is no evidence that either of these trees was growing in the region. *Pinus* pollen is a regular component of Weichselian assemblages in sites where pollen analysis has been possible: these sites are Upton Warren (Coope *et al.* 1961); the Tame Valley (Coope & Sands 1966), in which the highest value so far recorded in the Full-glacial was reached—10 %; Marlow (Bell 1968); and Earith.

It is well known that coniferous pollen travels far beyond the forest limit, and that in northern and mountain 'tundra' areas the low pollen productivity of the local vegetation exaggerates the proportion of this pollen. It has been assumed in these situations that values for coniferous pollen of 10 % or less certainly indicate long-distance transport (Faegri & Iversen 1964). In the Canadian Arctic values of 20 % were found for *Pinus* and *Picea* when the coniferous forest was 2000 km distant (Ritchie & Lichti-Federovitch 1967). At Full-glacial sites an additional source of coniferous pollen is secondary pollen from interglacial deposits.

In general, the preservation and quantity of pollen found in Full-glacial deposits, which in Britain are usually within the gravel of river terraces, are poor. This seems to be because of the oxidizing conditions in a gravel environment. In these circumstances, too much weight should not be given to low pollen sums; the consequently exaggerated non-British and derived elements can give a very confusing picture. At Earith, the macrofossils give reliable information as to the provenance and history of the organic material, and the micro- and macrofossils and stratigraphy may be combined to give a comprehensive picture of the site.

When considering the regional vegetation of Weichselian sites the question arises as to how far floras recovered from sites on river flood plains reflect the vegetation of the whole countryside, or how far these plains have a pioneer vegetation comparable with that of shingle banks in rivers today, an interpretation that would give an exaggerated impression of the openness of the vegetation. It is unlikely in the present case that other parts of the countryside—namely the sides and tops of hills—bore a more mature, closed vegetation, because no trace of it was picked up in the macrofossils nor, more significantly, in the pollen. This suggests that the hill slopes were no more favourable as a habitat than the flood plain, and must have borne similar or sparser vegetation. This is consistent with the expectation from the evidence of the contemporary climate (§2(*c*)) that the valley slopes would have been unstable.

Locally at least the vegetation can thus be considered as physiognomically a shrub-tundra, although the term 'tundra' is best avoided in further discussion here as there are important floristic differences between present-day tundra and the Weichselian vegetation.

(*b*) *Ecology*

(i) *General*

The flora from E 7, which contains the largest number of species, will chiefly be used to illustrate the relationships of the flora to the environment. Brief notes on the other beds will be given afterwards.

The macrofossils are completely consistent with a situation where vegetation grew around the braided channels of a river, in and around the pools of its plain and also in more stable areas either on the flood plain or alongside it. The vegetation of these more stable areas was rather luxuriant and shrubs in particular must have been well represented near to the incipient plant beds because of the large quantity and good preservation of their leaves.

The terrestrial herbs were numerous and varied. Only a few, such as *Lapsana communis* and *Urtica dioica*, tolerate shading and might have grown under the *Salix* scrub. *Urtica dioica* is associated with mature, organic soils and may have found a suitable habitat where animal activity had enriched the phosphorous and nitrogen content of the soil, or in the vicinity. The beetle genus *Aphodius*, which was present at Earith (Coope, personal communication) indicates the presence of large mammals (most *Aphodius* species live on the dung of the larger mammals) and the species *Thanatophilus dispar* is a carcass beetle (Coope *et al.* 1961). Dung pellets of an unidentified small mammal were also found in E 7.

Many herbs are basicoles, and the ground water was probably as base-rich as it is in the area today, or more so with increased erosion of the chalky boulder clay of the surrounding hills. *Scabiosa columbaria* specifically indicates a calcareous as opposed to base-rich substrate. The basiphilous, open vegetation element includes *Achillea millefolium*, *Allium schoenoprasum*, *Dianthus* cf. *gratianopolitanus*, *Euphorbia cyparissias*, *Helianthemum canum*, *Linum perenne* agg., *Leontodon autumnalis*, *Onobrychis viciifolia*, *Scabiosa columbaria* and *Festuca rubra*. In addition there is a more northern facies of the same basiphilous, short-turf vegetation, often associated with rather more open, mountainous habitats, with *Arenaria ciliata*, *Draba incana*, *Polygonum viviparum*, *Saxifraga oppositifolia*, *Potentilla crantzii*-Type, and *Thalictrum alpinum*.

Other herbs represent bare ground which may or may not have been basic: *Diplotaxis tenuifolia*, *Potentilla anserina*, *Linaria vulgaris*, and *Corispermum* sp. These would have extended farther out on to the fresh mineral ground around the river channels. *Corispermum* may be considered to indicate steppe-like conditions (Bell 1969).

Marsh vegetation is represented by *Lycopus europaeus*, *Ranunculus sceleratus*, *Eleocharis palustris* and *E. uniglumis*. An intermittently wet habitat of a pool or stream shore is represented by *Ranunculus hyperboreus*, *Damasonium alisma*, *Alisma plantago-aquatica*, and, in E 5, *Rumex maritimus*. Other helophytes, such as *Eleocharis palustris*, commonly grow in this situation and these waterside communities may have been very extensive. They would also be well represented in an aquatic sedimentary deposit; they may have grown around the same pools which were to become the plant beds.

Aquatic vegetation includes *Naias flexilis*, *Groenlandia densa*, *Potamogeton filiformis* and *acutifolius*, *Zannichellia palustris* and *Hippuris vulgaris*. Fossils of all these except *Naias flexilis*, of which only two fruits were found, were abundant. Various genera of the Characeae, including *Chara* and *Nitella* and perhaps others, are represented by oospores and probably formed part of the deeper water vegetation as well as that of shallow and intermittent water bodies.

There is a well-defined halophyte element. The obligate halophytes—*Glaux maritima*, *Suaeda maritima*, *Juncus gerardii* and *Triglochin maritima*—must have grown in damp areas with salt, probably in depressions in the ground surface where extensive evaporation occurred during the summer. This entails a retention of salt due to the overall upward movement of ground water followed by evaporation, a phenomenon found today in the Arctic, where permafrost underlies the surface and the climate is continental. The facultative halophyte species *Armeria maritima*, *Plantago maritima*, *Festuca rubra*, and others in the fossil list, could well have grown in quite high salt concentrations with the obligate halophytes. If terrestrial saline habitats were present, it is likely that there would have been brackish pools, and perhaps very saline water where these pools reduced their volume by partial drying up in the summer. In the brackish water *Zannichellia palustris* and *Potamogeton filiformis* could have grown, and around the margins such species as *Ranunculus sceleratus* and *Eleocharis uniglumis*.

(ii) *Relation to recent vegetation*

No close match of the vegetation described above exists in Europe; the fossil assemblage is a mixture of elements from very different present localities.

However, some similarity in the mixture of halophytes, steppe and northern and weedy plants can be found in the vegetation of the Middle and Upper Lena Valley of Siberia. The environment here is a wide flood plain under a very continental climate, with an annual range of temperature of 30 to 40 °C (Cajander 1903). There is permafrost just beneath the ground surface. The vegetation ranges from forest in the south, with *Larix*, *Picea*, *Alnus*, etc., through steppe, halophyte and luxurious herb communities in the central part, to tundra in the north. Several arctic and northern species occur in the steppe and halophyte communities.

The chief resemblances to Earith are, first, the great extent of *Salix viminalis* stands alongside the river channels. There are also areas of *Eleocharis palustris* and *Carex aquatilis* here. Secondly, the saline areas contain a number of species in common. Near Yakutsk one of the halophyte associations is Potentillieta anserinae with *Eleocharis palustris*, *Potentilla anserina*, *Primula farinosa*, *Glaux maritima* and others. The more extreme Salicornieta herbacea contains *Festuca rubra*, *Salicornia*, *Potentilla nivea*, two *Artemisia* species, and *Suaeda maritima*.

There are also resemblances in the non-saline herbs, but the comparisons which can be made, as also in considering the halophytes above, are limited by the extent of taxonomic identity between these Siberian plants and our European relatives. For example, Cajander's *Salix viminalis* must be *S. elaeagnos*, according to the distributions given in *Flora Europaea*, and *Primula farinosa sensu lato* covers a great range of species. Despite this, the general aspect of the vegetation seems to have much in common with the British glacial floras of the Earith type.

(iii) *Climate*

As noted at various points in §5, the present range of a species cannot be used directly to infer its climatic tolerances. Species with a southern range may be limited from spreading northward by factors other than a high temperature requirement, or they may have such a requirement. Those for which a temperature requirement has been postulated from observation or experiment may be called true thermophiles. The evidence for the species present at Earith comes only from observation, but it seems that *Naias flexilis*, *Lycopus europaeus* and *Groenlandia densa* may be true thermophiles, with a requirement equivalent to a mean July temperature of 16 °C. Iversen (1954) finds *Scirpus lacustris* to be a true thermophile in the sense used here, and to require a July temperature of 13 °C for fruiting. *Naias flexilis* and *Lycopus europaeus* occur in E 7; *Groenlandia densa* occurs in E 4, M 4 and E 7, and *Scirpus lacustris* occurs in E 1, E 5 and E 9.

The remarks all refer to the summer temperature, and it would seem that where such thermophiles occurred, here especially in E 7, the July temperature must have approached 16 °C, perhaps a little less if under conditions of less competition the plant species were more variable and more tolerant than today.

The winters were probably cold, and perhaps very cold if the presence of permafrost is accepted. There is little evidence of snow cover; *Salix herbacea* is regarded as chionophilous today but was very widespread in glacial times and occurs in almost every glacial site.

Armeria maritima occurs widely at Earith and in other Full- and Late-glacial sites and yet today it is found only in the oceanic north-west part of Europe, where the mean January temperature exceeds −8 °C. Because of this behaviour, Iversen (1954) believed that the late Pleniglacial and Late-glacial *sensu stricto* never had very cold winters. This is inconsistent with the bulk of the evidence supporting a continental climate for the Full-glacial, and the behaviour of *Armeria maritima* is as yet unexplained.

The climate is thus seen to have been continental as regards temperature and precipitation, although during the spring thaw there would have been saturated soil and humid air.

(iv) *Differences between the plant beds*

The major difference between E 7 and the other beds is the smaller amount of materia recovered and the smaller assemblages of plant species from the other beds. However, E 9 requires comment. This bed provided plentiful material although it was of a leafy nature and yielded fewer seed identifications. The E 9 assemblage differs from E 7 in that it contains only three southern species (only one, *Scirpus lacustris*, a true thermophile and requiring a 13 °C July temperature), many grasses (both caryopses and pollen) and many shoots of *Saxifraga oppositifolia*. This difference could be due to chance, a difference in the sedimentary characteristics of this deposit, or to a real difference in the flora. The pollen spectrum is most extraordinary (table 2) and this is not due to differential identification of easily recognized grains: the state of preservation was as in other beds. The large quantity of *Armeria maritima* pollen may be a chance occurrence of local origin of the plant, but this is unlikely as there was little macroscopic material of *Armeria*.

M 4 was a small site, but the environment represented is more extremely calcareous than the others. It yielded *Potamogeton filiformis* as the only *Potamogeton* species, and it was the only bed with *Myriophyllum spicatum*—both species that require base-rich waters.

(*c*) *The flora*

The flora is chiefly British, although with a minimum of six northern non-British species and one central European one (*Corispermum* sp.). The proportion of these exotics will tend to be underestimated, due to lack of knowledge and lack of reference material of non-British species compared with British, but the true proportion is unlikely to be significantly greater than that known at present.

The flora is closely related both to our present-day lowland chalk and limestone grassland flora, and to the basiphilous floras of the mountains of the north and west of Britain. This resemblance is due to the present floras of these localities containing the 'refuge' species, shade- and blanket-peat intolerant, which were widespread members of the glacial floras. The fossil flora is also related to our present weed flora, for similar reasons (Godwin 1959*a*).

During the Weichselian, it seems likely that there was a movement of species to the newly deforested lowlands from the mountains and from open habitats in Britain and perhaps from farther away, but there is no evidence that a great influx of species from outside Britain occurred. The exotics which do occur may well have been members of the British flora in the preceding Ipswichian interglacial period; such species as *Salix polaris* in the mountains and *Corispermum* on locally open ground of coastal or fluviatile situations.

7. Discussion

(*a*) *Interstadials and climates of the Weichselian*

There has recently been much discussion about the occurrence of an interstadial in the middle of the last glaciation, both in Britain and in the Netherlands. The demonstration that two main British tills of this glaciation, the Irish Sea and Holderness tills, fall within the later part of the glaciation, between 28000 and 15000 years ago (Shotton 1967; Penny, Coope & Catt 1969), adds credibility to the view that there existed in the Mid-Weichselian a period of more favourable climate.

The term interstadial has been used for periods of undoubted climatic amelioration sufficient at least for the growth of coniferous forest as in the Chelford Interstadial (Simpson & West 1958). More recently, the term 'Upton Warren Interstadial Complex' has been proposed for a period in the middle Weichselian, with no evidence of glaciation in the Midlands, from roughly 42000 to 28000 years B.P. At several times during this period the beetle faunas suggest a summer thermal environment similar to that in Britain today (Coope & Sands 1966).

Figures for the mean July temperature at sites falling within the Upton Warren Interstadial Complex have been obtained from plant species (§6 (*b*), iii) and from beetles. The temperatures relating to fossil beetle assemblages have been obtained by comparing them with modern assemblages from the floral zones of the Scandinavian mountains (Coope 1962). These zones are three alpine zones, the *Betula*, the *Pinus* and various deciduous forest zones. Some fossil beetle assemblages from the Interstadial Complex compare better with the modern assemblages below the tree line than with those of the alpine zones.

This might suggest that the plants of these forest zones are to be expected in the fossil sites. However, the plant zone names have been used merely because they provide a convenient classification of a complex environment, and in particular of the summer climate including such parameters as temperature sum, length of summer, and mean temperature of the warmest month. The dominant plants of the zones, the trees *Betula*, *Pinus* and *Picea* and the mixed oak forest, are dependent to a considerable extent on the winter temperature and its secondary effects. The action of winter cold on trees, which are enforced perennials, and especially cryoturbation and solifluction of the ground, is not paralleled to the same extent in its action on the beetles, which hibernate in winter. There are regions today where trees grow in unstable soil over permafrost, but at Earith the indications of desiccation and salt accumulation in the soil suggest that strong winds were present. The combined effects of low winter temperatures, soil instability and winds which would dry out both shoots and reproductive structures were probably sufficient to prevent the growth of any available tree species.

There is thus evidence both from flora and beetle fauna that there were episodes of climatic amelioration with summer temperatures as high as or higher than those associated with coniferous forest in Europe today. Nevertheless, trees were absent. The Earith beds, E 7 in particular, fall into this category. Such periods when the summer temperature rose to this high level may be regarded as interstadials. Their herbaceous vegetation should be regarded as a variety of steppe rather than as a tundra.

An interstadial defined in terms of summer temperatures presupposes the existence of stadia with lower summer temperatures. Evidence of cool summers is difficult to find from the plant species present in any Full-glacial flora, although the absence of thermophiles provides negative evidence for low temperatures. The overall poverty of a flora may also be evidence of an unfavourable climate (§7 (*b*)).

At Earith the presence of ice wedge casts at horizons younger than the interstadial plant bed dated to 42000 years suggests that the climate underwent a deterioration. It is unlikely that a mean annual temperature of −8 °C (§2 (*c*)) was achieved with a summer temperature of +16 °C, so that a lowering of this summer temperature seems to have occurred. No organic beds at Earith have been found which can be shown to be contemporaneous with a horizon containing ice wedge casts. The same lack of contemporaneity holds for other Weichselian sites and for earlier glacials; for example, in the Beestonian. Here, at West Runton in Norfolk (West 1968) an ice wedge cast closely but unconformably precedes an arctic plant bed. At the position of E 2 at Earith a plant bed is very shortly followed by a sterile bed and then by an ice wedge cast. This latter horizon may represent a stadial period. Bearing in mind that the arctic tundra today underlain by active ice wedges does support a substantial flora, there is no reason why the landscape should have been a polar desert at a time of ice wedge formation, as suggested for the Upper Weichselian of the Netherlands (van der Hammen, Maarleveld, Vogel & Zagwijn 1967).

It seems most likely that vegetation was sparse at these times and preserved in such small quantities that it has so far escaped detection.

(*b*) *Comparison with other British Full-glacial floras*

The flora and vegetation of Earith E 7 show the greatest affinity with the Upton Warren and Sidgwick Avenue sites. Other Earith beds more or less resemble E 7, generally depending on the size of their floras. These three sites have apparently truly thermophilous plants, a suggestion of steppe conditions, halophytes and several markedly northern or montane species. The proximity of the radiocarbon dates of Earith E 7 and Upton Warren confirm that interstadial conditions prevailed in Southern Britain around 42000 years B.P., although such a radiocarbon date is really a span of several thousand years.

Of the Full-glacial floras with younger radiocarbon dates, Barnwell Station and the Lea Valley are very similar to each other and to Earith. They show no easily recognized climatic differences, although Chandler (1921) originally suggested that the Barnwell Station flora was ‘colder’ than that of the Lea Valley beds. This was on the evidence that it contained 42% of arctic–alpine species compared with 22% in the Lea Valley. However, these figures can no longer be accepted in the light of corrections to the identifications from each of these sites, and in view of differing interpretations of the term arctic–alpine.

There are a number of smaller Full-glacial floras, including Brandon Terrace (Kelly 1968), Great Billing (Bell 1968) and Syston (Bell 1968). The majority of their component species are found at Earith and at the other sites mentioned above; they all contain northern and widespread species, and they all lack obligate halophytes although containing facultative ones (Bell 1969). However, they all lack true thermophiles, and the number of southern species is small: one species each in Brandon and Great Billing and none in Syston. The lack of thermophiles and of halophytes may be related to the total size of the floras: Brandon contained 28, Great Billing 44 and Syston 30 vascular plant taxa. In comparison, Earith E 7 contained 76. If the small size of a flora is due to an unfavourable environment for the accumulation and deposition of plant detritus, no climatic conslusions may be drawn. On the other hand, if the small size reflects an actual sparsity of species then deductions as to the climate may be made. In this case the deduction would be that the climate was cooler and also that there was less salinity than at Earith.

The flora from Dimlington, with its date of 18000 years (Penny *et al.* 1969), apparently lived during the period when the ice advance was nearing its maximum extent. This period might be expected to be climatically severe, and the flora to show a change from the Earith type. The flora itself is small, and contains exclusively aquatic and marsh species with the possible exception of a grass. It lacks thermophiles and obligate halophytes, and it also lacks any particularly northern species (Bell, unpublished). This site is unusual in not being situated in a large river valley, and it is possible that its fossil flora is that of a very restricted area, i.e. of the ponds where deposition occurred and their immediate surroundings, compared with the wide area from which fossils are thought to be collected before deposition in river terrace sediments.

This work was carried out in the Subdepartment of Quaternary Research in the Botany School, Cambridge, with the aid of studentships from N.E.R.C. and from Girton College. I am very grateful to Dr R. G. West, F.R.S., who supervised the work throughout and who has constantly helped me with the preparation of this paper. Discussions with Dr G. R. Coope concerning the site have been most valuable.

I was greatly helped in the early stages of my research by Mrs C. A. Dickson, who both handed on to me her preliminary results from Earith and also initiated me into the identification of plant macrofossils; and by Dr R. B. G. Williams who helped me with the fieldwork.

The assistance of Miss R. Andrew in matters of pollen identification was much appreciated, as was the help by the following people in macrofossil identification: Mrs Körber-Grohne (Gramineae), Dr J. Lid (*Salix*), Dr D. J. Ockendon (*Linum*), Dr A. J. Richards (*Taraxacum*), and Dr S. M. Walters (*Eleocharis*).

REFERENCES

Allison, J., Godwin, H. & Warren, S. H. 1952 Late-glacial deposits at Nazeing in the Lea Valley, North London. *Phil. Trans. Roy. Soc. Lond.* B **236**, 169.

Backman, A. L. 1948 *Naias flexilis* in Europa während der Quartärzeit. *Acta bot. fenn.* **43**, 3.

Bell, F. G. 1966 Plant remains from Earith, Huntingdonshire. *Ann. Rep. Hunts. fauna and flora Soc.* for 1965.

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

Bell, F. G. 1969 The occurrence of southern, steppe and halophyte elements in Weichselian (Last-glacial) floras from southern Britain. *New Phytol.* **68**, 3, 913.

Beug, H. J. 1957 Untersuchen zur spätglazialen und früh-postglacialen Floren und Vegetations-geschichte einige Mittelgebirge. *Flora, Jena* **145**, 167.

Böcher, T., Holmen, K. & Jakobsen, K. 1968 *The flora of Greenland.* Copenhagen: Haase and Son.

Cajander, A. K. 1903 Beiträge zur Kenntnis der Vegetation der Alluvionen des nördlichen Eurasiens. *Acta Soc. Sci. fenn.* **32**, 1, 1.

Chandler, M. E. J. 1921 The Arctic flora of the Cam Valley at Barnwell, Cambridge. *Q. Jl. geol. Soc. Lond.* **77**, 4.

Clapham, A. R., Tutin, T. G. & Warburg, E. F. 1962 *Flora of the British Isles*, 2nd ed. Cambridge University Press.

Coope, G. R. 1962 A Pleistocene coleopterous fauna with arctic affinities from Fladbury, Worcestershire. *Q. Jl geol. Soc. Lond.* **143**, 103.

Coope, G. R., Shotton, F. W. & Strachan, I. 1961 A Late Pleistocene fauna and flora from Upton Warren, Worcs. *Phil. Trans. Roy. Soc. Lond.* B **244**, 379.

Coope, G. R. & Sands, C. H. S. 1966 Insect faunas from the Last Glaciation from the Tame Valley, Warwicks. *Proc. Roy. Soc. Lond.* B **165**, 389.

Dickson, C. A. 1970 In D. Walker and R. G. West (eds.), *Studies in the vegetation history of the British Isles.* Cambridge University Press.

Faegri, K. & Iversen, J. 1964 *Textbook of pollen analysis*, 2nd ed. Oxford: Blackwell.

Florschütz, F. 1958 Steppen und Salzsumpfelementen aus den Floren der lezten und vorletzten Eizeit in den Niederland. *Flora, Jena* **146**, 489.

Fowler, G. 1933 Fenland waterways past and present. *Proc. Cambs. Antiq. Soc.* **33**, 108.

Godwin, H. 1956 *The history of the British flora.* Cambridge University Press.

Godwin, H. 1959*a* The history of weeds in Britain. In *The biology of weeds* (ed. J. L. Harper), 1*st Symp. Br. Ecol. Soc.* Oxford: Blackwell Scientific Publications.

Godwin, H. 1959*b* Plant remains from Hartford, Hunts. *New Phytol.* **58**, 85.

Godwin, H. 1964 Late-Weichselian conditions in southeastern Britain. *Proc. Roy. Soc. Lond.* B **160**, 268.

Godwin, H., & Willis E. H. 1964 Cambridge University natural radiocarbon measurements. VI. *Radiocarbon* **6**, 116.

van der Hammen, T., Maarleveld, G. C., Vogel, J. C. & Zagwijn, W. H. 1967 Stratigraphy, climatic succession and radiocarbon dating of the last glacial in the Netherlands. *Geologie Mijnb.* **46**, 79.

Iversen, J. 1954 The Late-glacial flora of Denmark and its relation to climate and soil. *Danm. geol. Unders* IIR, **80**, 87.

Jessen, K. & Farrington, A. 1938 The bogs at Ballybetagh, near Dublin, with remarks on the Late-glacial conditions in Ireland. *Proc. R. Ir. Acad.* B **4**, 10.

Kelly, M. R. 1968 Floras of Middle and Upper Pleistocene age from Brandon, Warwicks. *Phil. Trans. Roy. Soc. Lond.* B **254**, 401.

Körber-Grohne, U. 1964 *Probleme der Küstenforschung im südlichen Nordseegebiet*, Band 7. Hildersheim: August Lax.

Lambert, C. A., Pearson, R. G. & Sparks, B. W. 1963 A flora and fauna from Late Pleistocene deposits at Sidgwick Avenue, Cambridge. *Proc. Linn. Soc. Lond.* **174**, 1, 13.

Mitchell, G. P. 1953 The Late-glacial flora of Ireland. *Danm. geol. Unders.* IIR, **80**, 72.

Ockendon, D. J. 1967 *Experimental taxonomy of the* Linum perenne *group.* Ph.D. thesis, University of Cambridge.

Ockendon, D. J. 1968 Biosystematic studies in the *Linum perenne* group. *New Phytol.* **67**, 787.

Penny, L. F., Coope, G. R. & Catt, J. A. 1969 Age and insect fauna of the Dimlington Silts, East Yorkshire. *Nature, Lond.* **224**, 65.

Péwé, T. L. 1966 Palaeoclimatic significance of fossil ice wedges. *Biul. peryglac.* **15**, 65.

Proctor, M. C. F. 1956 Biological flora of the British Isles: *Helianthemum. J. Ecol.* **44**, 675.

Reid, E. M. 1949 The Late-glacial flora of the Lea Valley. *New Phytol.* **48**, 245.

Ritchie, J. C. & Lichti-Federovich, S. 1967 Pollen dispersal phenomena in arctic-subarctic Canada. *Rev. Palybotan. Palynol.* **3**, 255.

Rorison, I. H. 1960 Some experimental aspects of the calcicole—calcifuge problem. *J. Ecol.* **48**, 585.

Rousi, A. 1965 Biosystematic studies of the species aggregate *Potentilla anserina. Ann. Bot. Fenn.* **2**, 1.

Sharp, R. P. 1942 Periglacial involutions in northeastern Illinois. *J. Geol.* **50**, 113.

Shotton, F. W. 1967 Age of the Irish Sea glaciation of the Midlands. *Nature, Lond.* **215**, 1366.

Simpson, I. M. & West, R. G. 1958 On the stratigraphy and palaeobotany of a late-Pleistocene organic deposit at Chelford, Cheshire. *New Phytol.* **57**, 239.

Sterner, R. 1922 *The continental element in the flora of South Sweden.* Thesis, University of Uppsala.

Styles, B. T. 1962 The taxonomy of *Polygonum aviculare* and its allies in Britain. *Watsonia* **5** (4), 177.

Terasmae, J. 1968 Some problems of the Quaternary palynology in the Western Mainland region of the Canadian Arctic. *Geol. Survey of Canada*, Paper 68, 23.

Tralau, H. 1963 The recent and fossil distribution of some boreal and arctic-montane plants in Europe. *Arkiv för Botanik* (2), **5** (3), 533.

Vogel, J. C. & Zagwijn, W. H. 1967 Groningen radiocarbon dates. VI. *Radiocarbon* **9**, 63.

Walker, D. 1953 The interglacial deposits at Histon Road, Cambridge. *Q. Jl geol. Soc. Lond.* **108** (3), 273.

Walters, S. M. 1949 Biological Flora of the British Isles: *Eleocharis. J. Ecol.* **37**, 192.

Wayne, W. J. 1967 Periglacial climate in east-central United States. *VII INQUA Congress*, Abstracts.

West, R. G. 1968*a* *Pleistocene geology and biology.* London: Longmans, Green and Co.

West, R. G. 1968*b* Evidence for pre-Cromerian permafrost in East Anglia. *Biul. peryglac.* **17**, 303.

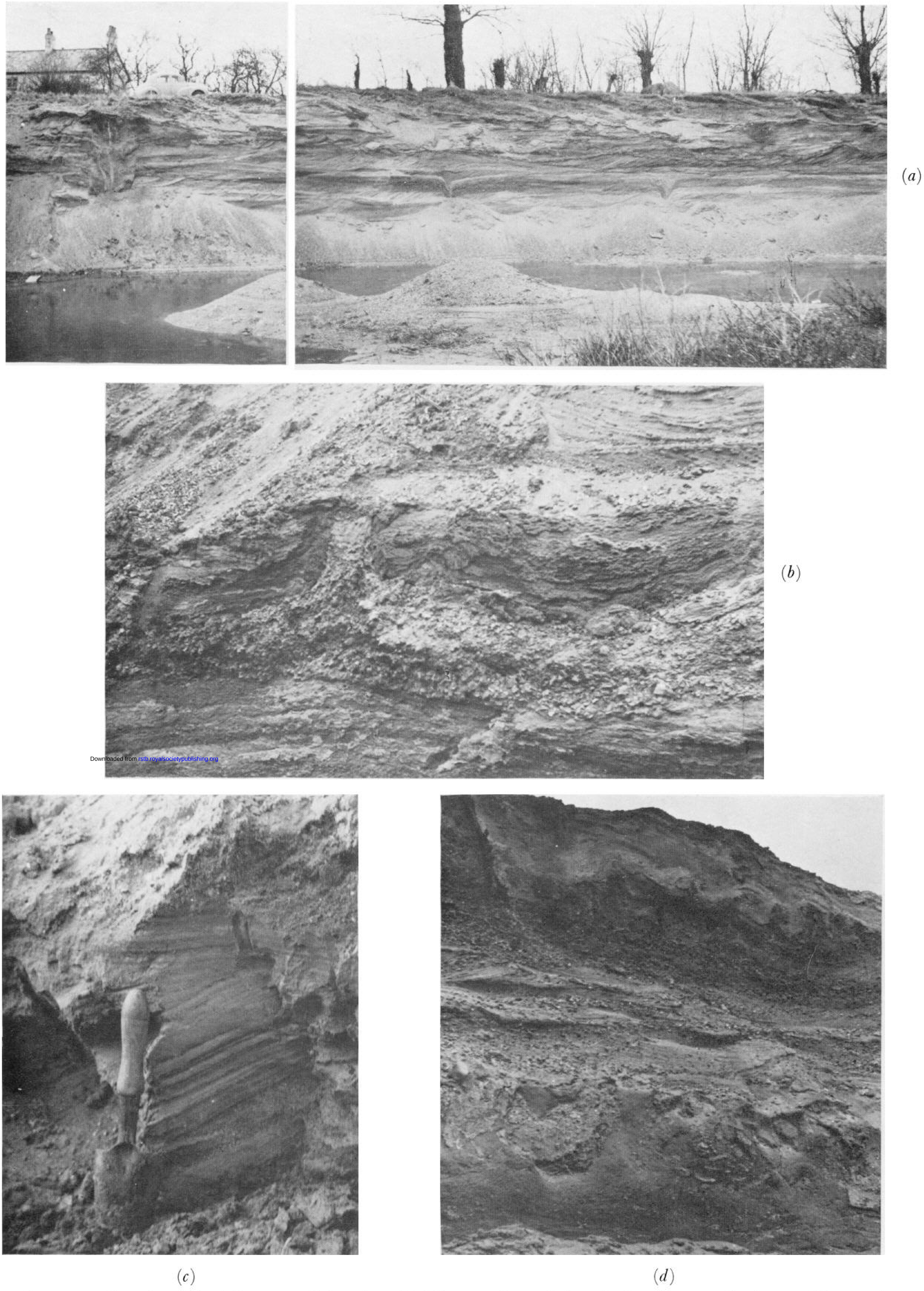
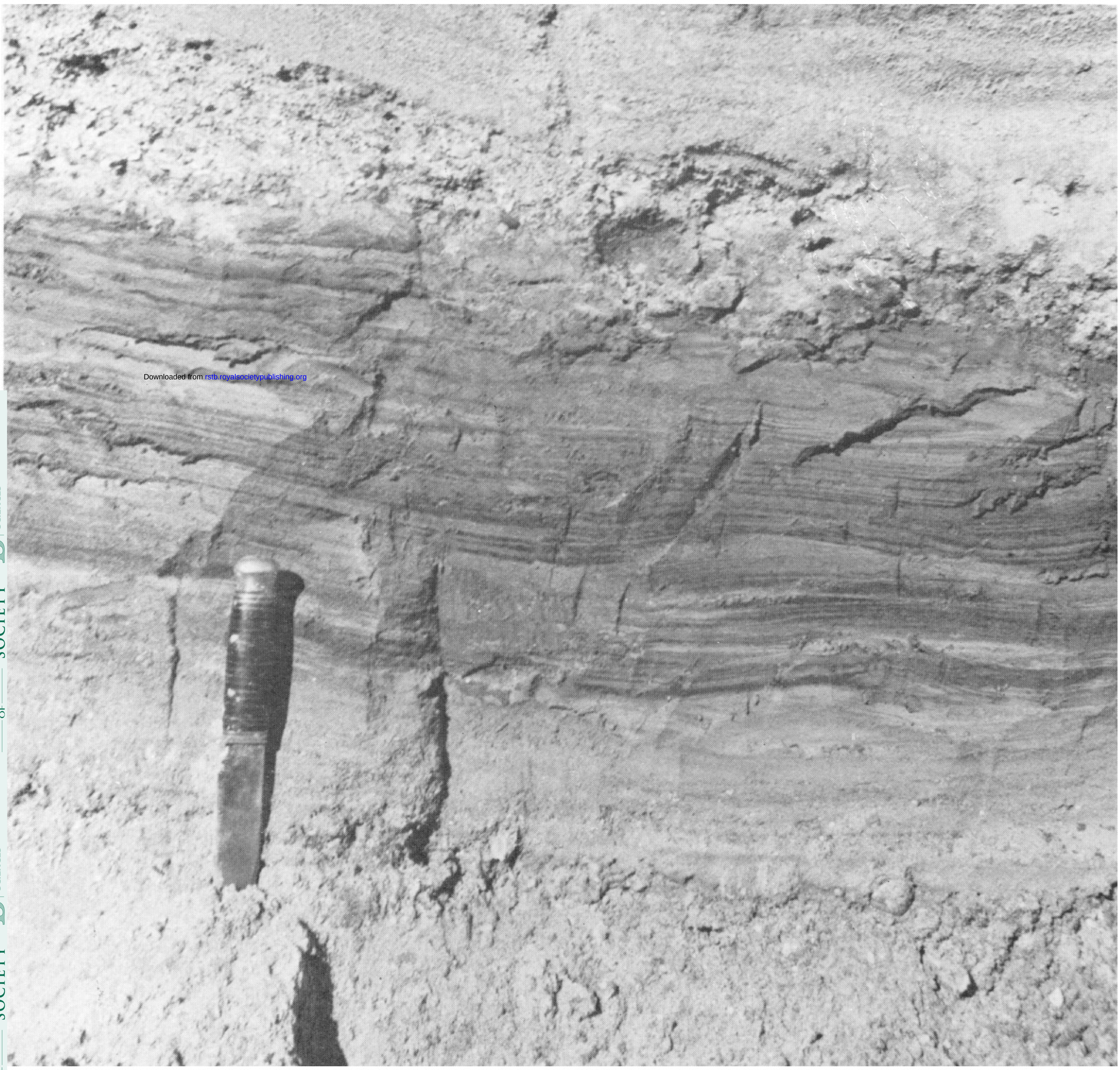


FIGURE 5. Stratigraphical features of the site. (*a*) The east face of the pit showing two horizons of ice wedge casts. (*b*) Injection of gravel through the plant bed E 5. (*c*) The plant bed E 4. (*d*) Flame type of involutions.

(*a*)



(*b*)

FIGURE 6. The plant bed E 2 and its context. (*a*) The bed in relation to an ice wedge cast and to a silt bed above it. (*b*) Detail of E 2.