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Studies of the Post-Glacial History of British Vegetation. XIV. Late-Glacial Deposits at Moss Lake, Liverpool

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STUDIES OF THE POST-GLACIAL HISTORY OF BRITISH VEGETATION

XIV. LATE-GLACIAL DEPOSITS AT MOSS LAKE, LIVERPOOL

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[Plates 3 and 4]

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Investigations of deposits at a built-over site near the centre of Liverpool disclose a basal stratigraphic sequence characteristic of the west-European Late-glacial period. Detailed pollen analyses confirm that the deposits extended from the Late-glacial (Zone I) to the Post-glacial thermal maximum (Zone VII *a*). The lake was overgrown in Zone VI by floating *Sphagna*, and in Zone VII a typical raised bog developed. Macroscopic remains of lake and fen plants were recovered in great abundance and together with frequent non-tree pollen these permitted a detailed reconstruction of the vegetational history of both the lake and the surrounding upland. Several species of notably disjunct or restricted present-day range have been recorded here, *Cotoneaster* cf. *integerrima* Medic., *Elatine hexandra* (Lapierre) D.C., *Lycopodium annotinum* L., *Pilularia globulifera* L., and *Linum anglicum* Mill., whilst tentative identification of species such as *Agropyron junceiforme*, A. & D. Löve, *Gentiana campestris* (L.), *Lotus uliginosus* Schkuhr, and *Vicia sepium* L. cast new light on the natural status of other British plants. Numerous further records confirm and extend our knowledge of the history of the British flora, especially in the Late-glacial and early Post-glacial periods.

1. Introduction

N. A. Cummins (1956) has recently described the geological features exposed in a series of temporary pits dug between Chatham Street and Peach Street, Liverpool. The site lies at the northern end of an area formerly known as Moss Lake, occupied by a peat bog exploited for fuel during the seventeenth century, subsequently drained, consolidated by the dumping of rubble, and finally built over in the nineteenth century.

Our attention was drawn to these deposits by Professor A. N. Burges. The stratigraphic sequence that he reported, and preliminary inspection of the pollen content of the peat samples he provided, both suggested the possibility that the bottom layers were of Late-glacial age. One of the trial pits adjacent to Walnut Street (Pit No. 8 in Cummins's fig. 1) was kindly left open, and it was from this that the records and samples now reported were obtained.

The section was recorded as follows:

cm	
0–150	Made ground, rubble.
150–170	Strongly mouldered surface, black peat. Clay pipe stem.
170–175	Very oxidized peat.
175–190	Very compressed peat, dark chocolate brown, highly humified. Probably *Sphagnum–Calluna* peat, cf. *Eriophorum*.
190–195	Very compressed highly humified, less oxidized. Probably aquatic *Sphagnum* pool peat.
195–199	Yellow brown, strongly laminated, aquatic *Sphagnum* peat with occasional dicot. leaves. *Sphagnum* capsule.
199–206	Similar, but becoming a coarse detritus mud and at 202 cm leaves of tree birch, occasional small pebbles, small twigs.
206–218	Small leaves (cf. *Salix*) at 210 cm; at 215 cm *Potamogeton* fruit.
218–227	As above but with appreciable content of silt; 220 cm ostracod.
227–245	Rather irregular surface at top: rather coarse sand with irregular organic material, abundant remains of large *Equisetum in situ* and not ascending into upper level. Sand includes occasional grains up to 1 or 2 mm. *Equisetum* stops at 239 cm.
245–255	Coarse yellow sand with small organic mud content and very little *Equisetum*.
255–262	Fine detritus to coarse detritus brown organic mud with horizontal laminations, high sand content. Occasional *Equisetum*.
262–269	Same material but dark grey (reduced). Occasional pebbles and some animal chitin.
269 down	Greenish-buff solifluxion material with coarse sand and abundant large pebbles.

It is clear from Cummins's report that the underlying Triassic sandstones are here overlaid by several feet of boulder clay, itself covered by a variable thickness of grey sand. The contact between the boulder clay and the sand shows cryoturbation and this agrees with our own determination of the layer below 269 cm at Pit 8 as solifluxion material.

The striking interposition of a dark-coloured organic mud layer (albeit sandy) at 255 to 269 cm, between the lower solifluxion layer and an upper layer of coarse sand (227 to 255 cm), is a feature represented in all the sections described on this site. This consistent alternation and the dimensions of the deposits again suggest the likelihood that this is a Late-glacial sequence. The solifluxion layer corresponding to Zone I of our pollen-analysis zonation (Older Dryas), the organic muds to Zone II (Allerød warm interstadial), and the upper sand layer to Zone III (Younger Dryas). Further evidence in support of this view is now adduced from pollen analyses and identifications of macroscopic plant remains.

Samples for pollen analysis were taken directly from the cleaned face of the section at intervals of 2 (or sometimes 3) cm, extending from the basal solifluxion material into the base of the oxidized *Sphagnum–Calluna* peat. These pollen analyses, carried out by Miss R. Andrew are the basis for the two pollen diagrams (figures 1 and 2).

Two monoliths of 9 in. (25 cm) cross-section were secured for transport to Cambridge from a position close beside the line of pollen samples. One extended from levels corresponding to 215 to 245 cm in the pollen series, and the other covered the levels between 257 and 275 cm: an intervening incoherent coarse sandy section (245 to 257 cm) was not taken. Subsequently, in Cambridge, Miss Andrew made short pollen analyses from marked horizons in the monoliths so that we were able to identify in them the zone boundaries already determined in the close pollen sequence. When this had been done both monoliths were divided into horizontal slices 2 cm thick. Sufficient material for radiocarbon dating

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was taken from each slice: it was dried and stored in sealed Cellophane bags. The residue from the slices was separately examined for macroscopic plant material by Miss C. A. Lambert. Unfortunately, it subsequently became clear that the material was inherently unsuitable for radio-carbon assay and the attempt to date by this means was abandoned.

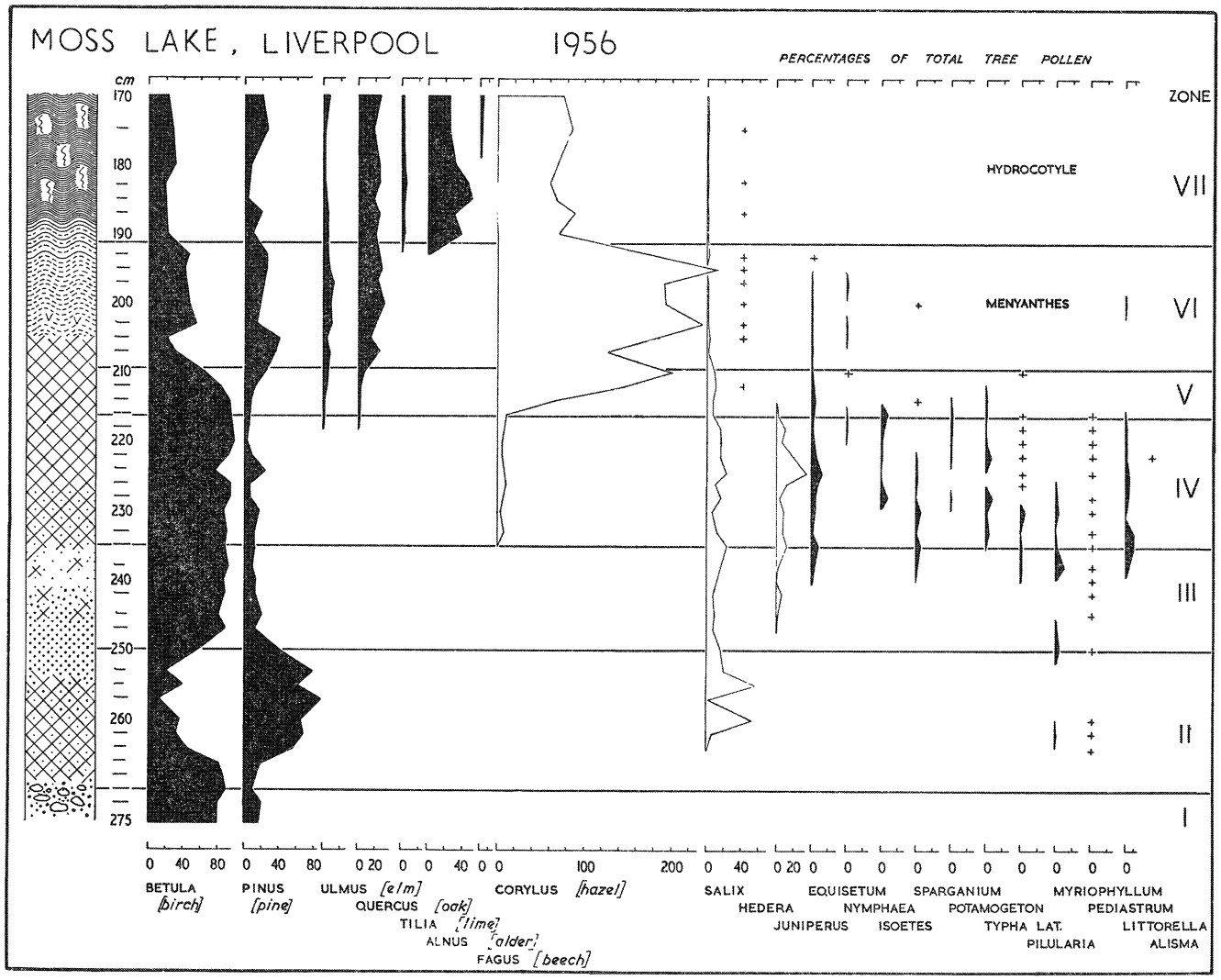

FIGURE 1. Pollen diagram of trees, shrubs and aquatic plants all expressed as percentages of total tree pollen.

2. ANALYSES AND IDENTIFICATIONS

Pollen analyses

The pollen analyses are presented in the form of two diagrams, the first of which (figure 1) includes pollen of trees, shrubs and aquatic plants with spores of the aquatic Pteridophyte genera, *Equisetum*, *Isoetes* and *Pilularia*: it has been convenient to express these results as percentages of the total tree pollen. In the second all frequencies are expressed as percentages of the total pollen of trees, shrubs and other land plants: this conveys a closer picture of the relative abundance of the vegetational components, which is of especial value for the Late-glacial and early Post-glacial periods in which herbaceous vegetation was characteristically abundant.

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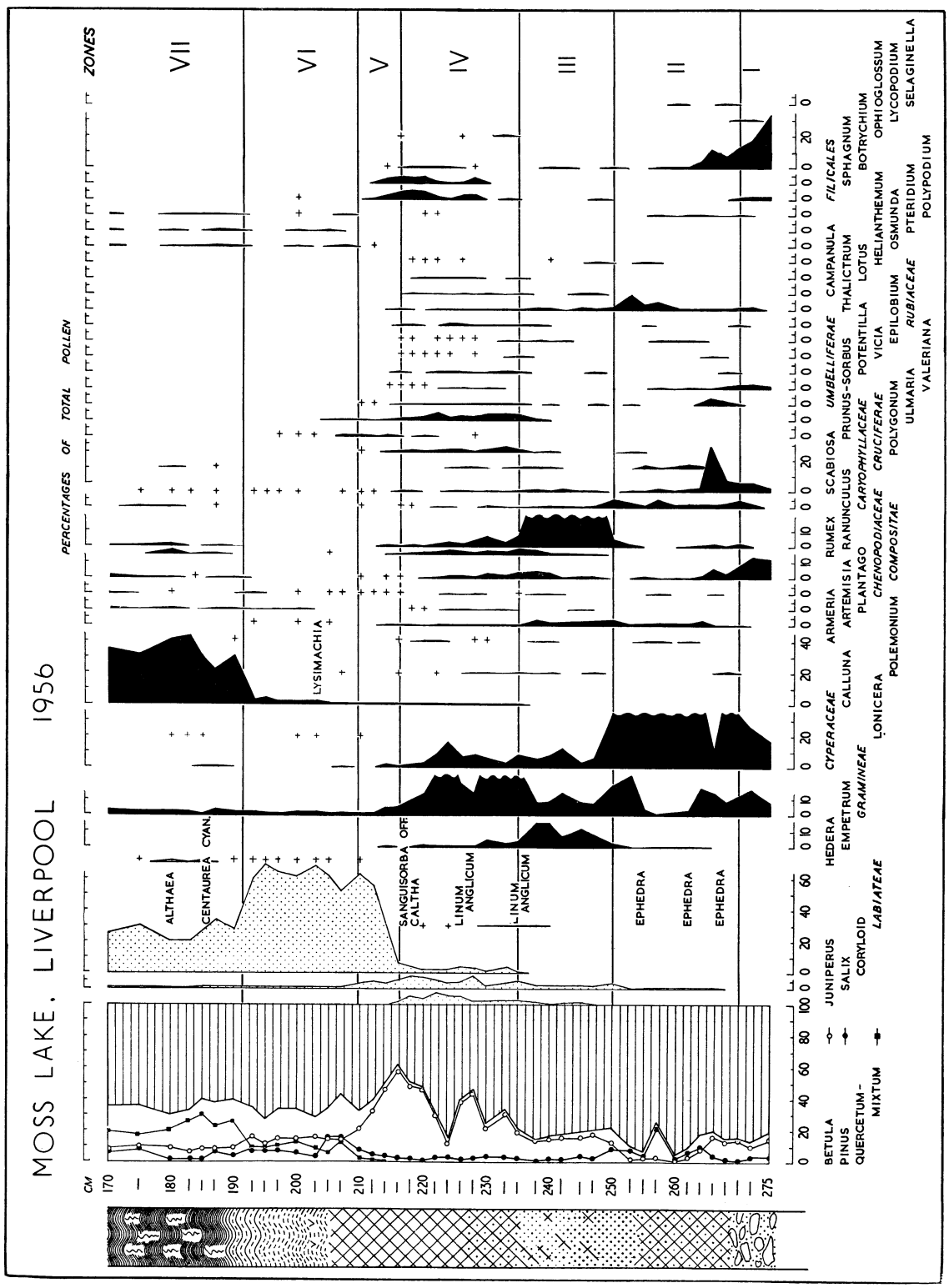

FIGURE 2. *Left*: diagram showing relative proportions of tree pollen (unshaded) and of other dry-land plants (shaded). *Right*: diagram showing changing frequencies of shrub pollen (dotted) and of dry-land herbaceous plants (solid), expressed as percentages of the total pollen of dry-land plants.

The criteria for determining the position of the respective zone boundaries may very shortly be given as follows:

VI/VII The sudden rise of *Alnus*, supported by the beginning of continuous *Tilia* curve.

V/VI The recession of *Betula*, with the corresponding increase of *Pinus*, *Ulmus* and *Quercus* and the initiation of very high values for *Corylus*.

IV/V The beginning of the increase of the *Corylus* to the high values sustained in Zone VI, and a general recession of pollen of herbaceous plants and shrubs.

III/IV The increase in the ratio of tree pollen to non-tree pollen corresponding with the onset of organic mud formation and decreased deposition of mineral sediment.

II/III The return of *Betula* to dominance over *Pinus* in the tree pollen, the substantial increases of *Empetrum* and *Juniperus*, closely associated with the deposition of coarse sand (which however commenced here in the later part of Zone II).

I/II The transition from a mineral solifluxion material to an organic mud, associated with the first appearances of many herbaceous types characteristic of the Late-glacial period.

We shall deal with the characterization of the zones themselves in §3, where pollen and macro-remains can be considered together.

Macroscopic remains

Table 1 gives the list of identifications from the bulk samples taken from the lower part of Zone VI downwards.

It should be noted that in making these analyses it was easy to recognize the strongly laminated leafy layers in the organic mud already noted in the field record. These clearly lay in the lowermost part of Zone VI and contained abundant leaves of tree birch and the royal fern (*Osmunda regalis*): between them were less frequent occasional leaves of *Cotoneaster* sp. and of *Salix*, cf. *aurita*.

Furthermore, in the preparation of the pollen samples the following macroscopic remains were recovered:

Betula sp., fruits from Zones IV, V, VI.
Elatine hexandra, seeds from Zones IV, V, VI.
Eleocharis palustris, fruits from Zones III, IV.
Empetrum nigrum, fruit stone from Zone III.
Isoetes echinospora, megaspores from Zones IV, V.
Juncus sp., seeds from Zones IV, V, VI, VII*a*.

Comments upon the identifications will be found in the next two sections.

3. Vegetational history

It will be necessary to distinguish, throughout this account, between the history of the vegetation actually growing upon the site of the former lake, and that of the mineral soil of the surrounding region. The macroscopic remains represent almost entirely plants in the former category, but the microscopic pollen and spores may clearly be derived either from plants growing directly on the spot, or may come from a general pollen rain representing the whole countryside. It is not, however, particularly difficult to refer most of the microfossils to one or other categories of origin.

The Late-glacial period as a whole is characterized here, as elsewhere in north-western Europe, by the general preponderance of herbaceous plants and shrubs over trees, by the presence of birch and pine as the only trees consistently represented, and with birch the

more abundant, by substantial amounts of *Juniperus*, *Empetrum* and *Salix*, and by the presence in varying (and often considerable) amounts of typical genera such as *Armeria*, *Artemisia*, *Campanula*, *Ephedra*, *Helianthemum*, *Plantago*, *Polygonum*, *Polemonium*, *Succisa*, *Thalictrum*, *Ulmaria*, *Valeriana*, *Botrychium*, *Lycopodium*, *Ophioglossum*.

Table 1. Macroscopic remains, Moss Lake

det. C. A. Lambert

Abbreviations: *c. sc.*, cone scale; *fr.*, fruit; *fst.*, fruit stone; *l.*, leaf; *Msp.*, megaspores; *p.*, perianth; *s.*, seed; *sh.*, shoot; *a.*, achene; *n.*, nut or nutlet; *o.*, oospore; *u.*, utricle.

Frequency: *r.*, rare 1–3; *o.*, occasional 4–6; *f.*, frequent 7–10; *a.*, abundant.

Zones ...		I	II	early III	mid to late III	III/IV	early IV	mid IV	late IV	V	late V and early VI
Betula pubescens Ehrh.	*fr.*	.	.	.	.	.	.	.	*o.*	*o.*	*a.*
B. verrucosa Ehrh.	*fr.*	.	.	.	.	.	.	.	*r.*	.	*f.*
Betula spp.	*fr.*, *c. sc.*	.	.	.	*r.*	.	*r.*	*o.*	*o.*	*f.*	*a.*
Betula spp.	*l.*	.	.	.	.	.	.	.	.	.	*a.*
Calluna vulgaris Hull	*s.*, *sh.*	.	.	.	.	.	.	.	.	.	*f.*
Carex rostrata Stokes	*n.*, *u.*	.	.	.	.	.	.	*f.*	.	.	*o.*
Carex spp.	*n.*	.	.	*r.*	*r.*	*r.*	.	.	*f.*	*o.*	.
Cladium mariscus (L.) Pohl	*n.*	.	.	.	.	.	.	.	.	.	*r.*
Corylus avellana L.	*n.*	.	.	.	.	.	.	.	.	.	*r.*
Cotoneaster sp.	*l.*	.	.	.	.	.	.	.	.	.	*o.*
Elatine hexandra D.C.	*s.*	.	.	.	.	*f.*	*o.*	*f.*	*a.*	*r.*	.
Eleocharis palustris (L) R.Br.	*n.*	.	.	*a.*	*o.*	*f.*	*a.*	*r.*	*r.*	.	.
Empetrum nigrum L.	*fst.*	.	.	*a.*	*o.*	.	*o.*	*o.*	*o.*	.	.
Equisetum sp.	*stem*	*o.*	.	.	*r.*	.	*r.*	*r.*	.	*r.*	.
Eriophorum sp.	*n.*	.	.	.	.	.	.	.	*r.*	.	.
Isoetes echinospora Durieu	*Msp.*	.	.	.	.	.	*r.*	*r.*	*r.*	*o.*	.
Juncus effusus or *conglomeratus* L.	*s.*	.	.	.	.	.	*o.*	*o.*	*r.*	.	.
Juncus spp.	*s.*	.	.	.	.	*r.*	*r.*	*r.*	*o.*	*r.*	.
Lycopus europaeus L.	*n.*	.	.	*r.*	.	.	.	*r.*	*r.*	.	.
Menyanthes trifoliata L.	*s.*	.	.	.	.	.	.	.	.	.	*r.*
Myriophyllum alterniflorum D.C.	*n.*	.	.	.	*r.*	.	.	.	.	.	.
Najas marina L.	*fr.*	.	.	.	.	.	.	.	.	*r.*	.
Nymphaea alba L.	*s.*	.	.	.	.	.	.	*r.*	*f.*	*f.*	*a.*
Osmunda regalis L.	*l.*	.	.	.	.	.	.	.	.	.	*a.*
Pilularia globulifera L.	*Msp.*	.	.	.	.	*o.*	*r.*	*o.*	*r.*	.	.
Pinus sylvestris L.	*s.*	.	.	.	.	.	.	.	.	*r.*	*r.*
P. sylvestris L.	*l.*	.	.	.	.	.	.	.	.	.	*f.*
Polygonum nodosum Pers. or *lapathifolium* L.	*n.*	.	.	*r.*	.	.	*r.*	.	.	.	.
Polygonum sp.	*n.*	.	.	.	*r.*	*r.*	.	.	.	.	.
Potamogeton crispus L.	*fst.*	.	.	.	.	.	.	.	*r.*	.	.
P. filiformis Pers.	*fst.*	.	.	.	.	.	.	.	*r.*	.	.
P. natans L.	*fst.*	.	.	.	*r.*	.	*r.*	.	*a.*	*a.*	*a.*
P. pectinatus L.	*fst.*	.	.	*o.*	*r.*	.	.	.	.	.	.
P. perfoliatus L.	*fst.*	.	.	.	*r.*	.	.	.	.	.	.
P. pusillus L. sec. Dandy & Taylor	*fst.*	.	.	.	.	.	.	.	*r.*	.	.
Potentilla palustris Scop.	*a.*	.	.	.	.	.	.	.	.	.	*r*
Ranunculus acris or *repens* L.	*a.*	.	.	.	.	.	*r.*	.	*r.*	.	.
R. (*Batrachium* sp.)	*a.*	.	.	*a.*	*a.*	*a.*	*f.*	*o.*	*o.*	.	.
Rorippa islandica (Oeder) Borbas	*s.*	.	.	*o.*	*r.*	*r.*	*r.*	*o.*	.	.	.
Rumex maritimus L.	*n.*, *p.*	.	.	*r.*	.	.	.	*r.*	.	.	.
Rumex sp.	*n.*	.	.	.	*r.*	.	.	.	.	.	.
Ruppia spiralis Dum.	*fr.*	.	.	.	.	.	.	.	.	.	*r.*
Salix cf. *aurita* L.	*l.*	.	.	.	.	.	.	.	.	.	*r.*
Schoenoplectus lacustris (L.) Palla	*n.*	.	.	*r.*	.	.	.	.	.	.	*a.*
Viola cf. *palustris* L.	*s.*	.	*o.*	.	.	.	.	.	.	.	.
Viola sp.	*s.*	.	.	.	.	.	*r.*	.	.	.	.
Characeae	*o.*	.	.	.	.	*o.*	.	.	*r.*	*o.*	.

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Zone I

Only the close of Zone I is represented in the Moss Lake samples. Solifluxion was bringing coarse mineral soil into the basin, trees were sparse and mostly birch, and the open character of the vegetation is shown by the presence of the dwarf pteridophytes, *Selaginella*, *Ophioglossum*, *Lycopodium*, and *Botrychium*, the latter in remarkably high frequency diminishing upwards into Zone II. Pollen referable to the *Taraxacum* type within the Compositae behaves much as the *Botrychium*, but we cannot more closely identify it; *Valeriana officinalis* and *Succisa pratensis* were frequent, but the commonest plants were clearly grasses and sedges, probably regionally as well as locally.

Zone II

The increasing warmth of Zone II is indicated by the formation of organic muds above the solifluxion material of Zone I. The water plants identified include *Myriophyllum verticillatum* or *M. spicatum* at the end of the zone, along with colonies of the algae *Pediastrum* and *Botryococcus*.

The zone opens with birch pollen preponderant over that of pine, but as in other west-European diagrams, the relative positions are reversed higher in the zone. There is no evidence here of the development of closed woodland in Zone II and the tree pollen/non-tree pollen ratio remains low. However, *Empetrum* was present in low frequencies and pine in high frequencies accompanied by substantial amounts of willow. Another shrub present infrequently appears to have been *Ephedra distachya*, along with *Helianthemum* sp. There was an increased representation of Late-glacial herbaceous plants in the genera *Polemonium*, *Armeria*, *Artemisia*, *Rumex*, *Potentilla*, and *Thalictrum*, and in several families.

If, as seems likely, we cannot attribute the decrease of *Botrychium* and *Taraxacum*-type Compositae to the development of birch woods, it seems likely that it was here due to the increased density and luxuriance of taller herbs, especially the grasses and sedges.

Zone III

Throughout Zone III birch pollen heavily outweighs that of pine, the tree pollen/non-tree pollen ratio remains low, but macroscopic remains prove birch to have been present locally. *Empetrum nigrum* pollen is abundant throughout the zone and since fruit stones are also present, the plant must have grown close at hand. *Salix* and *Juniperus* pollen occurs in smaller frequency. Sand now washed freely into the lake and it seems probable that the soil was kept disturbed or open by frost action. Macroscopic remains show that the lake shallows and margins grew *Eleocharis palustris* or carices, *Rorippa islandica*, *Lycopus europaeus* and *Rumex maritimus*. In more open water grew *Potamogeton natans*, *P. pectinatus* and *P. perfoliatus* and all three British species of *Myriophyllum*. Towards the top of the zone *Equisetum*, *Sparganium*, *Pilularia*, *Littorella* and *Polygonum amphibium* occur, but the most abundant aquatic flowering plants appear to have been the water buttercups, for their very abundant achenes are accompanied by remarkably large frequencies of *Ranunculus* pollen.

In many west-European sites Zone III shows an increase in variety and frequency of Late-glacial herbaceous plants, after their suppression in Zone II by the birch or birch-pine woodland. At Moss Lake the herbaceous land plants appear to decrease, save

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Artemisia, and indeed the decrease in frequency of *Thalictrum* and *Scabiosa* at the opening of the zone is striking. One suspects that the explanation may lie in the local physiographic conditions, perhaps such as deep snow cover. Pollen is present sporadically of *Plantago maritima*, *P. major*, *Polygonum* cf. *bistorta*, *Polemonium caeruleum*, *Armeria maritima*, *Epilobium*, *Jasione montana*, *Campanula*, *Helianthemum* and of several families commonly associated with the Late-glacial period, Caryophyllaceae, Cruciferae, Rubiaceae, Compositae, Gramineae and Cyperaceae. The great decrease in pollen of Cyperaceae from Zone II may be explicable in the changed conditions of the lake rather than the surrounding upland, but *Carex* nutlets are, nevertheless, recorded throughout Zone III, though not in Zone II.

Zone IV

The field notes indicate a somewhat abrupt lithological change at the level where the contact between Zones III and IV has been placed, but it is unlikely that there was any substantial discontinuity. Coarse detritus organic mud was laid down throughout Zone IV, with a rapidly diminishing sand content reflecting the stabilized vegetation cover of the landscape.

In the lake itself the zone was marked by a profuse development of aquatic plants (see figure 1). *Equisetum* remains are abundantly present at the III/IV zone boundary and spores are present throughout Zone IV. Other aquatics present in varying amount are *Isoetes echinospora* (represented both by megaspores and microspores), *Pilularia globulifera* (also with two spore types), *Typha latifolia*, *Sparganium* sp., *Nymphaea alba* (pollen and seeds). *Potamogeton crispus*, *P. filiformis*, *P. natans*, *P. pusillus*, batrachian ranunculi, *Littorella lacustris*, *Elatine hexandra*, *Eleocharis palustris*, *Carex rostrata*, *Juncus* sp., *Myriophyllum alterniflorum* and *Polygonum amphibium*. The presence of the Characeae and of occasional ostracods points to some lime content in the water, and the profuse aquatic vegetation indicates a degree of eutrophy, although *Elatine hexandra*, *Isoetes echinospora* and *Pilularia globulifera* are most commonly found in oligotrophic habitats, and we have *Sphagnum* spores present throughout most of the zone and *Eriophorum* sp. recorded from the end of it.

This great expansion of water plants, some of them thermophilous, in Zone IV, is a feature remarked upon by Iversen (1954) in reviewing the Late-glacial flora of Denmark. It fully accords with the deduction of warmer conditions after Zone III. Macroscopic remains of *Lycopus europaeus*, *Rorippa islandica*, *Rumex maritimus* and *Juncus effusus* or *conglomeratus*, presumably came from the lake margins.

Turning now to consideration of conditions on the dry land we note at once the substantial continuing rise throughout the zone of the tree-pollen/non-tree-pollen ratio. *Betula* pollen strongly preponderates over that of pine, and there are macroscopic remains of tree birches throughout Zone IV, both *Betula verrucosa* and *B. pubescens* being present late in the zone. The inference is of the progressive closure of birch woods. The considerable frequency of *Juniperus*, a distinctly shade-intolerant shrub, throughout the zone, and the continuing though diminished representation of *Empetrum*, as well as the frequency and variety of herbaceous plants indicate that closed forest even of birch was not yet established. No thermophilous forest trees are yet present, but *Corylus* pollen is present consistently through the zone. Parallel evidence for this early presence of the hazel appears to be accumulating, but until macroscopic remains are identified some uncertainty of the

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precise pollen source will persist. In this zone pollen referable to *Prunus* and to *Sorbus* is present.

Figure 2 shows the remarkable persistence throughout Zone IV of many dry-land herbaceous plants characteristic of the Late-glacial vegetation. Some indeed are represented here in increased frequency, for example, *Ulmaria palustris*, *Rumex* cf. *acetosa*, and *Polygonum* (of the *persicaria* and *maritimum* type as well as *amphibium*). *Pastinaca* occurs for the first time, and in relation to the indications of eutrophy in the aquatic flora, we may note the presence of the calcicolous *Helianthemum* and *Polemonium*, together with a species not hitherto recognized in British deposits, *Linum anglicum*. One supposes that the local drift supplied areas of relatively high base status.

Another pollen type not hitherto recorded and appearing in this zone is *Vicia* cf. *sepium*: towards the top of the zone isolated grains of *Caltha palustris* and *Sanguisorba officinalis* are recorded and there reappears *Circaea*, already seen in Zone II.

Zone V

Zone V shows the impact of great vegetational changes in the countryside. The mixed oak-forest genera, *Ulmus* and *Quercus* are present in increasing frequency throughout the zone and with an increasing proportion of *Pinus*, the *Betula* curve correspondingly decreases. *Corylus* pollen increases through the zone to values twice those of the total tree pollen. Macroscopic remains of tree birches are now accompanied by the seeds of *Pinus sylvestris*. It is difficult to resist the interpretation of establishment of closed woodland and closed hazel scrub, for at the end of Zone IV the pollen curves for grasses, sedges and the majority of dry-land herbs fall away to low values or cease entirely. Likewise the shade-intolerant *Juniperus* and *Empetrum*. The explanation of the strong diminution in the pollen of water plants may rest partly in the increased absolute frequency of the tree pollen employed as standard. Fruit stones of *Potamogeton natans* are still abundant, and mega-spores of *Isoetes echinospora* occur occasionally along with seeds of *Elatine hexandra*, *Nymphaea alba*, nutlets of *Carex* and fruits of Characeae, but colonies of *Botryococcus* and *Pediastrum*, present throughout Zones III and IV cease about this time. Of particular interest is the presence of fruits of the thermophilous *Najas marina* and we note that the first grains of ivy, *Hedera helix*, occur in this zone also.

Zone VI

In Zone VI the tree birches amount to no more than 40% of the total tree pollen, but macroscopic remains of both *Betula pubescens* and *B. verrucosa* are abundant, especially in the leafy layers at the level 205 to 210 cm in the pollen series. They are accompanied by both seeds and leaves of *Pinus sylvestris*, a species contributing substantially more to the tree pollen in this zone than in either the preceding or succeeding zone, and reaching 40% of the total tree pollen in the leafy layer. *Ulmus* and *Quercus* also show values substantially above those of Zone V, and very high percentages of *Corylus* pollen are maintained. This is a normal picture for the woodland history of Zone VI. Early in this zone a transformation to oligotrophic bog becomes apparent in the formation of very strongly laminated aquatic *Sphagnum* peat. It seems likely that the 'leafy layers' represent the mesotrophic transition from open water to floating *Sphagnum* mat. These layers contain besides the leaves and twigs of birch and seeds and leaves of pine, abundant leaves of *Osmunda regalis*

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and leaves of a willow resembling *Salix aurita*. The tendency of *Osmunda* to occur in such a transition to oligotrophic bog was noted in analyses of the Meare Pool region of the Somerset Levels (Godwin 1955). Between the leafy layers were found a few leaves of *Cotoneaster* sp.: these are discussed later. Also from the deposits near the V/VI zone boundary were recovered macroscopic remains of *Calluna vulgaris*, *Carex rostrata*, and *Corylus avellana*. Among other aquatic plants similarly represented are *Potamogeton natans*, *Schoenoplectus lacustris*, *Potentilla palustris*, *Nymphaea alba*, *Menyanthes trifoliata*, *Lysimachia* sp. *Ruppia spiralis* and *Cladium mariscus*. The last two-named are species of southerly range in Scandinavia and their appearance at the Zone V/VI boundary accords with what is already known of their Post-glacial expansion elsewhere in Britain. It will be noted, similarly, that pollen of *Lonicera* and spores of *Pteridium* occur sparsely from the beginning of Zone VI; both are somewhat thermophilous.

Zone VII

An abrupt rise in the *Alnus* pollen curve to sustained high values and the beginning of continuous records for *Tilia cordata* clearly indicate the opening of Zone VII, and, as often elsewhere, the *Corylus* pollen curve falls from the high values of Zone VI, presumably because the closure of the alder-mixed oak forest was suppressing the hazel scrub. Little attention was paid to the deposits of this zone, since they were very much dried out, decayed and penetrated from above by secondary rootlets. However, it is clear that highly humified *Sphagnum–Eriophorum–Calluna* peat extends upward from the base of Zone VII, and that a typical raised moss occupied the site, as the historical records of course indicate. The sustained high values for pollen of *Calluna* reflect the bog condition. It is interesting to note the presence in Zone VII of a single pollen grain of *Althaea officinalis*. Pollen of *Centaurea cyanus* and *Plantago lanceolata* was present in the lowermost samples of Zone VII.

4. Records of individual species

Cf. Agropyron junceiforme (*A. & D. Löve*) *A. & D. Löve*

It is seldom possible to recognize a grass by its pollen grains, and even generic identification escapes us. However, the sand couch-grass, *Agropyron junceiforme*, is apparently exceptional. The germ pore is large in proportion to grain size and its raised margin projects to an unusual extent for grass pollen, and the wall is unusually thick.

A single pollen grain, and that rather badly damaged but clearly showing the pore structure, was recovered from the 264 cm sample in Zone II. Although the pore morphology and surface texture correspond exactly with those of type material of *A. junceiforme*, the identification must be extremely tentative.

A. junceiforme is a plant highly typical of the embryonic or fore-dunes of British coasts. If we recall the likelihood that during Zone II, in which this pollen was deposited, the world sea-level was lower than it now is by perhaps 300 ft. (100 m), it will appear that Moss Lake was far distant from the contemporary coast. The interesting possibility remains that *A. junceiforme* in Late-glacial time grew upon inland dune systems such as are represented in Holland by the 'cover-sands' and which possibly have analogues in the Shirley Hill Sands of Cheshire. *A. junceiforme* is a southern and western European plant extending north on the continental mainland to about 63° N.

Althaea officinalis *L.*

Discoveries of the subfossil pollen of *Althaea officinalis* have not been published hitherto, although there are unpublished records from Zone VII*a* at Burnham-on-Sea, Somerset. A single grain was recovered from the same zone at Moss Lake. A pollen grain of *A. officinalis* is distinguishable from the pollen of other British members of the Malvaceae by its smaller size and the wider spacing of the spines of the exine. *A. officinalis* is a coastal plant closely associated with brackish soils. At the time of the Moss Lake record, rising sea level had brought the coast approximately to its present position, and salt-marsh habitats were not far from the site.

Armeria maritima *Willd.*

Pollen of *Armeria* was found at Moss Lake in Zones II, III and IV and pollen of both 'A' and 'B' types was present. These early records accord with other abundant British evidence for the Late-glacial prevalence of this species. A single grain from the opening of Zone VII*a* contributes to our evidence, already strong, for the persistence of the plant.

Betula nana *L.*

Although it is difficult to make a completely satisfactory separation between *Betula nana* and the tree birches, *B. verrucosa* and *B. pubescens*, on pollen morphology, nevertheless it was possible to recognize that pollen of the dwarf birch was present along with that of the tree birches at various levels in Zone IV, and again at the V/VI boundary. The greater observed frequency of dwarf birch in Zone IV than in the preceding Late-glacial zone parallels the behaviour of *Juniperus*, and might well relate to similar causes.

Cf. Bidens cernuus *L.*

A single pollen grain from Zone IV was identified as *Bidens cernuus* with some confidence, as fossil grains of this species have recently been found from a Post-glacial Kentish site in considerable frequency at a level at which fruits of the same plant were also present. In this category of pollen grains, *B. cernuus* has characteristically long curved spines with concave outline.

B. cernuus occurs freely (like *Rorippa islandica*) on sites with standing water in the winter, but not during the growing season (Clapham, Tutin & Warburg 1952). It occurs throughout the British Isles and extends northwards to 60° N. in Scandinavia.

There are no British records of the plant before Roman time.

Botrychium lunaria (*L.*) *Sw.*

Botrychium lunaria is the only species of *Botrychium* now growing in Britain, and the subfossil spores resemble those of this species. It is already known from all zones of the Late-glacial period in Britain, but not with the high frequencies it displays at Moss Lake in Zone I. Its presence in such amount must indicate a very open condition of the vegetation, and the quick decline in abundance at the transition to Zone II is presumed to indicate the thickening of tall herbaceous vegetation at that time.

Campanulaceae

A number of pollen grains of the '*Campanula*' type were found between the levels of 218 and 247 cm. Of them six were between 17 and 22 μ in diameter and can be tentatively

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identified as *Jasione montana* L.: these were in Zone IV and at the III/IV transition. A few larger grains (24 to 29 μ) occurred in both Zone III and Zone IV and these are referable to a restricted number of species in the genus *Campanula*.

Circaea *sp.*

From Zone II, the top of Zone IV, and Zone VII there are records of a few pollen grains of *Epilobium* type but far too small to belong to that genus: it can be matched with those of the genus *Circaea*, pollen of which has only once before been noted in British deposits (Kirkby Thore, Westmorland, Zone VI).

Cotoneaster *sp.*

From the organic detritus mud between the leafy layers at the base of Zone VI, Miss Lambert extracted the well-preserved portions of four leaves which are illustrated in plate 3. They correspond in close detail with the short-petioled, broadly elliptic, ovate or orbicular leaves of *Cotoneaster integerrima* and one of them exhibits the retuse apex often found in that species. Close as agreement is in all respects with *C. integerrima* it is not possible with so small a sample to rule out the possibility that they might alternatively belong to *C. melanocarpa*, which has in general larger leaves somewhat more obovate and less often retuse. *C. integerrima* is a Euro-Siberian species extending from south Scandinavia and Finland south to Spain and Italy and eastwards into Asia, but in the British Isles it is restricted to a very sparse growth upon Great Orme's Head in north Wales. It grows there upon limestone, but upon the continent it is not limited to limestone though preferring it. It appears to favour open, dry, sunny and stony slopes, and on the continent often occurs in open coniferous woodland. *C. melanocarpa* is also a Euro-Siberian species, but has a less southern range than *C. integerrima* and it does not now grow in Britain.

The probability is that the fossil leaves belong to *C. integerrima*, but whether to this species or *C. melanocarpa* they prove a Post-glacial modification of range.

Elatine hexandra *D.C.*

The highly recognizable curved seeds of *Elatine hexandra* were present in considerable numbers from deposits at the III/IV zone boundary, throughout Zones IV, V and part of VI. They have been described by Watts (1958) who recovered them from interglacial deposits at Kilbeg. They had previously been identified from the Cromer Forest Bed, but have not hitherto been known from the British Post-glacial period.

E. hexandra is a small annual aquatic plant growing on exposed wet mud or submerged along with other small plants of similar habit, such as *Isoetes echinospora* and *Littorella uniflora*, both of which are indeed found along with it in Zone IV at Moss Lake, and both of which share its own preference for oligotrophic habitats.

Empetrum nigrum *L.*

Pollen of the crowberry is present from Zone II to V at Moss Lake and attains considerable abundance in Zone III: its seeds are also abundant in this zone and present, though less abundantly, in Zone IV. This plant is very well known from the whole of Late-glacial time in the British Isles, and Jessen has commented upon its very high frequency in Zone II,

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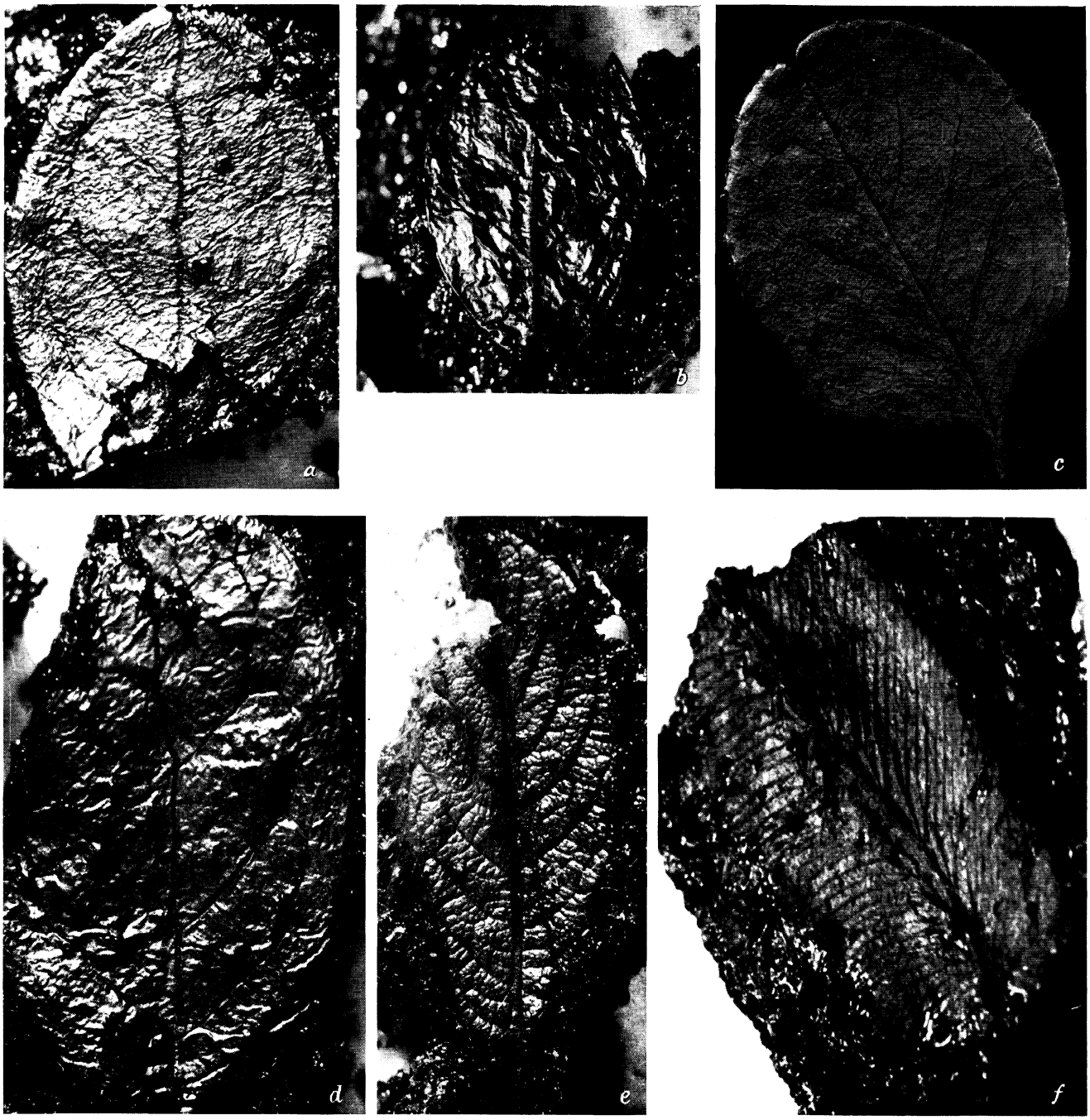

FIGURES *a*, *b*, *d*, leaves of *Cotoneaster* sp. from the Zone V/VI transition at Moss Lake; *c*, leaf of living *C. integerrima*, which the fossils closely resemble; *e*, fossil leaf of *Salix* (cf. *S. cinerea*); *f*, fossil leaf of *Osmunda regalis* L.

(*Facing p.* 138)

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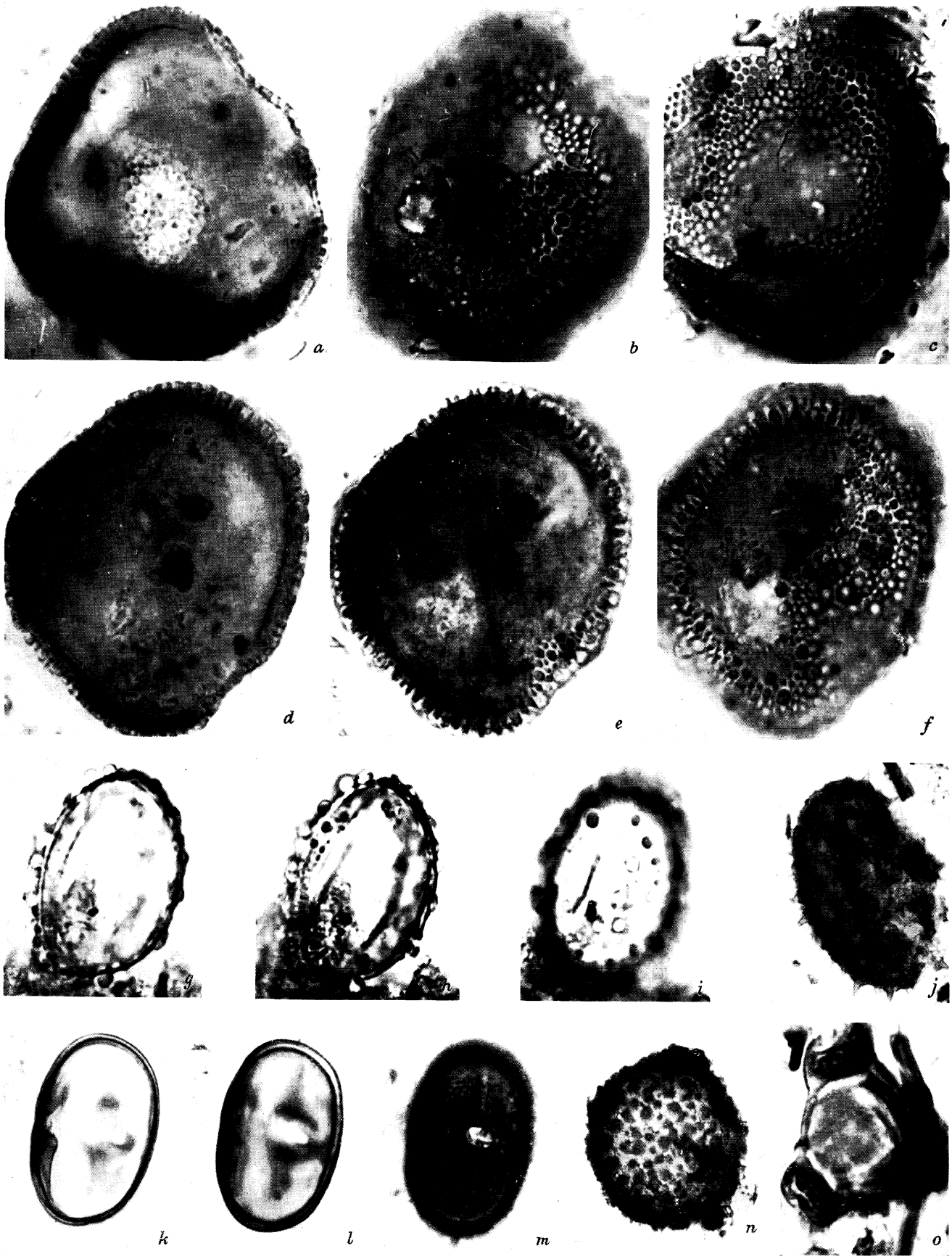

FIGURES *a* to *f*, fossil pollen of *Linum anglicum* Mill. seen at different focal depths: they show the ill-defined pores and the clear heteromorphy of the exine elements (magn. ×1130); *g*, *h*, *i*, fossil pollen of *Nymphaea alba* L. bearing exclusively gemmate processes (magn. ×1500); *k*, *l*, *m*, fossil pollen of *Vicia* cf. *sepium* L. (magn. ×1270); *j*, *n*, two fossil grains of *Althaea officinalis* L. (magn. ×640); *o*, fossil grain of *Circaea* sp. (magn. ×1000).

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attributing this to the presence of *Empetrum* heaths. In the Netherlands, as at Moss Lake, it seems that a comparable importance was reached by *Empetrum* in Zone III. In the Moss Lake vicinity there must have been big stretches of Triassic sandstone exposed, or of tills much affected by it, just as in many Late-glacial Dutch sites the cover-sands were exposed. These soil conditions might be expected to have favoured *Empetrum*.

Ephedra distachya *s.l.*

Three pollen grains of *Ephedra distachya* found in Zone II add to the now considerable number of Late-glacial records for this plant in north-western Europe.

Cf. Gentiana campestris (*L.*) *H.Sm.*

In the sample at 266 cm in Zone II there was found a large tricolporate grain clearly belonging to the genus *Gentiana*. Its wall was of exceptional thickness, the ektexine showing long robust columellae tending to expand and fuse near the apex, thus giving a striking subreticulate pattern in surface view. This pattern we could match in British gentians only in *G. campestris* (L.) H.Sm.

G. campestris (L.) H.Sm. is a plant of distinctly northern range in Britain although widespread in Ireland. On the Continental mainland it occurs from Iceland and western Finland southwards to northern Denmark and Bornholm, and has a separate area in the mountains of central and southern Europe.

Pollen of '*Gentiana* cf. *campestris* s.l.' has been recorded by Iversen (1954) from the Late-glacial in Jutland.

Isoetes echinospora *Durieu*

Microspores of *Isoetes* were frequent in Moss Lake in Zone IV and the beginning of Zone V and they were accompanied throughout by megaspores recognizable by the residual pattern left after shedding of the outer layer with its long, sharp spines, as those of *I. echinospora*. The microspores were consistently small, falling within the size range of *I. echinospora*. This species has been found in the Allerød muds at Hawk's Tor, Cornwall, and Mr B. Seddon has unpublished records of it from the Nant Ffrancon. *I. echinospora* has a disjunct distribution in Europe and in the British Isles themselves: the present localities nearest to Liverpool are in north Wales.

Juniperus communis *s.l.*

The pollen records from Moss Lake strengthen the view that *Juniperus* was an important component of the vegetation in Late-glacial and early Post-glacial time. In many sites in Denmark and Britain it is present in Zone II, diminishes in frequency in Zone III and reaches its greatest values at the Zone III/IV boundary, a time where it is assumed to suffer neither the climatic severity of Zone II nor the tree competition of Zone IV. At Moss Lake we have seen reason to suppose that the woodlands only consolidated slowly in Zone IV, and the continued abundance of *Juniperus* may well be associated with this. We may note Iversen's comment (1954), 'A high juniper curve in Late-glacial diagrams, therefore, indicates the borderline between the subarctic, open park-tundra and the temperate dense forest.'

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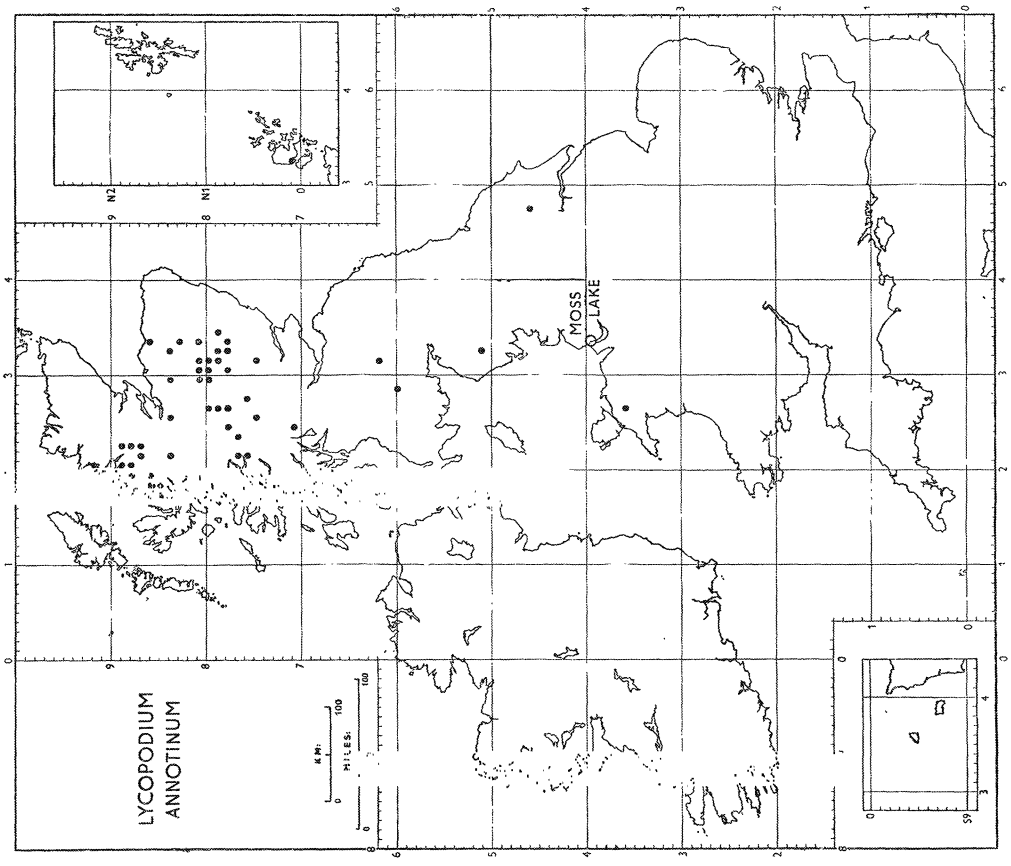

FIGURE 4. Map showing the site of Moss Lake where *Lycopodium annotinum* L. was identified in the Late-glacial Zone I, and the present British range of this plant.

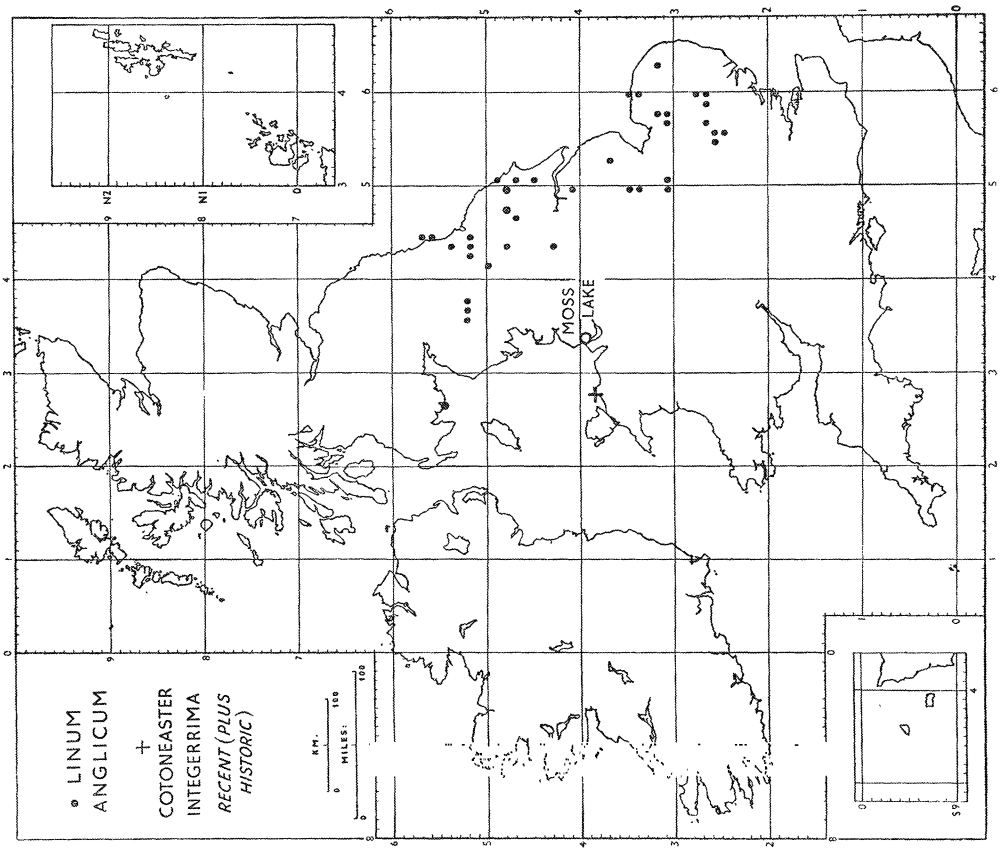

FIGURE 3. Map showing the site of Moss Lake (open circle), the sole present natural locality for *Cotoneaster integerrima* in Britain (+), and the known recent and historic localities for *Linum anglicum*.

Supplied by the Director of the Distribution Maps Scheme of the Botanical Society of the British Isles.

Linum anglicum *Mill.*

At the beginning and middle of Zone IV occurred three pollen grains clearly belonging to the genus *Linum*, and finally determined as those of *Linum anglicum*. Mill. They are large grains with five of six pores of indefinite outline and their margins, like those described by Erdtman for *L. heterosepalum* ('foramina tenuimarginate, not sharply defined'). The wall structure is characterized by 'excrescences dimorphic', a description given by Erdtman to the grains of *L. flavum* f. *longistylum* (Erdtman 1952). In *L. anglicum* the elements of the exine are large gemmoid elements on the one hand, and in between them much narrower rod-like elements, more or less pointed apically, and not quite so long (perhaps five-sixths) as the gemmoid elements (see plate 4). Different grains in the type-material of *L. anglicum* differ in the proportion of large to small excrescences, but the heteromorphy is very pronounced, and in this character the grains of *L. anglicum* are easily distinguishable from those of other British species of flax. Still more evident is the fact that whereas *L. bienne* and *L. catharticum*, the other native British species, have clearly tricolpate grains, those of *L. anglicum* are, as we have said, polyforate. The fossil grains are approximately 50 to 55 μ in diameter, falling within the size range of the type material. The intine is much thinner than the exine.

L. anglicum is a perennial flax of calcareous grassland found very locally in eastern England from Durham to Essex and extending westwards to Cambridge, Leicester and Westmorland. It occurs also in eastern and central France and at one place in Baden. Already it has been shown (Godwin 1956) that many of the seeds recovered from Full-glacial deposits in the Lea Valley and originally referred to *L. praecursor* Reid (a species not known living) are extremely similar to seeds of *L. anglicum*, as are others from East Anglian interglacial deposits. The possibility is now clearly increased that these fossil seeds represent *L. anglicum* which thus appears to have been present in this country right through from Full-glacial times.

Littorella uniflora (*L.*) *Aschers*

Pollen of *L. uniflora* was found at Moss Lake at the close of Zone III, and abundantly throughout Zone IV: it was found early in Zone V, and a single grain was recovered from Zone VI. Its chief expansion was in Zone IV along with many other aquatics of comparable ecological range, notably *Pilularia globulifera*, *Isoetes echinospora* and *Elatine hexandra*.

It was already apparent that this species was present in Britain in Late-glacial time: this evidence indicates a local expansion under suitable environmental conditions.

Lotus *cf.* uliginosus *Schkuhr or* hispidus *Desf.*

From various levels in the deposits of Zone IV, there were recovered eleven small tricolporate pollen grains corresponding closely in structure with those of the genus *Lotus*. It was impossible to discern a wall pattern in surface view, but in optical section at the poles a few widely spaced elements were visible radially crossing the exine.

The grains ranged between 10 to 13 μ in length, and even allowing for the shrinkage that is very commonly found in our preparations of fossil pollen, this seems to exclude identification with *L. corniculatus* L. in which the mean pollen-grain length is about 16 μ. The fossil grains do, however, fall within the size range of grains of *L. uliginosus* (11 to 14 μ) and *L. hispidus* (14 μ) though still somewhat smaller.

L. uliginosus is a plant of damp meadows, fens and marshes, and, on the Continent of moist to dry woodland. It is notable that Hegi (1925) writes 'besonders auf kalkarmen Boden', and we might suppose the shore conditions of Moss Lake in Zone IV already described (p. 134) to have been very suitable to this species. *L. uliginosus* is found throughout the British Isles except the extreme north, and has a limited southern range in Scandinavia. It is placed by Salisbury (1932) and by Matthews (1937) among the species of 'Continental southern range'.

Lotus hispidus is a much rarer plant in Britain, occurring only in six south-western counties of England, and favouring 'dry grassy places near to the sea' (Clapham *et al.* 1952). It is placed by Matthews (1937) in his category of 'Oceanic Southern' species.

Iversen (1954) has recorded pollen of *Lotus* cf. *corniculatus* from Zone III of the Late-glacial in Bornholm, but we are unaware of other published fossil records for the genus.

Lycopodium annotinum *L.*

It is interesting to recover the spores of *L. annotinum* from Zone I, for this is the scarcest of the British club-mosses, and it has a pronouncedly northern and high altitudinal range both in the British Isles and on the Continental mainland. It has recently been identified by B. Seddon (unpublished) from various Late-glacial localities in north Wales, where the plant no longer grows. It has been found in all three zones of the Late-glacial in Denmark. it is not found south of Yorkshire or in Ireland.

Myriophyllum *spp.*

All three British species of *Myriophyllum* were present in Moss Lake in the Late-glacial period, as they have already been proved to have been elsewhere in Britain and in Denmark. *M. alterniflorum* fruits were found in middle and late Zone III, and pollen occurred late in Zone III also. Pollen of *M. verticillatum* was found in Zones II and III, and that of *M. spicatum* in Zone III.

Nymphaea alba *L.*

In his *Introduction to pollen-analysis*, Erdtman (1943) indicates that *Nymphaea alba* and *N. candida* are distinguishable on pollen morphology, the grains of *N. alba* being covered with spines and those of *N. candida* with small warts instead of spines. Furthermore, Clapham *et al.* (1952) indicate that in Scottish forms of *N. occidentalis* (Ostenf.) Moss 'the uniformly short processes are all about as long as wide'. *N. candida* appears not to be native to the British Isles and *N. occidentalis* has a very limited range. It was, therefore, with particular interest that Miss Andrew noted that, contrary to all previous experience with British subfossil *Nymphaea* pollen, that from Moss Lake (Zones IV to VI) appeared to be entirely of a type covered with widely spaced and almost spherical gemmae or warts attached by a very constricted base (plate 4). The grains are also somewhat smaller in size than type material of *N. alba*.

We were fortunate at this stage in being able to call upon the help of Mrs Y. Heslop-Harrison whose extensive taxonomic and ecological work upon British water lilies had just been published (1955), and she kindly furnished us with stamens of type material from many collections of *N. alba* populations. We also examined Scottish material kindly supplied by Dr McVean, and Dr H. Fletcher. Among these we were able to confirm what

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Mrs Heslop-Harrison recognized, viz. that within one plant of *N. alba* there can be considerable range in the sculpturing pattern of the pollen, and that different populations may show grains with gemmae only, or gemmae with rods in varying proportions, but that there seem to be no grains with rods exclusively. We agreed also that there are existing populations with pollen grains of the subfossil type within *N. alba*. Mrs Heslop-Harrison does not recognize *N. occidentalis* as a useful taxon, nor does the pollen character in question seem to be restricted to plants that might be referred to *N. occidentalis* on other grounds. We also agree with Mrs Heslop-Harrison that the sculpturing pattern on grains of *N. candida* is always much finer than that in *N. alba*. The Moss Lake material is certainly therefore not *N. candida*.

It is interesting to discover an early Post-glacial example of the kind of population differentiation that Mrs Heslop-Harrison finds still to exist in the British Isles. It is to be noted that the pollen is accompanied by seeds which increase in frequency to abundance at the Zone V/VI transition, the stage at which also idioblasts of *Nymphaea* occur in the pollen preparations.

Pilularia globulifera *L.*

The record of *Pilularia globulifera* from the Irish interglacial deposits at Kilbeg has been amply confirmed by Watts (1958), but we have not hitherto had records of it from the Post-glacial period. The easily recognizable megaspores were found at the Zone III/IV boundary and throughout Zone IV, whilst the microspores figure in the pollen counts from the later part of Zone III to the end of Zone V, being especially frequent early in Zone IV. We have already pointed to the association of this plant with *Elatine hexandra*, *Isoetes echinospora* and *Littorella lacustris*. Watts has commented upon the presence of a similar aquatic community in the Kilbeg deposits. *Pilularia globulifera* is classed by Hultén as a Sub-atlantic species: it has a southern range in Scandinavia like a number of other aquatic species now known to have been present in Britain in Late-glacial time.

Plantago *spp.*

A considerable proportion of fossil grains of plantain can be referred to their species. *Plantago maritima* grains occurred in Zones III, IV, and V: this accords with previous records of it in the Late-glacial in Denmark and the British Isles.

Plantago major was identified in Zones III and IV again in conformity with earlier British records. Grains referable to either *P. major* or *P. media* were found in Zones VI and VII*a*, *P. lanceolata* occurred in Zone VII*a*, one grain at the opening of it.

Polygonum *spp.*

Pollen of *Polygonum* occurred from Zone III onwards, but it was particularly abundant in Zone IV along with the abundant pollen of many other aquatics. In this zone, and extending somewhat into Zones III and V, pollen of *P. amphibium* was recognizable in every sample.

Pollen of the *P. bistorta* type (which includes *P. viviparum*) was found in Zone III. That of *P. persicaria* type (which includes the species *P. nodosum* and *P. lapathifolium*, see table 1) occurred in Zones IV, V and VII*a*.

Pollen comparable in all respects (save somewhat smaller size) with that of *P. maritimum* occurred in Zone IV and at the very end of Zone III. This is a rare and extremely southern

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species in Britain and the identification must be regarded as very tentative. *P. maritimum* is the smallest of the British *Polygonum* species with a size range of 22 to 26 μ for grain length. The fossil material is even smaller (18 to 20 μ), but has the same notable thickness of wall (see Hedberg 1946) and identical wall pattern.

Potamogeton *spp.*

The Moss Lake material was rich in the fruit stones of *Potamogeton* and six species of the genus were recognized, viz: *P. crispus* (Zone IV), *P. filiformis* (Zone IV), *P. natans* (Zones III to VI), *P. pectinatus* (Zone III), *P. perfoliatus* (Zone III), and *P. pusillus* (Zone IV). These all conform to existing records for these species in these respective zones in the British Isles.

Rosaceae, Prunus *and* Sorbus *types*

From Zones IV, V and VI pollen grains were recovered which clearly belonged to the categories *Prunus* and *Sorbus*, but we found it impossible to make a closer identification. One or two further grains showed some resemblance to those of *Crataegus* or *Malus*.

Rorippa islandica (*Oeder*) *Borbás*

Seeds of *Rorippa islandica* were found occasionally or rarely in Zones III and IV. This is a plant of great catholicity of habitat, and is particularly common on sandy habitats flooded in winter. It is very likely, judging from the lithology of the deposits, that Moss Lake provided suitable situations for it in Zones III and IV. *R. islandica* is a cosmopolitan species which extends north to Iceland and the Varanger peninsula. It is already known from the Full-glacial and Late-glacial periods in Britain (Godwin 1956).

Rumex maritimus *L.*

The fruits of *Rumex maritimus* are very easily recognizable when they retain their enclosing sepals. They have hitherto been known in Britain from the Full-glacial period, and thereafter only from Zone VII*a*. The Moss Lake records from early in Zone IV and the middle of Zone IV fill in the Post-glacial story of the species. It is a plant of rather southerly range both in the British Isles and Scandinavia.

Ruppia spiralis *Dum.*

A fruit of *Ruppia spiralis* was recovered from the bulk sample crossing the Zone V/VI boundary. This record accords with numerous Post-glacial discoveries of which the earliest is one from the North Sea moorlog (Zone IV or V).

Saxifraga (*hypnoides type*)

From three samples in Zone II there were recovered five pollen grains of the genus *Saxifraga*. They are tricolpate grains approximately 25 to 28 μ long, finely patterned and with slightly thickened furrow margins. They can be closely matched within the British saxifrage species by pollen of *S. hypnoides* (agg.), and *S. rivularis*.

S. hypnoides has already been recorded from a few Late-glacial sites in Britain on a basis of leaf and seed identifications.

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Solanum nigrum *L.*

A single pollen grain from Zone IV belongs to a very small category of tricolporate grains with no surface pattern, and with deeply inturned furrows. Seen in lateral view the furrows retract in a straight line from the pores towards the poles, thus giving a sharply triangular shape, kinked at the pore. The grain is too large (23 μ) and too thin-walled for it possibly to be referred to *S. dulcamara*, a species already identified in the Danish Late-glacial (Iversen 1954).

S. nigrum is a species which is strongly southern in its British range, being absent from most of Scotland. It extends northwards in Scandinavia to 63° N. In Britain it strongly favours light well-drained sandy soils.

The present identification is supported by a seed identification from the pollen-zone boundary IV/V at the Mesolithic settlement site of Star Carr in east Yorkshire (Godwin 1956).

Vicia *cf.* sepium *L.*

From the uppermost sample of Zone III, and at various levels throughout Zone IV, there were recovered in all, nine pollen grains which could be recognized with considerable confidence as those of the genus *Vicia*. The tricolporate grains varied little in length from 25 μ. The furrow walls (as may be seen in figures *k*, *l*, *m*, plate 4) are strongly thickened internally when they meet the circular pores. The surface pattern is a faint, shallow and irregular reticulum which is more apparent near the equator, where it becomes resolved into a series of irregular strands tending to radiate from the pores.

Apart from *V. sepium* and *V. hirsuta* other British species of *Vicia* have rather larger grains than the fossil type, and the pollen of *V. hirsuta* is more strongly reticulate. This leads to the qualified identification we have given.

V. sepium is a British member of that remarkable category of plants (recently considered by Clapham (1953)) which it is difficult or impossible to refer to natural communities, at least within this country. *V. sepium* is here a typical hedgerow and scrub plant, found commonly in wayside situations, 'grassy places, hedges and thickets'. On the Continent it also occurs in grazing meadows, open woodland and scrub, and it favours fresh, moist to fairly dry soils of high mineral status.

It is a plant which extends north to Iceland and to high latitudes in Scandinavia and throughout Europe, though 'rare and local in the Mediterranean region'.

It has not hitherto been identified in subfossil condition.

5. General floristic considerations

The Moss Lake deposits have proved to be both comprehensive and productive. Pollen analyses showed that they extend from the end of Zone I continuously through to Zone VII, and in the bottom deposits the evidence of microscopic and macroscopic plant remains upholds the view suggested by the lithology, that the characteristic Late-glacial sequence is present. One can follow both the vegetational history of the surrounding upland and the progress of the lake through its moderately eutrophic open stages rich in aquatic plant life, through its transient birch–willow–pine fen woods to the ombrogenous raised moss which persisted from the beginning of Zone VII onwards.

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TABLE 2. COMPREHENSIVE LIST OF PLANT REMAINS FROM MOSS LAKE, LIVERPOOL

Abbreviations as given in Table 1.

British pollen zones ...		I	II	III	IV	V	VI	VII*a*
Cf. *Agropyron junceiforme* (A. & D. Löve) A. & D. Löve	*p.*	.	×	.	.	.	.	.
Alisma sp.	*p.*	.	.	.	×	.	.	.
Alnus sp.	*p.*	.	.	.	.	.	.	×
Althaea officinalis L.	*p.*	.	.	.	.	.	.	×
Armeria maritima (Mill.) Willd.	*p.*	.	×	×	×	.	.	.
Artemisia sp.	*p.*	.	×	×	×	×	×	×
Betula nana L.	*p.*	.	.	.	×	×	.	.
B. pubescens Ehrh.	*fr.*	.	.	.	×	×	×	.
B. verrucosa Ehrh.	*fr.*	.	.	.	×	×	×	.
Betula spp.	*fr.*, *c.sc.*, *l.*, *p.*	×	×	×	×	×	×	×
Cf. *Bidens cernuus* L.	*p.*	.	.	.	×	.	.	.
Botrychium lunaria (L.) Sw.	*sp.*	×	×	.	×	×	.	.
Calluna vulgaris (L.) Hull	*l.*, *sh.*, *p.*	.	.	.	.	—	×	— ×
Caltha sp.	*p.*	.	.	.	×	.	.	.
Campanula sp.	*p.*	.	.	.	×	.	.	.
Carex rostrata Stokes	*n.* + *u.*	.	.	.	×	×	×	.
Carex spp.	*n.*	.	.	×	×	×	.	.
Centaurea cyanus L.	*p.*	.	.	.	.	.	.	×
Caryophyllaceae	*p.*	×	×	×	×	×	×	×
Chenopodiaceae	*p.*	.	×	×	×	×	×	×
Circaea sp.	*p.*	.	×	×	×	.	.	×
Cladium mariscus (L.) Pohl	*n.*	.	.	.	.	—	×	— .
Compositae: (residual) *Arctium* type	*p.*	.	.	.	×	.	.	.
Bellis type	*p.*	.	.	×	×	.	.	.
Cirsium type	*p.*	.	.	.	×	.	.	×
Matricaria type	*p.*	×	×	×	×	×	.	×
Taraxacum type	*p.*	×	×	×	×	×	×	×
Corylus avellana L.	*p.*, *n.*	.	.	.	×	×	×	×
Cotoneaster cf. *integerrima*	*l.*	.	.	.	.	—	×	— .
Cruciferae	*p.*	.	×	×	×	.	.	×
Cyperaceae	*p.*	×	×	×	×	×	×	×
Elatine hexandra D.C.	*s.*	.	.	.	×	×	×	.
Eleocharis palustris L. (R.Br.)	*n.*	.	.	×	×	.	.	.
Ephedra distachya s.l.	*p.*	.	×	.	.	.	.	.
Epilobium sp.	*p.*	.	×	×	×	.	.	.
Empetrum nigrum L.	*p.*, *s.*	.	×	×	×	×	.	.
Equisetum sp.	*st.*, *sp.*	.	.	×	×	×	×	.
Eriophorum sp.	*n.*	.	.	.	×	.	.	.
Fagus sylvatica L.	*p.*	.	.	.	.	.	.	×
Filipendula ulmaria (L.) Maxim.	*p.*	.	.	×	×	×	×	.
Cf. *Gentiana campestris* (L.) H.Sm.	*p.*	.	×	.	.	.	.	.
Gramineae	*p.*	×	×	×	×	×	×	×
Hedera helix L.	*p.*	.	.	.	.	×	×	×
Helianthemum sp.	*p.*	.	×	×	×	.	.	.
Hydrocotyle vulgaris L.	*p.*	.	.	.	.	.	.	×
Isoetes echinospora Durieu	*msp.*, *Msp.*	.	.	.	×	×	.	.
Jasione montana L.	*p.*	.	.	.	×	.	.	.
Juncus effusus L. or *conglomeratus* L.	*s.*	.	.	.	×	.	.	.
Juncus spp.	*s.*	.	.	×	×	×	×	×
Juniperus communis s.l.	*p.*	.	.	×	×	.	.	.
Labiatae	*p.*	.	.	×	×	.	.	.
Linum anglicum Mill.	*p.*	.	.	×	×	.	.	.
Littorella uniflora (L.) Aschers.	*p.*	.	.	×	×	×	×	.
Lonicera periclymenum L.	*p.*	.	.	.	.	.	×	×
Lotus cf. *uliginosus* Schkuhr or *hispidus* Desf.	*p.*	.	.	×	×	.	.	.
Lycopodium annotinum L.	*sp.*	×	.	.	.	.	.	.
Lycopus europaeus L.	*fr.*	.	.	×	×	.	.	.
Lysimachia vulgaris L.	*p.*	.	.	.	.	.	×	.
Menyanthes trifoliata L.	*p.*, *s.*	.	.	.	.	.	×	×
Myriophyllum alterniflorum D.C.	*p.*, *n.*	.	.	×	×	.	.	.
M. spicatum L.	*p.*	.	—	×	— .	.	.	.
M. verticillatum L.	*p.*	.	×	×	.	.	.	.
Najas marina L.	*fr.*	.	.	.	.	×	.	.
Nymphaea alba L.	*p.*, *s.*	.	.	.	×	×	×	.
Ophioglossum vulgatum L.	*sp.*	.	×	.	×	.	.	.
Osmunda regalis L.	*l.*, *sp.*	.	.	.	.	×	×	×

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TABLE 2 (*cont.*)

British pollen zones ...		I	II	III	IV	V	VI	VII*a*
Pastinaca satira L.	*p.*	.	.	.	×	.	.	.
Pilularia globulifera L.	*msp.*, *Msp.*	.	.	×	×	×	.	.
Pinus sylvestris L.	*s.*, *l.*, *p.*	×	×	×	×	×	×	×
Plantago lanceolata L.	*p.*	.	.	.	.	.	.	×
P. major L.	*p.*	.	.	.	×	.	.	.
P. major L. or *media* L.	*p.*	.	.	.	.	.	×	×
P. maritima L.	*p.*	.	.	×	×	×	.	.
Polemonium caeruleum L.	*p.*	.	.	×	×	.	×	.
Polygonum amphibium L.	*p.*	.	.	×	×	×	.	.
P. bistorta L. type	*p.*	.	.	×	.	.	.	.
P. cf. *maritimum* L.	*p.*	.	.	×	×	.	.	.
P. nodosum Pers. or *lapathifolium* L.	*n.*	.	.	×	×	.	.	.
P. persicaria L. type	*p.*	.	.	.	×	—	×	— ×
Polygonum sp.	*n.*	.	.	×	.	.	.	.
Polypodium vulgare L.	*sp.*	.	×	.	×	.	×	×
Potamogeton crispus L.	*fst.*	.	.	.	×	.	.	.
P. filiformis Pers.	*fst.*	.	.	.	×	.	.	.
P. natans L.	*fst.*	.	.	×	×	×	.	.
P. pectinatus L.	*fst.*	.	.	×	.	.	.	.
P. perfoliatus L.	*fst.*	.	.	×	.	.	.	.
P. pusillus L.	*fst.*	.	.	.	×	.	.	.
Potamogeton sp.	*p.*	.	.	.	×	.	.	.
Potentilla palustris Scop.	*fr.*	.	.	.	.	—	×	— .
Potentilla sp.	*p.*	.	.	×	×	.	.	.
Prunus type	*p.*	.	.	.	×	×	×	.
Pteridium aquilinum (L.) Kuhn	*sp.*	.	.	.	.	.	×	×
Quercus sp.	*p.*	.	.	.	.	×	×	×
Ranunculus acris L. or *repens* L.	*fr.*	.	.	.	×	.	.	.
Ranunculus—batrachium spp.	*fr.*	.	.	×	×	.	.	.
Ranunculus sp.	*p.*	.	×	×	×	×	.	×
Rorippa islandica (Oeder) Borbás	*s.*	.	.	×	×	.	.	.
Rosaceae (residual)	*p.*	.	.	.	×	.	×	.
Rubiaceae	*p.*	.	×	×	×	.	.	.
Rumex maritimus L.	*n.* + *per.*	.	.	×	×	.	.	.
Rumex sp.	*n*, *p.*	.	.	×	×	.	×	×
Ruppia spiralis Dum.	*fr.*	.	.	.	.	—	×	— .
Salix cf. *aurita* L.	*l.*	.	.	.	.	—	×	— .
Salix sp.	*p.*	.	×	×	×	×	×	×
Sanguisorba officinalis L.	*p.*	.	.	.	×	.	.	.
Saxifraga (*hypnoides* type)	*p.*	.	×	.	.	.	.	.
Schoenoplectus lacustris (L.) Palla.	*n.*	.	.	×	.	—	×	— .
Cf. *Scleranthus annuus* L.	*p.*	.	.	×	.	.	.	.
Selaginella selaginoides (L.) Link	*sp.*	.	×	.	.	.	.	.
Solanum nigrum L.	*p.*	.	.	.	×	.	.	.
Sorbus type	*p.*	.	.	.	.	×	×	.
Sparganium sp.	*p.*	.	.	×	×	.	×	.
Succisa pratensis Moench.	*p.*	×	×	×	×	×	×	×
Thalictrum sp.	*p.*	×	×	×	×	.	.	.
Tilia cordata Mill.	*p.*	.	.	.	.	.	×	×
Typha latifolia L.	*p.*	.	.	×	×	.	.	.
Ulmus sp.	*p.*	.	.	.	.	×	×	×
Umbelliferae (residual)	*p.*	.	×	×	×	×	.	.
Valeriana officinalis L.	*p.*	×	×	×	×	×	.	.
Vicia cf. *sepium* L.	*p.*	.	×	×	×	.	.	.
Viola cf. *palustris* L.	*s.*	.	×	.	.	.	.	.
Viola sp.	*s.*	.	.	.	×	.	.	.
ALGAE								
Botryococcus sp.		.	.	×	×	×	.	.
Characeae	*o.*	.	.	×	×	×	.	.
Pediastrum spp.		.	×	×	×	.	.	.
FUNGI								
Microthyruim sp.	*fr. b.*	.	.	.	.	.	.	×
Ophiostoma pini		.	.	×	.	.	.	.
Tetraploa sp.	*sp.*	.	.	.	×	.	.	.
BRYOPHYTA								
Sphagnum sp.	*l*, *sp.*	.	.	.	×	×	×	×

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There is such a substantial total list of identifications referrable to particular pollen zones (see table 2), that the Moss Lake deposits could be made to illustrate most of the major features already known of the history of the British flora. In fact, besides substantiating a large number of species histories already fairly well known, there is a considerable number of additions to the British records of species hitherto unidentified, or not identified from the time-periods where they are represented here.

It is now well established that in addition to the expected Arctic-alpine, Sub-arctic and northern species, the Late-glacial period in Britain already had seen the establishment of many relatively thermophilous species, such for instance as now do not grow north of Denmark or southern Sweden. The Moss Lake identifications include a good number of confirmations and additions in both categories with *Gentiana campestris* (Zone II), *Lycopodium annotinum* (Zone I), *Elatine hexandra* (Zone III/IV transition), and cf. *Agropyron junceiforme* as the least familiar.

Zone IV is of especial interest in Moss Lake on account of the great diversity of aquatic and fen species that suddenly flourished there. Some of them, such as *Littorella uniflora*, *Pilularia globulifera*, *Isoetes echinospora* and *Elatine hexandra* are indicative of clear shallow water tending towards oligotrophy. Others such as *Bidens cernuus* and *Rorippa islandica* suggest shallow sandy margins flooded in winter, and there were certainly extensive fringing beds of *Eleocharis palustris*, *Carex rostrata* and *Equisetum*, besides a wealth of true aquatics. From the lake and its surroundings in this zone we have numerous confirmations of existing British records of thermophilous plants, but in addition the following are identified for the first time in Post-glacial time: *Linum anglicum*, *Bidens cernuus*, *Solanum nigrum*, *Polygonum* cf. *maritimum*, *Lotus* cf. *uliginosus* or *hispidus* and *Pilularia globulifera*.

From just above the Zone V/VI boundary come the fossil leaves of *Cotoneaster*, very possibly those of *C. integerrima*, and in Zone VII*a* the pollen of *Althaea officinalis*. These also are new to British published records.

We are familiar with the notion, now amply established by the fossil record, that many Arctic-alpine and northern species that were present in our lowlands in Late-glacial time have subsequently become restricted and disjunct in range. The evidence now given for thermophilous plants prevalent in the early Post-glacial suggests that possibly some of them also have suffered similarly. The evidence is still slight, but *Linum anglicum* and *Cotoneaster integerrima* are both plants of open habitat that would hardly withstand forest cover, and Liverpool is well outside their present British range. If the identification of *Polygonum maritimum* were certain that would furnish a similar example.

The tentative recognition of *Vicia sepium* appears to add a new historical record for another species of uncertain natural status to join those such as *Pastinaca sativa* and *Plantago major* and *P. lanceolata* already known from the Late-glacial.

It is worth noting that in the neighbourhood of Moss Lake, where Triassic sandstones are exposed, it seems likely that there was much blowing sand in Late-glacial time: a number of the plant identifications suggest the presence of dunes, for instance *Agropyron junceiforme*, *Polygonum maritimum*, and possibly *Armeria maritima*, and *Ephedra distachya*.

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References

Clapham, A. R. 1953 Human factors contributing to a change in our flora: the former ecological status of certain hedgerow species. *The changing flora of Britain* (ed. J. E. Lonsley). Arbroath: Botanical Society of the British Isles.

Clapham, A. R., Tutin, T. G. & Warburg, T. G. 1952 *Flora of the British Isles*. Cambridge University Press.

Cummins, W. A. 1956 New Quaternary sections in Liverpool. *Lpool Manch. Geol. J.* **1**, 502.

Erdtman, G. 1943 *An introduction to pollen analysis*. Waltham, Mass.: Chronica Botanica.

Erdtman, G. 1952 *Pollen morphology and plant taxonomy: Angiosperms*. Stockholm: Almquist and Wicksell, Waltham, Mass.: Chronica Botanica.

Godwin, H. 1955 Studies of the Post-glacial history of British vegetation. XIII. The Meare Pool region of the Somerset Levels. *Phil. Trans.* B, **239**, 161.

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

Hedberg, O. 1946 Pollen morphology in the genus *Polygonum* L. S. lat., and its taxonomical significance. *Svensk. bot. Tidsk.* **40**, 371.

Hegi, G. 1925 *Illustrierte Flora von Mittel-Europa*. München: Lehmanns.

Heslop-Harrison, Y. 1955 Biological Flora of the British Isles: Nymphaea. *J. Ecol.* **43**, 719.

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

Matthews, J. R. 1937 Geographical relationships of the British flora. *J. Ecol.* **25**, 1.

Salisbury, E. J. 1932 The East Anglian flora. *Trans. Norf. Norw. Nat. Soc.* **13**, 191.

Watts, W. A. 1958 Interglacial deposits at Kilbeg and Newtown, Co. Waterford. *Proc. R.I. Acad.* **60**, B 2.

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CORRIGENDUM

Philosophical Transactions of the Royal Society of London
Series B, No. 689, Vol. **242**, pp. 127–149. (1959)

Re-examination of the leaves referred in this paper to *Cotoneaster* sp., and of a wider range of herbarium material, indicates the strong probability that the correct identification is with *Vaccinium vitis-idaea* L., an attribution which would accord better with the local ecological conditions.

This re-identification affects pages 127, 131, 136, 138, 148; tables 1, 2; and figure 3.

H. Godwin

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FIGURES *a*, *b*, *d*, leaves of *Cotoneaster* sp. from the Zone V/VI transition at Moss Lake; *c*, leaf of living *C. integerrima*, which the fossils closely resemble; *e*, fossil leaf of *Salix* (cf. *S. cinerea*); *f*, fossil leaf of *Osmunda regalis* L.

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FIGURES *a* to *f*, fossil pollen of *Linum anglicum* Mill. seen at different focal depths: they show the ill-defined pores and the clear heteromorphy of the exine elements (magn. ×1130); *g*, *h*, *i*, fossil pollen of *Nymphaea alba* L. bearing exclusively gemmate processes (magn. ×1500); *k*, *l*, *m*, fossil pollen of *Vicia* cf. *sepium* L. (magn. ×1270); *j*, *n*, two fossil grains of *Althaea officinalis* L. (magn. ×640); *o*, fossil grain of *Circaea* sp. (magn. ×1000).