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Late-Glacial Deposits at Llyn Dwythwch and Nant Francon, Caernarvonshire

B. Seddon

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LATE-GLACIAL DEPOSITS AT LLYN DWYTHWCH AND NANT FFRANCON, CAERNARVONSHIRE

By B. SEDDON, Ph.D.*
University Subdepartment of Quaternary Research, Cambridge

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[Plate 23]

CONTENTS

The stratigraphy of sediments in two lake basins in the Caernarvonshire mountains at 600 and 900 ft. o.d. is described and it is shown that the basal layers were deposited in the Late-glacial Period. The deposits of a third site occupying a kettle-hole in morainic gravels at 1223 ft. o.d. are described and here the Late-glacial Period is not represented. The relation of these sites to the youngest corrie moraines of the district indicates that the latter were formed during the post-Allerød climatic regression (Zone III).

The vegetation history of the district was studied by means of pollen analysis of lacustrine deposits from the two first-mentioned sites (above). The vegetation of the Late-glacial Period at first formed tundra (Zone I) in which arctic-alpines, notably *Betula nana*, flourished together with species of oceanic and oceanic-northern distribution and calcicolous, eutrophic and moderately thermophilous plants. The spread of juniper scrub preceded the arrival of tree birches, which form 'park-tundra' in Zone II at Nant Ffrancon but failed to grow as high as Llyn Dwythwch. The birch 'park-tundra' is considered to have covered Britain south of the Forth–Clyde at low altitudes and to have occupied central and eastern Ireland at this time. The climatic deterioration of Zone III is clearly registered by the decline of juniper and tree birch and the local severity of conditions is demonstrated by the increased abundance of the chianophilous fern, *Cryptogramma crispa*, *Lycopodium selago*, *Saussurea alpina* and other montane herbs. The extensive occurrence of solifluxion, augmented by glacier streams, brought down silt and clay into the lakes. The ensuing amelioration in climate and the course of forest development through the Post-glacial Period is briefly traced and the persistence of certain elements of the present mountain flora from the Late-glacial Period demonstrated.

A description is given of the spores of *Cryptogramma crispa* which together with *Lycopodium annotinum* and *Saussurea alpina* are new to British Late-glacial records.

Introduction

At two lake sites in the mountains of Caernarvonshire borings through the lacustrine sediments revealed a basal stratification reminiscent of the north-west European Late-glacial sequence. One of the sites, Llyn Dwythwch, is a lake situated at 900 ft. o.d. in a

* Now at Department of Botany, National Museum of Wales, Cardiff.

large glacial cwm (cirque), two miles south-south-west of Llanberis and indicated on the map (figure 1). From the west side of the lake a broad tract of alluvium covered by *Sphagnum-Polytrichum* bog extends towards the head of the cwm. On the other sides of the lake there are boulder-strewn shores, that on the east side being the base of the massive terminal moraine which impounds the lake. A north-south line of borings across the alluvium demonstrated the existence at a depth of 1·0–1·5 m of a layer of stream-deposited gravel, which was penetrated to reach the underlying deposits only in those borings close to the present lake margin where the stratigraphy is as shown in figure 2.

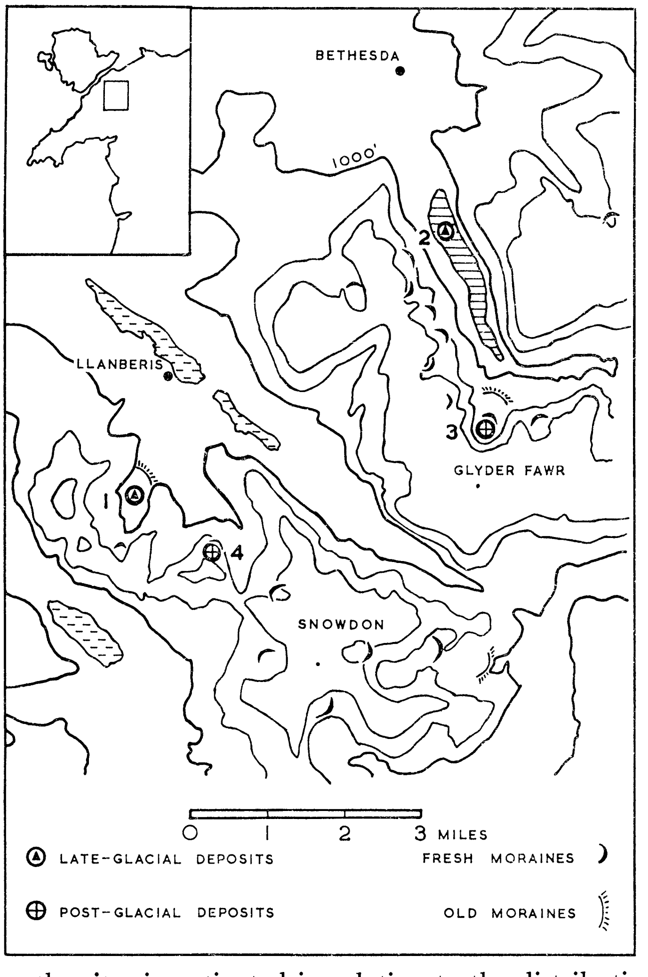

FIGURE 1. Map showing the sites investigated in relation to the distribution of cwm moraines on Snowdon and the Glyders. (1) Llyn Dwythwch, (2) Nant Ffrancon, (3) Cwm Idwal, (4) Cwm Cynghorion. The contours shown are at 1000 ft. (305 m), 1500 ft. (457 m), and 2000 ft. (610 m) O.D. Existing valley lakes are shown thus ⁻⁻⁻, and the former lake in Nant Ffrancon thus ═.

The other site, Nant Ffrancon, is a straight valley extending three and a half miles in a south-south-east direction from Bethesda. The floor of the valley is a glacially excavated basin which was formerly occupied by a lake approximately $2\frac{1}{2}$ miles in length and is now completely filled by lacustrine sediments. These are described by means of a series of borings sited across the former lake about $\frac{1}{2}$ mile from its northern end, where the surface level is at just over 600 ft. above sea level, and the resulting stratigraphy is shown in figure 3.

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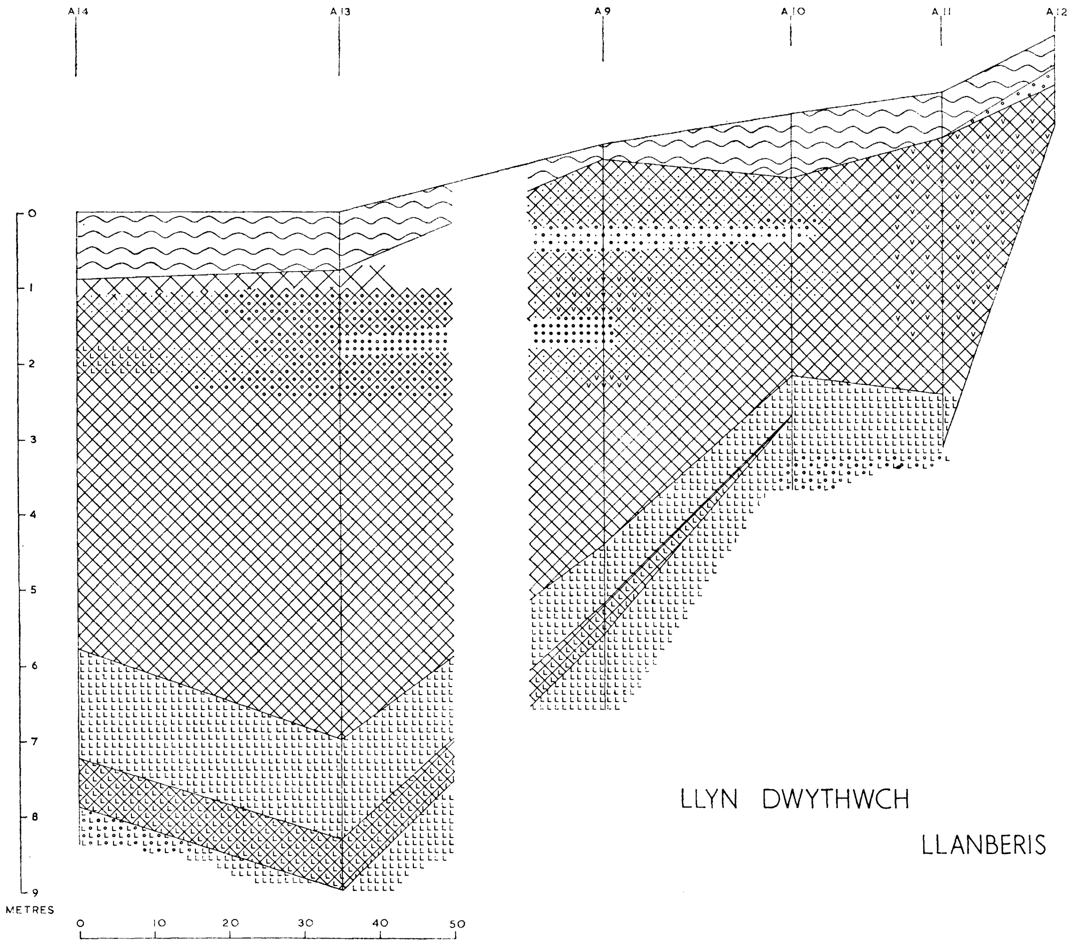

FIGURE 2. Stratigraphy of Llyn Dwythwch. The Allerød layer of clay-mud is intercalated between two layers of solifluced clay and above this are Post-glacial lacustrine sediments.

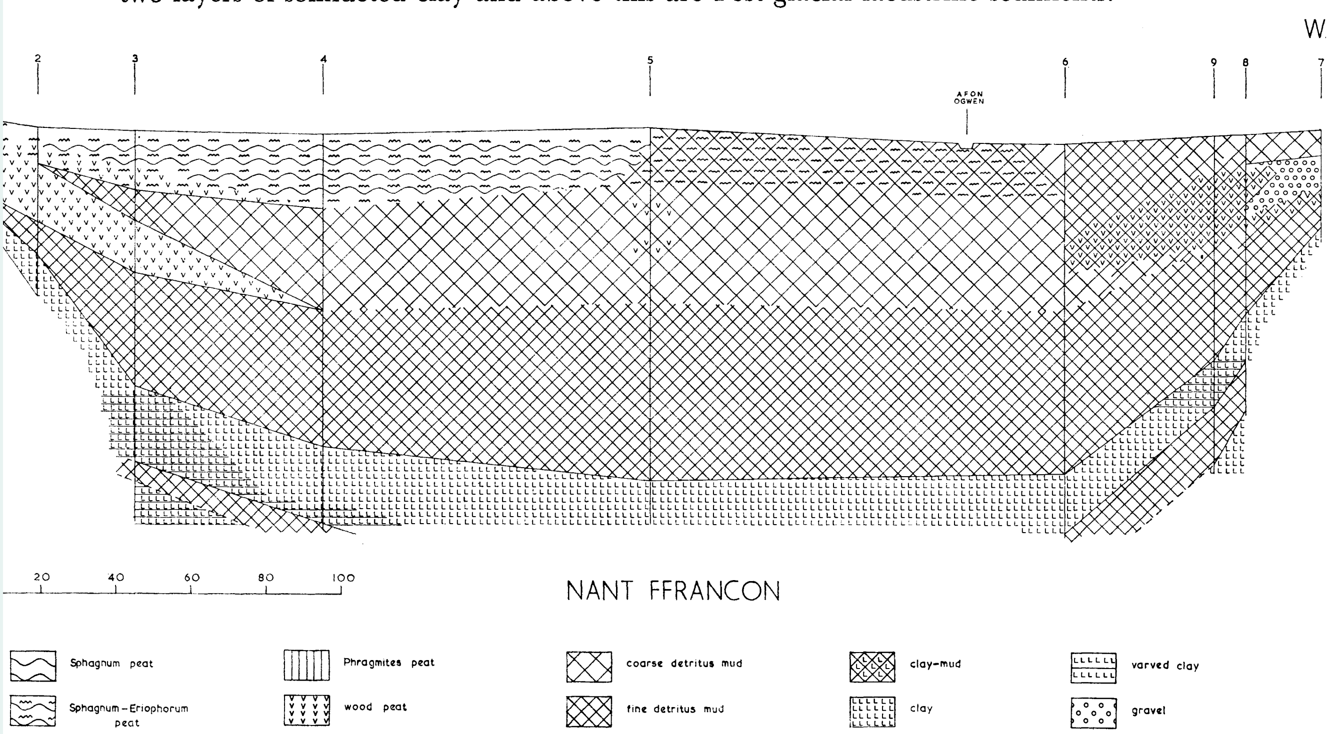

FIGURE 3. Stratigraphy of Nant Ffrancon. The former lake is now completely filled by organic sediments, at the base of which are Late-glacial deposits consisting of two clay layers and the intercalated Allerød layer of fine organic mud.

Stratigraphy

The deposits recorded at these two sites are closely comparable both in composition and in stratification and for the purpose of description will be treated together. The basal layer is of stiff blue clay representing material soliflucted from the surrounding slopes and deposited in the lakes by sedimentation. It is quite distinct at both sites from stream-carried material which forms deltas of coarse gravel. The basal clay was penetrated in only a few borings, in which it appeared to rest on coarse gravel. It was overlaid by clay-mud, grey or buff in colour and friable in texture. The presence of an organic component, for which the term mud is used here, indicates an amelioration in climate sufficient to permit algal growth in the lakes. This layer had a thickness of 80 cm in Llyn Dwythwch and 140 cm in Nant Ffrancon. A climatic retrogression next produced a return of solifluxion which deposited a second layer of clay up to 130 cm in thickness in the lakes. In borings numbers 3 and 9 at Nant Ffrancon the clay was laminated with thin dark bands of silt suggestive of seasonal sedimentation of material carried into the lake by glacier streams.

This tripartite sequence consisting of organic material sandwiched between two layers of soliflucted inorganic material is typical of Late-glacial sites in north-west Europe and reflects a climatic oscillation in which a phase of amelioration intervened between two periods of climatic severity. The milder Allerød phase, named after the type site in Zealand (Hartz & Milthers 1901), marks the warmest phase of the Gotiglacial Period (Gross 1954) during which the Scandinavian ice sheet retreated across southern Sweden. The temporary halt at the Fenno-scandian moraines coincides with the ensuing ('Upper Dryas') cold period (Donner 1951).

Above the upper clay layer there is a series of wholly organic deposits derived from successive phases in the development of aquatic vegetation. The greater part of the total thickness of Post-glacial deposits is a compact, structureless mud or gyttja composed almost entirely of algal material and formed under open water conditions. This was followed by fine detritus mud derived from the remains of species of *Potamogeton*, *Nuphar* and *Nymphaea* and then by coarse detritus mud formed from species of *Carex*, *Scirpus* and *Phragmites*. At Nant Ffrancon this was superseded by the development of *Sphagnum–Eriophorum* peat representing the formation of raised bog, which is also to some extent indicated in figure 3 by the contours of the surface although it has been affected by peat-cutting on the west side. Wedges of wood peat extend into the Nant Ffrancon lake deposits from both sides, showing that fen carr became established on the marginal mud at one stage in the hydrosere. The gravel wedge intercalated between layers of organic mud on the west side of Nant Ffrancon is part of the delta of a stream which descends from one of the cwms situated high on the mountainside above this point. The several layers of sand and gravel in the upper part of the Llyn Dwythwch sequence are presumed to have been deposited by the stream which flows across the alluvium and which must have changed its course frequently in the past.

The detailed stratigraphic descriptions of the cores from which pollen samples were taken at Llyn Dwythwch and Nant Ffrancon are as in table opposite.

The sequences described above may be contrasted with the series of deposits found in a kettle-hole in morainic gravel on the east shore of Llyn Idwal, a lake situated at 1223 ft. O.D. in a cwm at the head of Nant Ffrancon (figure 1). Here, there formerly existed a

Llyn Dwythwch, boring No. 14:

cm	
0– 90	water
90–110	coarse detritus mud
110–140	sandy detritus mud
140–175	fine brown detritus mud
175–180	grey clay-mud
180–185	green-grey clay
185–190	green-grey silty clay
190–207	grey clay-mud
207–210	grey clay
210–215	grey clay-mud
215–450	fine brown detritus mud with frequent fine rootlets
450–515	fine grey detritus mud
515–560	black silty mud with slate fragments at 540 cm
560–580	buff and grey layered silty mud
580–590	grey silty clay
590–710	fine grey clay
710–790	dark grey and buff clay-mud, with abundant moss stems at 725 cm and 785 cm
790–840	stiff blue clay, not penetrated.

Nant Ffrancon, boring No. 9:

cm	
0–100	brown coarse detritus mud
100–300	coarse detritus mud with occasional pieces and abundant small fragments of wood
300–396	fine detritus mud with seeds of *Nymphaea alba* and fruitstones of *Potamogeton natans*
396–408	very fine grey gyttja
408–600	very fine khaki gyttja
600–725	light blue-grey plastic clay with intermittent thin bands of slate fragments
725–870	grey and khaki gyttja
870	light grey tenacious clay, not penetrated

small pool in which the deposits represented in figure 4 were proved by means of a line of borings. The fine detritus mud contained fruitstones of *Potamogeton natans* and seeds of *Scirpus lacustris* and at the transition to coarse detritus mud the abundance of stems of *Phragmites communis* indicates that the water had become sufficiently shallow for reedswamp to spread completely across the pool. At this level too seeds of *Potentilla palustris* were common. The coarser mud above this was composed mainly of monocotyledonous leaf remains, probably of *Carex* species. Peat of *Sphagnum* and *Eriophorum angustifolium* covers the aquatic deposits and at the higher levels *Calluna* and *Polytrichum* enter into its composition. The notable feature of this sequence is the presence of only one clay layer which was penetrated in all borings and proved to rest directly on the gravel of the moraine. The same sequence was also proved to occur in the deposits impounded behind a fresh moraine in Cwm Cynghorion (figure 1). This basal layer of stiff grey silty clay represents a single period of solifluxion which clearly corresponds with the later of the two episodes described in Llyn Dwythwch and Nant Ffrancon as it is followed immediately by the Post-glacial series of organic deposits. The absence of the Late-glacial sediments from these sites in Cwm Idwal and Cwm Cynghorion is of great significance when their situation is considered in relation to the distribution of moraines (p. 479).

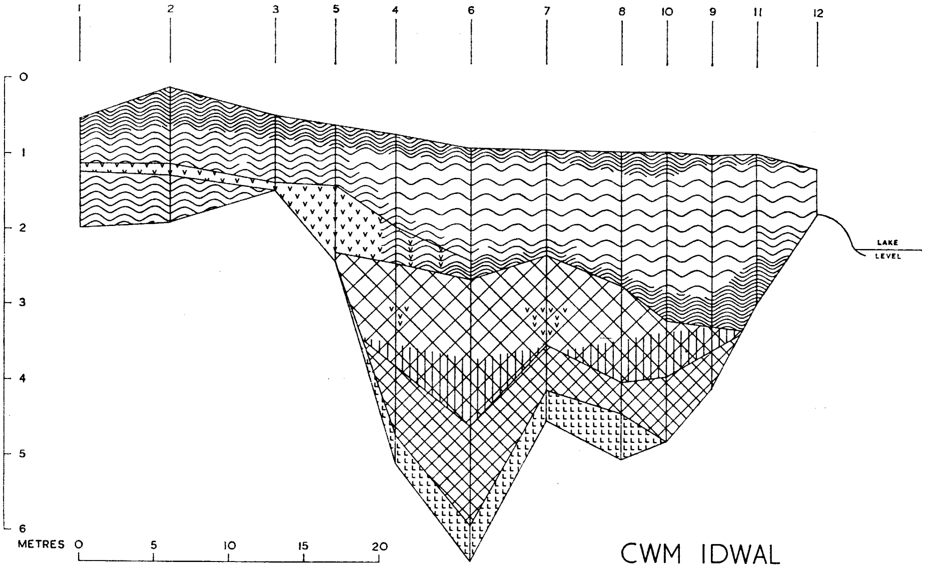

Figure 4. Stratigraphy of Cwm Idwal. The Post-glacial lacustrine muds and overlying bog peat occupy a trough between the gravel mounds of a fresh moraine. A single clay layer lines the basin.

Pollen analyses and macroscopic identifications

The results of pollen analyses are presented in two pollen diagrams for each site. Figures 5 and 6 show the pollen percentages of the genera of trees and shrubs throughout the Late- and Post-glacial Periods at Llyn Dwythwch and Nant Ffrancon respectively, together with a graph showing the ratio of the pollen of trees plus shrubs to that of herbs and dwarf shrubs, e.g. *Ericaceae*. This reflects the changing proportion of forest and unforested land respectively.The percentages for the individual graphs are calculated on the total tree pollen sum of 150 pollen grains except in the Late-glacial Period where owing to the low absolute frequency of tree pollen the total is generally between 50 and 100 and in Zone I even less. Figures 7 and 8 present the pollen record of individual familes, genera and species as percentages of the total pollen sum of all dry land plants excluding the spores of pteridophytes and, of course, the pollen of aquatics. These two diagrams cover the Late-glacial and the early Post-glacial Periods when the herbaceous flora was most extensive and varied. The pollen sum for every sample is usually between 350 and 500 but exceptionally totals outside this range are used.

The zones employed are those generally adopted in Britain (Godwin 1940, 1956) for the Post-glacial Period, Zones IV to VIII inclusive. The zone boundary III/IV is placed at the sharp lithological boundary between inorganic and organic sediments in accordance with Donner (1957). The Late-glacial Zones I to III are defined on the basis of the tree pollen curve as in Denmark (Iversen 1954), the boundary between Zones I and II being placed at the distinct rise, and that between Zones II and III at the marked decline in total tree pollen.

The number of plants identified from macroscopic remains is small, chiefly because the borings were sited to provide detailed pollen sequences and were therefore rather distant from the marginal lake deposits which are richer in seeds, fruits, leaves and other plant remains. Those records which have been made from such material are listed in table 2, which also gives complete zone records based on pollen identification.

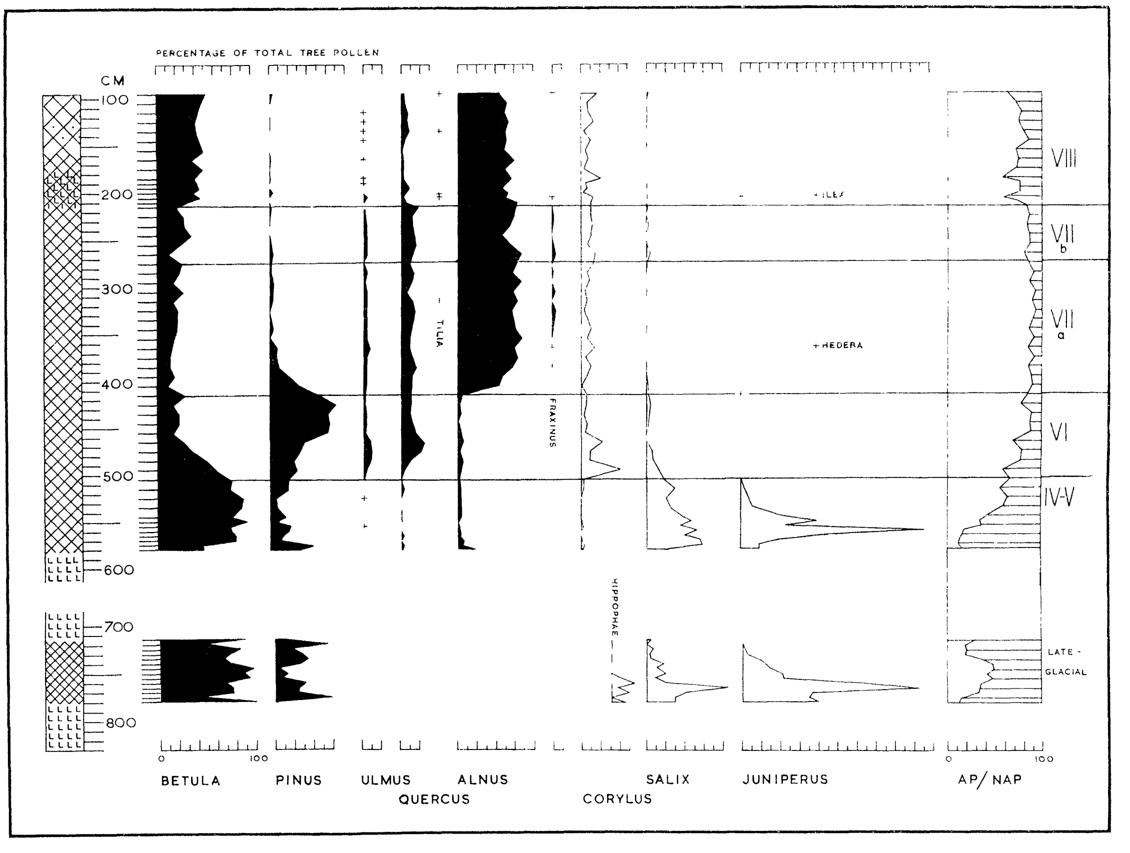

Figure 5. Llyn Dwythwch. Tree pollen diagram. The curves shown black comprise the total on which percentages are calculated. The ratio *AP/NAP* shows the changing proportions of arboreal pollen (representing forest) and non-arboreal pollen (representing other vegetation) through the Late- and Post-glacial Periods.

Vegetational history

The Late-glacial Period

The period represented by the deposit of clay-mud or gyttja intercalated between the two clay layers provides the first evidence of aquatic vegetation in the lakes. The presence of the algal genera *Pediastrum*, *Chara* and *Nitella* is demonstrated at both sites and at Nant Ffrancon macroscopic remains prove the occurrence of *Isoetes echinospora*, *Montia fontana* spp. *fontana*, *Potamogeton polygonifolius* and *Ranunculus repens*. Pollen records indicate *Littorella uniflora*, batrachian *Ranunculus* spp., *Sparganium* sp. and *Typha latifolia* as members of the aquatic flora with *Myriophyllum alterniflorum* present in addition at Nant Ffrancon.

The Late-glacial climatic oscillation is reflected very clearly by the course of the total tree pollen curve, which from consistently low values rises to a maximum and then declines. This is the basis of the subdivision into Zones I, II and III. The trees of the Late-glacial

Period were birch, pine and willow but altogether they formed only a small proportion of total vegetation cover. The low frequencies of *Quercus* and *Alnus* pollen are considered to be due to contamination in the Hiller borer as they do not occur in samples taken from open sections.

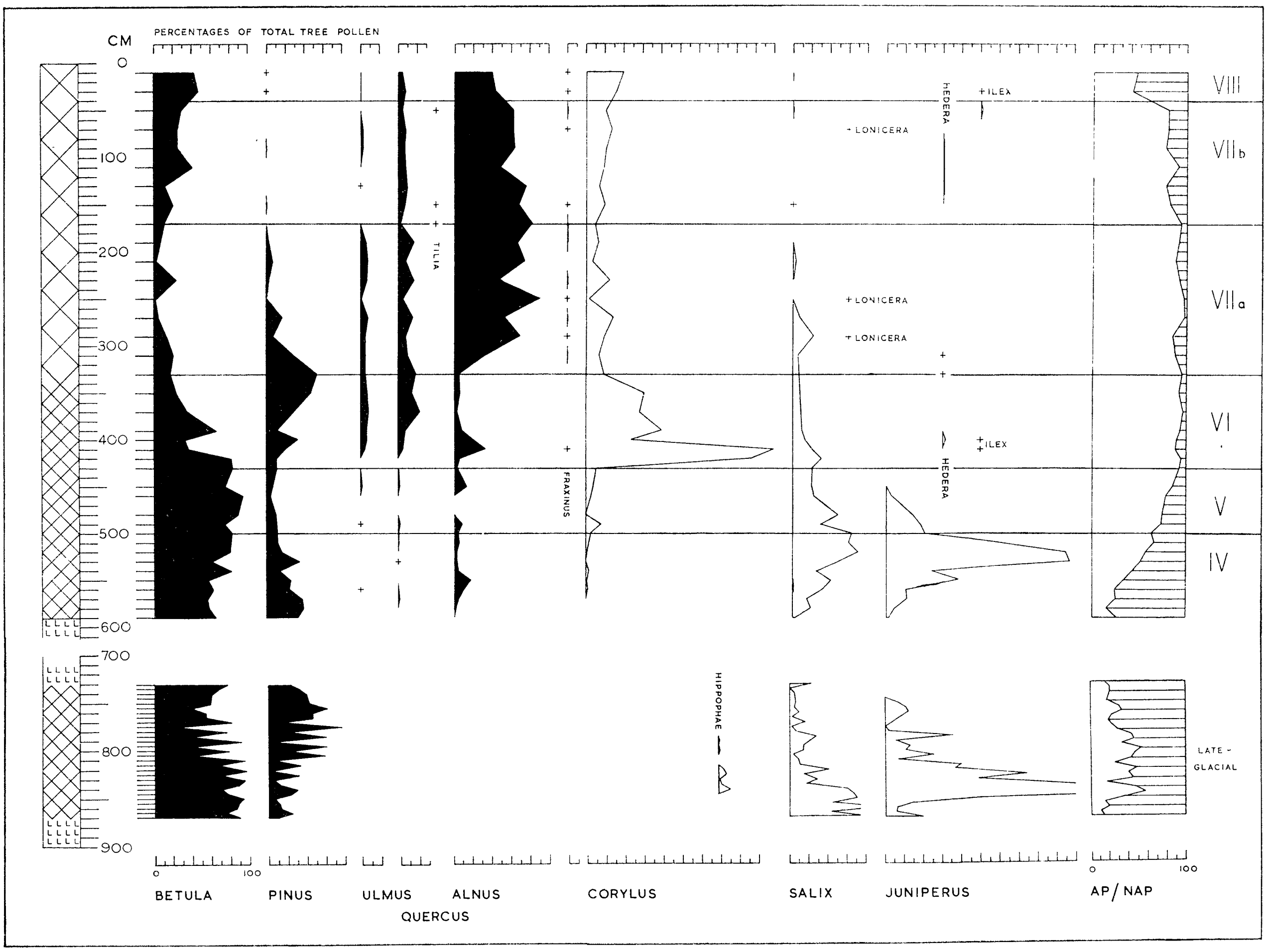

FIGURE 6. Nant Ffrancon. Tree pollen diagram. The curves shown black comprise the total on which percentages are calculated. The ratio *AP/NAP* shows the changing proportions of arboreal pollen (representing forest) and non-arboreal pollen (representing other vegetation) through the Late- and Post-glacial Periods.

The *Betula* pollen curve follows the same pattern at both sites, reaching a maximum (25 % at Llyn Dwythwch, 30 % at Nant Ffrancon) in the middle of Zone II and declining towards the end of the zone. Even at the maximum of the Late-glacial climatic amelioration birch can scarcely have formed continuous woodland but more probably occurred in groves in what has been termed 'park-tundra' by Iversen (Degerbøl & Iversen 1945). It is interesting to find that in Zone I the dwarf birch *Betula nana* contributed a high proportion of all birch pollen, especially at Llyn Dwythwch, as the figures in table 1 show.

The distinction between the pollen grains of the dwarf birch and that of the tree birches has been made by Walker (1955 *a*) on the basis of the ratio of grain diameter to depth of pore. The percentages given in table 1 are based on the separation of the birch pollen grains by the recognition of the same features subjectively, a method found useful by van der Hammen (1951). Thus grains of *Betula nana* are circular rather than triangular in optical section and have less protuberant pores than grains of the tree birches. The recovery of fruits of *Betula nana* and of *B. pubescens* from the same sediments at Nant Ffrancon substantiates the pollen records.

TABLE 1. PROPORTION OF *BETULA NANA* IN LATE-GLACIAL SAMPLES

	sample depth (cm)	zone	*B. nana* (%)	other *Betula* (%)
Llyn Dwythwch	715	III	11	89
	735	II	12	88
	770	I	66	33
Nant Ffrancon	755		32	68
	765	III	14	86
	775		21	79
	785		10	90
	795		18	82
	815	II	6	94
	825		7	93
	835		47	53
	845	I	21	79
	855		33	67
	865		25	75

The *Pinus* curve follows a pattern characteristic of Late-glacial sites in north-west Europe, that is it rises at a point about half-way through Zone II and maintains a significantly higher level through the latter part of that zone and through Zone III. The delayed arrival of pine indicated by this increase is generally ascribed to its slow rate of migration (Iversen 1954). It is not known whether pine was growing in north-west Wales as no macroscopic remains have been found and its pollen is susceptible to long-distance transport. In samples of the present-day pollen rain in Swedish Lapland van der Hammen (1951) recorded 15% *Pinus* pollen in a typical 'park landscape' pollen spectrum from a site 20 km distant from the nearest stands of the tree. He also found that from samples in treeless vegetation *Pinus* is dominant in the tree-pollen spectrum. In the light of these observations we may reasonably assume that pine was not present here in the Late-glacial Period and that in Zone III there was a return to an almost treeless landscape.

Having considered briefly the basic features of the Late-glacial Period as a whole it will be convenient now to examine the details of the flora of each of the three zones.

Zone I

This zone, the earliest phase of the Late-glacial Period, is characterized at both sites, as elsewhere in Britain, by the predominance of herbaceous vegetation and by the extremely low percentages of tree pollen. In only one sample does *Betula* pollen exceed 10%, of which *Betula nana* contributes a considerable portion as already noted. The small number of *Pinus* pollen grains is not regarded as an indication of local presence and may be attributed to long distance transport.

The large herbaceous element is composed mainly of Gramineae, Cyperaceae, Compositae, Caryophyllaceae, Chenopodiaceae and by the genera *Armeria*, *Artemisia*, *Empetrum*, *Epilobium*, *Filipendula*, *Helianthemum*, *Lycopodium*, *Plantago*, *Polemonium*, *Rumex*, *Thalictrum* and *Valeriana*. Godwin (1959) has remarked on the presence of the dwarf pteridophytes *Botrychium*, *Lycopodium*, *Ophioglossum* and *Selaginella* as indicators of the open character of the vegetation and to these may be added *Armeria maritima*, *Helianthemum* sp.; *Plantago maritima*, *P. media*, *Polemonium caeruleum*, *Poterium sanguisorba* and *Thalictrum* sp. Indeed, a preference for situations where rock weathering is rapid and where the soil nutrient supply is constantly replenished appears to be common to many plants of the Late-glacial flora.

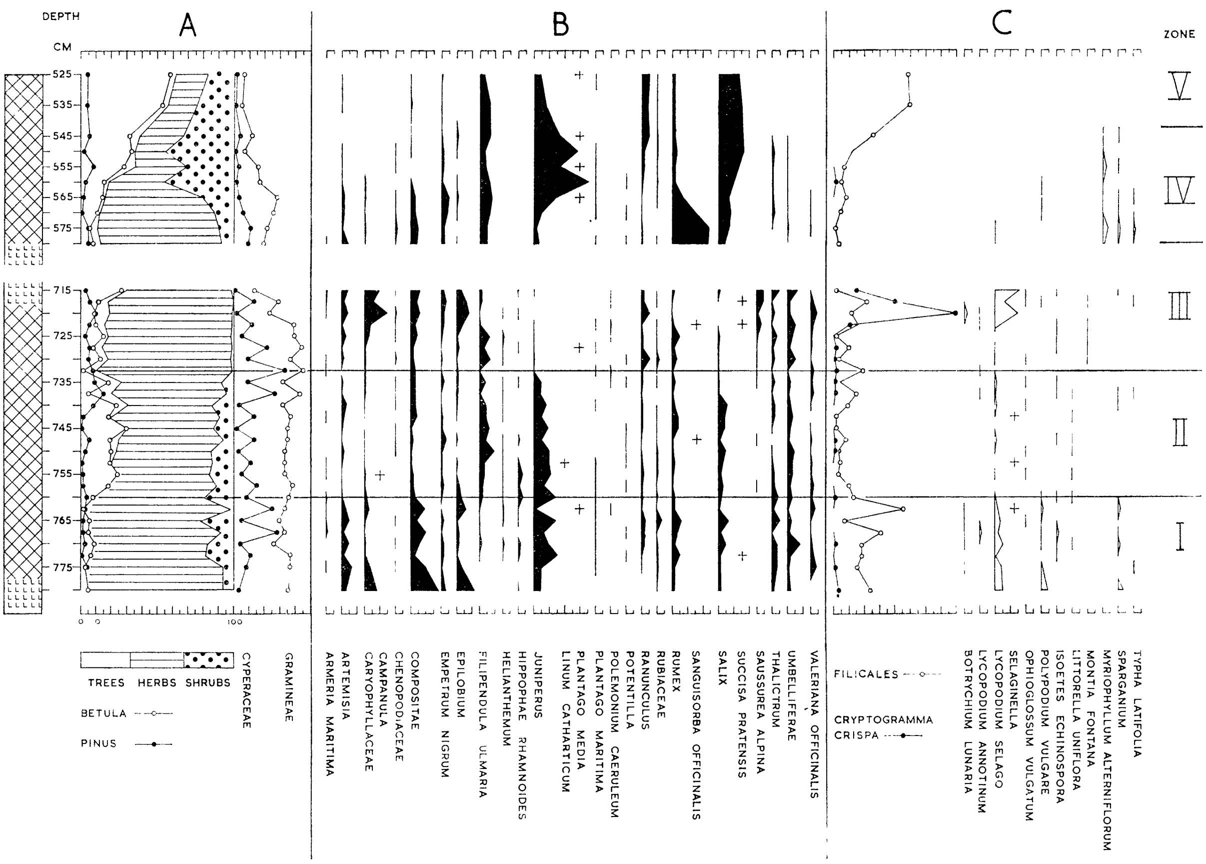

FIGURE 7. Llyn Dwythwch: total pollen diagram of the Late-glacial and early Post-glacial Periods. Section A shows proportions of tree, shrub and herb pollen and graphs of the main tree and herb constituents. Section B shows individual curves for all families, genera and species included in the pollen total. Section C shows individual curves for Pteridophyta and aquatics, which are not included in the total pollen sum.

A feature of particular interest is the behaviour of *Juniperus communis*, which is present from the beginning of the zone and increases to a maximum just before the transition to Zone II, i.e. before the increase in birch. *Hippophae rhamnoides* follows a parallel course and we may assume that the shrubs sea buckthorn, juniper and dwarf birch formed low scrub in an open sward of herbs (tundra).

Zone II

Tree birches now increase and the dwarf birch, while persisting throughout the zone, occupies a subordinate role. *Juniperus* and *Hippophae* are also consistently present but decline in abundance as tree birches become established. Thus there is a tendency towards

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the formation of birch woodland though it does not progress beyond the stage described as park-tundra.

The herbaceous vegetation remains substantially the same in composition as in the preceding zone, the most notable change being the first appearance and rapid increase in abundance of meadowsweet, *Filipendula ulmaria*. This is regarded by Iversen (1954) as an indication of a rise in temperature as *Filipendula* is a thermophilous plant in Scandinavia. Pollen of *Campanula* cf. *rotundifolia*, *Linum catharticum* and *Sanguisorba officinalis* was recorded

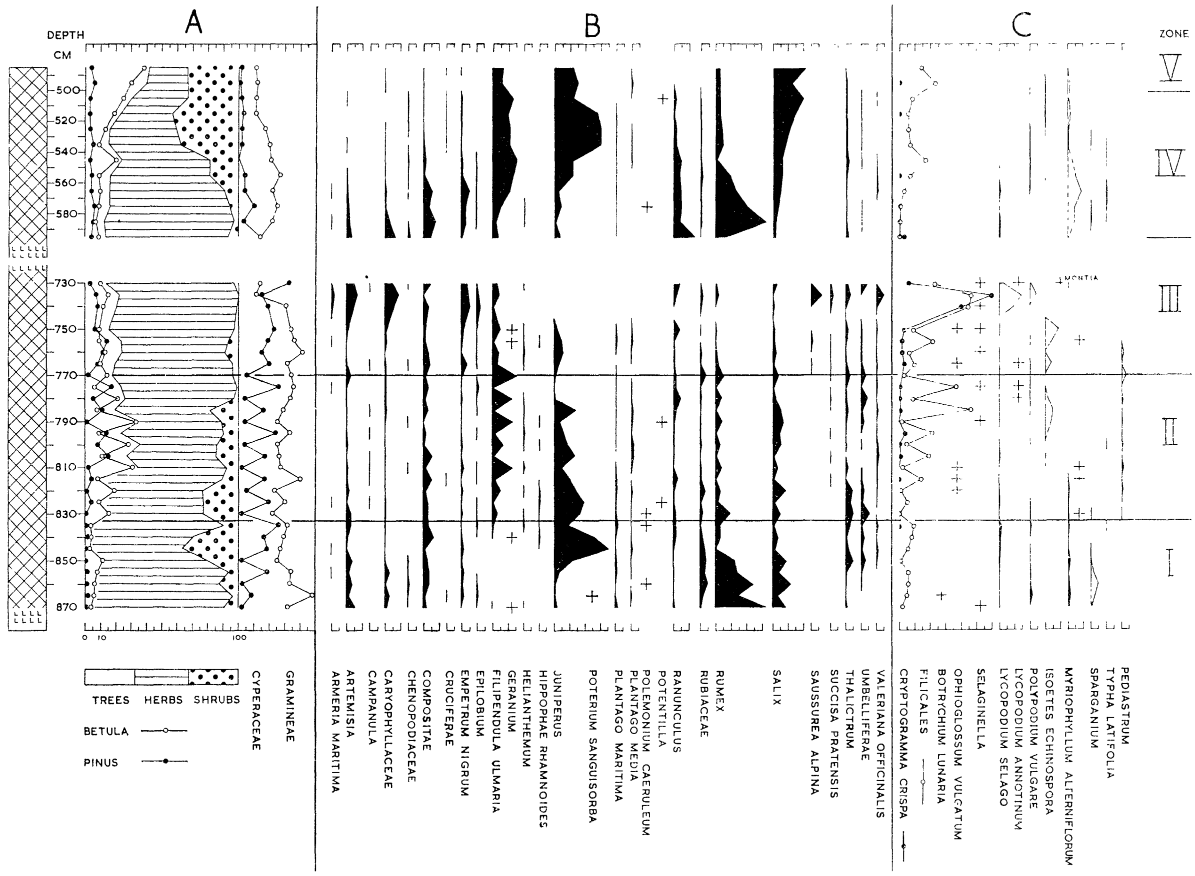

FIGURE 8. Nant Ffrancon: total pollen diagram of the Late-glacial and early Post-glacial Periods. Section A shows proportions of tree, shrub and herb pollen and graphs of the main tree and herb constituents. Section B shows individual curves for all families, genera and species included in the pollen total. Section C shows individual curves for Pteridophyta and aquatics, which are not included in the total pollen sum.

from this zone, the last two from Llyn Dwythwch only. The variety of herbs, many of which are exacting in terms of mineral requirements, remains unimpoverished: the apparent slight decrease in their representation through this zone is a statistical consequence of the increase in birch pollen. Amongst aquatic species there appears to be a real increase in the abundance of *Littorella uniflora*, which is thermophilous in comparison with *Sparganium* and *Myriophyllum alterniflorum*, the predominant aquatics in Zone I.

Zone III

The end of Zone III in both diagrams is an artificial one created by the spread into the lakes of the soliflucted clay which does not contain pollen in sufficient quantity to permit analysis. It should be distinguished from the natural end of the zone, i.e. the boundary with Zone IV, which is not represented here vegetationally owing to the locally severe effect of the climatic recession in producing soil creep and minor glaciation. The same phenomena were common to elevated sites in northern England, southern Scotland and Ireland, e.g. Lunds, Yorkshire (Walker 1955 *b*), Whitrig Bog, Berwickshire (Mitchell 1948) and Ballybetagh, Co. Dublin (Jessen & Farrington 1938), and in Scotland north of the Forth–Clyde were widespread even outside the mountain districts (Donner 1957).

A rapid decline of the *Betula* pollen curve and of the ratio of tree pollen to non-tree pollen marks the beginning of Zone III and is a positive indication of the onset of less favourable climatic conditions. The vegetation indicates a reversion to tundra, trees possibly surviving only in the most sheltered situations. Together with the decrease in birch there is also a real decrease in willow. The abundance of juniper is greatly diminished and towards the end of the zone its pollen is completely lacking. In Norway at the present day juniper is intolerant of long snow cover (Professor R. Nordhagen, personal communication) and this fact accords well with its disappearance immediately preceding the deposition of clay by solifluxion and glacial meltwater. At the same time there is a considerable expansion (equal to 60% at Nant Ffrancon and 80% at Llyn Dwythwch of the total of all other pollen) of the parsley fern, *Cryptogramma crispa*, and a smaller contemporaneous expansion of *Lycopodium selago*. The parsley fern is characteristic at the present day of late snow patch vegetation in Norway (Nordhagen, personal communication), and in Scotland (Ratcliffe, & McVean 1962). There is a corresponding increase in *Saussurea alpina*, a sub-alpine plant of north-facing screes of basic rocks in Snowdonia, as in the Central Alps.

The general composition of the flora closely resembles that of Zone I with even stronger representation of *Empetrum nigrum* (at Nant Ffrancon), *Epilobium* and Caryophyllaceae (including several grains of *Silene* type, (*a–c*, plate 23) cf. Jessen & Farrington 1938). The former abundance of *Rumex* (at Nant Ffrancon) does not recur. The consistently higher pollen frequencies of Caryophyllaceae, Compositae and *Epilobium* at Llyn Dwythwch suggests that in these categories we are dealing mainly with montane plants which unfortunately are not specifically identifiable by their pollen. Abundance of *Empetrum nigrum* in Zone III is a characteristic feature of sites in north-west Ireland (Jessen 1949) and to some extent in the Netherlands also (van der Hammen 1949) and points to oceanicity of climate. Its higher frequency at Nant Ffrancon of the two Caernarvonshire sites may indicate its greater prevalence on the lowlands where the tendency to prolonged snow cover would be counteracted by the ameliorating influence of the sea. Amongst the dwarf pteridophytes *Lycopodium annotinum* seems to have become more abundant in this zone than previously.

Zone IV *The Post-glacial Period*

At Llyn Dwythwch and at Nant Ffrancon this zone has several features in common with Zone I. This is accounted for by the fact that both zones are phases of vegetational recovery following periods in which climatic conditions were sufficiently severe to cause the formation of glaciers. At first birch values were as low as 10% and herbaceous elements were correspondingly abundant. However, the flora was not as varied in composition as it had been during the Late-glacial Period. *Rumex* pollen has very high percentages at both sites initially as it had at Nant Ffrancon in Zone I. *Artemisia*, *Armeria maritima*, *Plantago maritima*

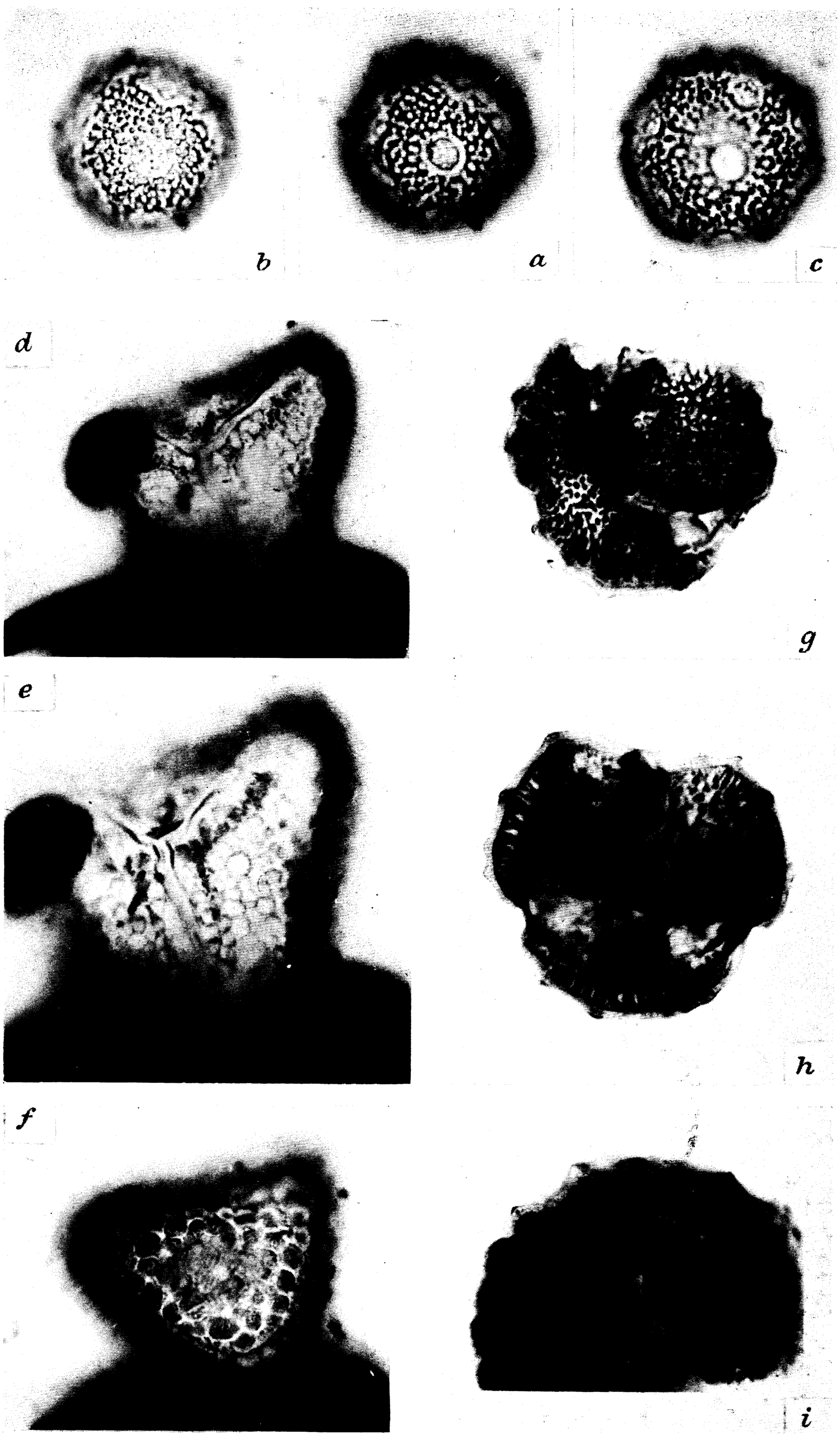

FIGURE 10. (*a*), (*b*), (*c*) Pollen grain of the genus *Silene* from Nant Ffrancon, 855 cm (Zone I) magn. × 1000: in (*a*) small bright points around margin of focused area are spinulae projecting from surface of outer wall, dark points within focused area are perforations in the outer wall, bright spots within focused area are columellae supporting the outer wall; in (*b*) at a lower level of focus below the outer wall or tectum only the columellae are visible.

(*d*), (*e*), (*f*) Spore of *Cryptogramma crispa* from Llyn Dwythwch, 720 cm (Zone III) magn. × 500: (*d*) and (*e*) show the tri-radiate scar, (*f*) shows reverse side of spore.

(*g*), (*h*), (*i*) Pollen grain of *Saussurea alpina* from Nant Ffrancon, 765 cm (Zone (III) magn. × 1000; (*g*) and (*h*) are in polar view showing the wall surface and optical section respectively; (*i*) shows equatorial view of one furrow.

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and the families Caryophyllaceae, Chenopodiaceae, Compositae, Cyperaceae and Gramineae reappeared with their former abundance but there are no pollen records of *Hippophae rhamnoides*, *Poterium sanguisorba* and *Saussurea alpina*. The latter survives at the present day in suitable localities in the Caernarvonshire mountains and hence the absence of pollen records cannot be taken to imply the disappearance of the plant though its retraction to refugia more distant from the sites sampled is probable. *Poterium sanguisorba* survived through Zone IV at Cwm Idwal (Godwin, 1955) and *Helianthemum* sp. and *Polemonium caeruleum* reappeared briefly at Nant Ffrancon. These three plants are no longer present in the mountains of Caernarvonshire and while *Helianthemum chamaecistus* and *Poterium sanguisorba* grow on limestone on the Menai Straits coast, the nearest natural locality for *Polemonium caeruleum* is on the Carboniferous limestone of Derbyshire (Pigott 1958).

Preceding the recovery of birch from the setback of Zone III juniper increased rapidly and to judge from its pollen frequency it achieved an even greater expansion now than in Zone I. Amongst the birch pollen the presence of some grains of *Betula nana* indicates its persistence from the Late-glacial Period. It is no longer extant in Wales and is now confined in the British Isles to the Scottish Highlands.

Zone V

During Zone V the total tree pollen increased from 63 to 93% of all pollen at Nant Ffrancon but reached only 66% at the end of the zone at Llyn Dwythwch, 300 ft. higher. Birch was the dominant tree and it gradually displaced juniper, which was able to survive only above the tree-line where it remains at the present day. This was a period of forest expansion in the mountains of North Wales although the lowlands of England and the Welsh Marches were already forested in Zone IV (Hardy 1939; Godwin 1956). Hazel had not yet reached Llyn Dwythwch and was only sparingly present at Nant Ffrancon and at Cwm Idwal (Godwin 1955). Amongst the herbs *Plantago maritima* and *Plantago media* remained present throughout this zone as through the preceding zones. The latter is not found in the county at all at the present day but *Plantago maritima* still survives as a relict at a few isolated stations in the mountains.

Zone VI

The arrival of the thermophilous trees, *Quercus* and *Ulmus*, and the rapid expansion of *Corylus* and of *Pinus* mark the establishment of the mixed oak forest, which suppressed the hitherto abundant *Betula* and *Salix*. The different development of forest at Llyn Dwythwch and Nant Ffrancon provides information on the variation of forest composition with altitude. *Quercus*, *Ulmus* and *Corylus* were more abundant at Nant Ffrancon where they were accompanied by *Ilex aquifolium* amd *Hedera helix*, two species which have well-defined ranges of temperature tolerance (Iversen 1954). At the higher site, Llyn Dwythwch, *Pinus* was much more conspicuous and perhaps was dominant at the upper limit of tree growth. The persistence of some elements of the Late-glacial flora is demonstrated by the presence of *Artemisia*, Chenopodiaceae, Compositae, *Empetrum nigrum*, *Filipendula ulmaria*, *Rumex* and *Succisa pratensis* at Llyn Dwythwch and in addition to these by *Epilobium*, *Plantago maritima* and *Thalictrum* at Nant Ffrancon. Notable additions to the flora at Nant Ffrancon are

Plantago lanceolata (one of its earliest British records), *Lythrum salicaria* and *Pilularia globulifera*, the latter previously recorded only from Moss Lake, Liverpool, amongst British Post-glacial sites (Godwin 1959).

Zone VII (a) and (b)

Throughout this zone the mixed deciduous forest was augmented by the presence of *Fraxinus excelsior*, sparse *Tilia cordata* and at Nant Ffrancon *Lonicera periclymenum*, the latter appearing also at Cwm Idwal (Godwin 1955). The pollen of *Alnus* exceeded that of every other species in quantity and the forest as a whole was more continuous during Zone VII (*a*) than at any other time in the Post-glacial Period. *Plantago lanceolata* maintained its presence at Nant Ffrancon while a single grain of *Plantago media* in Zone VII (*a*) at Llyn Dwythwch is the last record of this species in Caernarvonshire. Plants whose persistence is demonstrated through this period of maximum forest expansion include *Artemisia*, *Empetrum nigrum*, *Filipendula ulmaria*, *Potentilla*, *Ranunculus*, *Rumex*, *Succisa pratensis* and members of the families Caryophyllaceae, Chenopodiaceae, Rubiaceae and Umbelliferae.

Zone VIII

The decrease in the proportion of total tree pollen indicates a retrogression of forest, which permitted a resurgence of all those herbaceous elements which had survived the previous period of forest dominance either in the forest or above the tree-line. All the plants named as present through the preceding zones now appeared in greater abundance. In addition, pollen of *Thalictrum*, *Ophioglossum vulgatum*, *Cryptogramma crispa* and *Lycopodium selago* reappeared showing almost certainly that these plants of open communities had survived the forest optimum at higher altitudes.

Biogeographical implications of individual species

The Betula *curve*

The pollen curves for *Betula* demonstrate the Late-glacial climatic oscillation with a degree of clarity which can be accounted for only by the conclusion that north-west Wales occupied a critical position in relation to the distribution of birch during this period. Very similar evidence of the climatic oscillation has been described from Kentmere in north-west England (Walker 1955*a*), a site closely comparable in its situation and stratigraphy to Nant Ffrancon.

Caernarvonshire certainly lay within the range of tree birches, cf. fruits of *Betula pubescens* at Nant Ffrancon (see table 2), but the mountainous situation of the two sites made them extremely sensitive to fluctuations in the altitudinal limit of tree growth. The probability that the tree line in the Allerød Period lay near or between the altitudes of Llyn Dwythwch and Nant Ffrancon is suggested by the differences detectable in the percentage representation of birch at these two sites. The *Betula* maximum is on average at least 5 % higher at Nant Ffrancon than at Llyn Dwythwch and the Nant Ffrancon values closely approach the figure of 36 % *Betula* obtained at Gors Goch, 250 ft. above present sea level, in the lowland county of Anglesey. The failure of the *Betula* curve to exceed 20 % and the absence of the typical oscillation in the Scottish sites described by Donner (1957) led him to conclude that Scotland north of the Forth–Clyde line lay beyond the northern limit of tree birches. Late-glacial sites in Ireland might be expected to show trends more similar to those demonstrated in Caernarvonshire, and indeed birch pollen percentages at the optimum of Zone II in central and eastern Ireland are comparable (> 30 %) but at sites in the west values of 20 % indicate treeless tundra here also.

These indications of the variation in the importance of birch during Zone II over the British Isles are presented in the map (figure 9). Apparent discrepancies may be due to a number of factors, for example the altitudes of the various sites and the proportion of *Betula nana*, which is liable to be heavily over-represented (Iversen 1947). However, the general diminution of values both northward and westward is clearly shown.

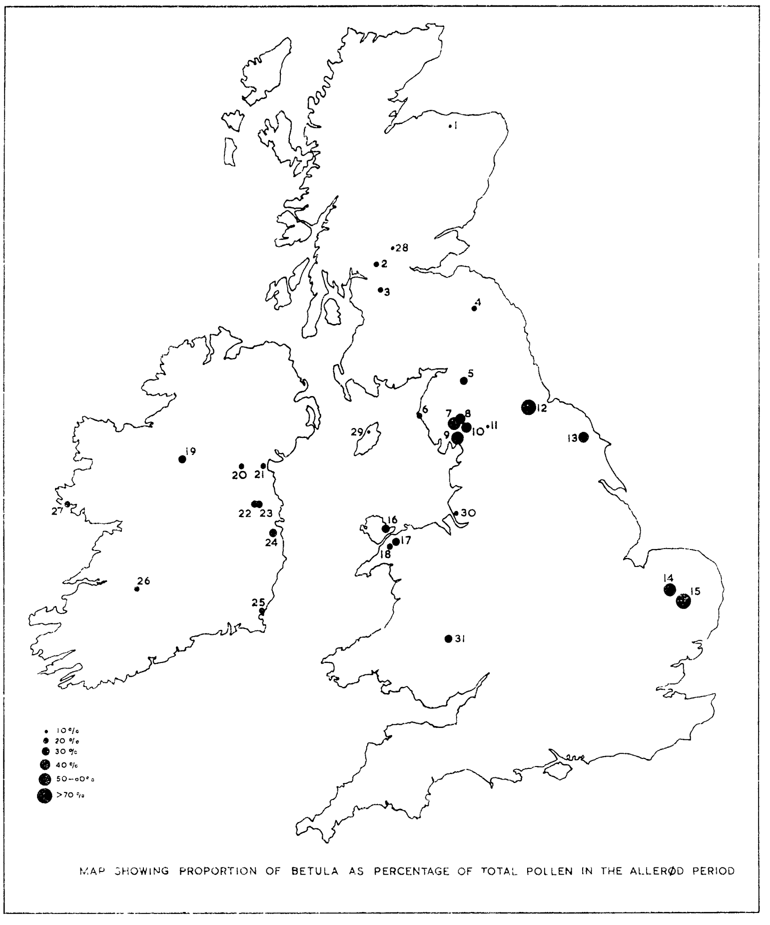

Figure 9. Map showing the distribution and importance of birch in Britain and Ireland during Zone II. The sites included are as follow: (1) Garral Hill (Donner 1957), (2) Drymen (Donner 1957), (3) Garscadden Mains (Donner 1957), (4) Whitrig Bog (Mitchell 1948), (5) Moorthwaite (Walker, unpublished), (6) St Bees (Walker 1956), (7) Kentmere (Walker 1955 *a*), (8) Windermere (Pennington 1947), (9) Helton Tarn (Smith 1958), (10) Skelsmergh Tarn (Walker 1955 *a*), (11) Lunds (Walker 1955 *b*), (12) Neasham (Blackburn 1952), (13) Seamer (Clark 1954), (14) Hockham Mere (Godwin & Tallantire 1951), (15) Lopham Fen (Tallantire 1953), (16) Gors Goch (Seddon, unpublished), (17) Nant Ffrancon, (18) Llyn Dwythwch, (19) Carrowreagh (Jessen 1949), (20) Ralaghan (Jessen & Farrington 1938), (21) Newtownbabe (Mitchell 1951), (22) Ratoath (Mitchell 1941), (23) Dunshaughlin (Mitchell 1940), (24) Ballybetagh (Jessen & Farrington 1938), (25) Kilmacoe (Mitchell 1951), (26) Kilteely (Jessen 1949), (27) Roundstone (Jessen 1949), (28) Loch Mahaick (Donner 1958), (29) Ballaugh (Mitchell 1958), (30) Liverpool (Godwin 1959), (31) Rhosgoch (Bartley 1960).

Cryptogramma crispa *(L.) Hook. & Bauer*

The spores of this fern are recorded for the first time in British Late- and Post-glacial deposits. However, the spores are quite distinctive, being bluntly triangular, 70 μ in diameter, with a boldly verrucate surface, the verrucae diminishing in size towards the margins of the triradiate scar on one side, as shown in the photographs (plate 23). *Cryptogramma* is found in late snow patch vegetation in Norway and in Scotland, as already noted on p. 470. In Wales at the present day it is locally common as a colonist of scree and boulder terrain, a habitat which it also occupies in Norway, the Swiss Alps and the Black Forest. In the Swiss Alps it is not common and does not ascend above the 'sub-alpine' zone of *Picea* forest.

Isoetes lacustris *L. and* I. echinospora *Dureau*

The microspores of *Isoetes* species are often encountered in large numbers in the sediments of oligotrophic lakes, e.g. up to 3000% of total tree pollen (Frey 1951). Specific determination of the microspores depends upon the different size range found in the two species. However, this character is liable to alteration by the chemical preparation of the sample and a degree of uncertainty is bound to result. The megaspores are clearly distinguishable by the form and pattern of the tubercles on the thick outer spore coat and where this is missing by the corresponding pattern on the thin inner wall. The zonal distribution of the two species given in table 2 is based entirely on megaspore identifications from which it appears that *Isoetes echinospora* was present in the Late-glacial zones and that it was joined by *I. lacustris* in Zones V, VI and VII (*a*), i.e. the period of the Post-glacial climatic optimum. This conclusion was also reached by Lang (1955) for lakes in the Vosges and the Black Forest. The only Late-glacial record of *I. lacustris* is from Ralaghan in Ireland (Jessen & Farrington 1938). Both species have an oceanic-northern distribution, but *I. echinospora* has a more western bias, reaching Iceland, while *I. lacustris* penetrates eastwards into White Russia (Diels & Samuelsson 1926).

Juniperus communis *L.*

It is only within recent years that pollen of *Juniperus* has been recognized (Godwin 1956) and consequently the full extent of its Late-glacial range in Britain is not yet known. There are records of its seeds, mainly from Zones II and III, from Hawk's Tor, Cornwall (Conolly, Godwin & Megaw 1950), Neasham, Co. Durham (Blackburn 1952) and from a number of sites in Counties Cavan, Dublin, Louth and Monaghan, indicating a wide distribution in Ireland. More recently *Juniperus* pollen has been recorded at Helton Tarn, Westmorland (Smith 1958), Malham Tarn Moss, W. R. Yorkshire (Pigott & Pigott 1959), Moss Lake, Liverpool (Godwin 1959), Scaleby Moss, Cumberland (Godwin, Walker & Willis 1957), and Whitrig Bog, Berwickshire (Godwin, unpublished). It is notable that Donner did not find *Juniperus* pollen in any of his Scottish sites except Loch Mahaick (Donner 1958) where, as at Llyn Dwythwch, it scarely exceeded 10% and did not exhibit a pronounced peak.

The plant does not extend above the 'sub-alpine' zone of *Picea* forest in the Alps, e.g. 2100 m in Wallis, and even there it occurs as a dwarf form. This is also characteristic of juniper in the sub-arctic belt of Scandinavia, where it grows under *Betula tortuosa*. In view of these facts it is suggested that where climatic amelioration permitted a sudden expansion

Table 2. List of plant records from Llyn Dwythwch and Nant Ffrancon

In the columns under the zone headings finds of plant remains at Llyn Dwythwch are indicated by the Letter *D*, and those at Nant Ffrancon by the letter *N*. The following abbreviations are used to denote the nature of the plant remains: *csc* = catkin scale, *fr* = fruit, *fst* = fruitstone, *msp* = microspore, *Msp* = megaspore, *n* = nut, *oosp* = oospore, *p* = pollen, *s* = seed, *sp* = spore.

plant	plant remains	zones I	II	III	IV	V	VI	VII*a*	VII*b*	VIII
Alnus sp.	*p*	...	...	...	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*
Armeria maritima (Mill.) Wild.	*p*	*D N*	*D N*	*D N*	*D N*	...	...	...	...	...
Artemisia sp.	*p*	*D N*	*D N*	*D N*	*D N*	*D N*	*D*	*D*	*N*	*D N*
Betula nana L.	*fr*		←— *N* —→		...	...	...	...	...	...
Betula pubescens Ehrh. or *verrucosa*	*fr, csc*		←— *N* —→		...	...	*N*	*D*	...	...
Calluna vulgaris (L.)Hull.	*p*	...	...	...	*D*	*D*	*D N*	*D N*	*D N*	*D N*
Caltha sp.	*p*	...	...	...	*N*	*N*	...	...	...	*N*
Campanula cf. *rotundifolia* L.	*p*	...	*D N*	*N*	...	...	...	...	...	...
Caryophyllaceae	*p*	*D N*	*D N*	*D N*	*D N*	*N*	*N*	*D N*	*N*	*D N*
Centaurea nigra L.	*p*	...	...	...	...	...	*N*	...	...	*N*
Chenopodiaceae	*p*	*D N*	*D N*	*D N*	*D N*	...	*D*	*D*	...	*N*
Compositae	*p*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*N*	*N*	*D N*
Corylus avellana L.	*n, p*	...	...	...	...	*N*	*D N*	*D N*	*D N*	*D N*
Cruciferae	*p*	*D N*	*D N*	*D*	*N*	...	...	...	...	...
Cyperaceae	*p*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*
Empetrum nigrum L.	*p*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D*	...	*D*
Epilobium sp.	*p*	*D N*	*D N*	*D N*	*D N*	...	*N*	...	...	...
Ericaceae (residual)	*p*	...	...	...	*N*	*N*	*N*	*N*	*N*	...
Filipendula ulmaria (L.) Maxim.	*p*	*N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*
Fraxinus excelsior L.	*p*	...	...	...	...	...	*N*	*D N*	*D N*	*D N*
Geranium sp.	*p*	*D N*	...	*D N*	...	...	...	...	...	...
Gramineae	*p*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*N*	*D N*	*D N*
Hedera helix L.	*p*	...	...	...	...	...	*N*	*D N*	*N*	...
Helianthemum sp.	*p*	*D N*	*D N*	*D N*	*N*	...	...	...	...	...
Hippophaë rhamnoides L.	*p*	*D N*	*D N*	*D N*	...	...	...	...	...	...
Ilex aquifolium L.	*p*	...	...	...	...	...	*N*	...	*N*	*D N*
Juncus effusus L.	*s*	...	...	...	...	...	*D N*	*D N*	*D N*	*N*
Juniperus communis L.	*p*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	...	...	...
Labiatae	*p*	...	...	...	*N*	...	...	...	...	...
Linum catharticum L.	*p*	...	*D*	...	...	...	...	...	...	...
Littorella uniflora (L.) Aschers	*p*	*D*	*D N*	*N*	*D N*	*N*	*N*	...	...	...
Lonicera periclymenum L.	*p*	...	...	...	...	...	...	*N*	*N*	...
Lythrum salicaria L.	*p*	...	...	...	...	...	*N*	...	...	...
Menyanthes trifoliata L.	*s*	...	...	...	...	...	*N*	*N*	...	...
Montia fontana L. ssp. *fontana* Walters	*p, s*	...	...	*D N*	...	...	...	...	...	...
Myriophyllum alterniflorum D.C.	*p*	*N*	*N*	*N*	*D N*	*D N*	*D N*	*D N*	*D*	...
Nuphar lutea (L.) Sm.	*p, s*	...	...	...	*D*	...	*N*	*N*	*D*	*D*
Nymphaea alba L.	*p, s*	...	...	...	*D*	...	*N*	...	...	*D*
Pinus sp.	*p*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*
Plantago coronopus L.	*p*	...	...	...	...	...	...	...	...	*N*
Plantago lanceolata L.	*p*	...	...	...	...	...	*N*	*N*	*N*	*D N*
Plantago maritima L.	*p*	*D N*	*D N*	*D N*	*D N*	*D N*	*N*	...	...	*D*
Plantago media L.	*p*	*D N*	*N*	*D N*	*D N*	*D N*	...	*D*	...	...
Polemonium caeruleum L.	*p*	*D N*	*D N*	*D*	*N*	...	...	...	...	...
Polygonum cf. *aviculare* L. *s.l.*	*p*	*N*	...	...	...	...	...	...	...	...
Polygonum cf. *bistorta* L.		...	*N*	...	...	...	...	...	...	...
Potamogeton natans L.	*fst*	...	...	...	*N*	...	*N*	*D*	...	...
Potamogeton sp.	*p*	...	...	...	*D N*	*N*	*D N*	*D*	*D*	*D*
Potamogeton polygonifolius Pourr.	*fst*		←— *N* —→		...	...	...	...	...	...
Potamogeton cf. *pusillus* L.	*fst*	...	...	...	...	...	*N*	...	...	...
Potentilla palustris Scop.	*fr, p*	...	...	...	*D N*	...	*N*	*N*	...	...
Potentilla sp.	*p*	...	...	...	...	*N*	*N*	*D N*	*N*	*D N*
Poterium sanguisorba L.	*p*	*N*	...	...	...	...	...	...	...	...
Quercus sp.	*p*	...	...	...	...	*N*	*D N*	*D N*	*D N*	*D N*
Ranunculus repens L.	*fr*		←— *N* —→		...	...	...	...	...	...
Ranunculus sp.	*p*	*D N*	*D N*	*D N*	*D N*	*N*	*N*	*D N*	*N*	*D N*

TABLE 2—*cont.*

plant	plant remains	zones: I	II	III	IV	V	VI	VII*a*	VII*b*	VIII
Rubiaceae	*p*	*D N*	*D N*	*D N*	*D N*	...	...	...	*D N*	*D N*
Rubus fruticosus L. *s.l.*	*fst*	...	...	...	...	...	...	*N*	...	...
Rumex acetosella L. type	*p*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*N*	*D N*
Salix sp.	*p*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*
Sanguisorba officinalis L.	*p*	...	*D*	*D*	...	...	...	...	...	...
Saussurea alpina (L.) DC.	*p*	...	*D*	*D N*	...	...	...	...	...	...
Scirpus lacustris L.	*n*	...	...	...	...	...	*N*	...	...	...
Sparganium sp.	*p*	*D N*	*D*	*D*	*D N*	*N*	...	*D*	...	*D*
Succisa pratensis Moench.	*p*	*D*	*N*	*D N*	...	*D*	*D N*	...	*D*	*D N*
Thalictrum sp.	*p*	*D N*	*D N*	*D N*	*D N*	*N*	*N*	...	...	*D*
Tilia cordata Mill.	*p*	...	...	...	...	...	...	*D*	*N*	*D*
Typha latifolia L.	*p*	*D*	*D*	*D*	*D N*	...	...	...	...	...
Ulmus sp.	*p*	...	...	...	...	*N*	*D N*	*D N*	*D N*	*D N*
Umbelliferae	*p*	*D N*	*D N*	*D N*	*D N*	...	*D N*	*D N*	*N*	*D N*
Valeriana officinalis L.	*p*	*D N*	*D N*	*D N*	*N*	*D*	...	...	...	...
Viola palustris L.	*s*	...	...	...	*D*	...	...	...	...	...
PTERIDOPHYTA										
Botrychium lunaria (L.) Sw.	*sp*	*D N*	...	*D*	...	...	...	...	...	...
Cryptogramma crispa (L.) Hook & Bauer	*sp*	*D*	*D N*	*D N*	*D N*	*N*	...	...	...	*D*
Equisetum sp.	*sp*	...	...	...	*N*	*N*	*N*	*N*	...	...
Filicales	*sp*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*
Isoetes echinospora Durieu	*Msp*	...	*N*	...	...	...	...	*D*	...	...
Isoetes lacustris L.	*Msp*	...	...	...	...	*N*	*N*	*D*	...	...
Isoetes sp.	*msp*	*D*	*D N*	*D N*	*D N*	*D N*	*D N*	*D*	*D*	*D N*
Lycopodium annotinum L.	*sp*	*D*	*D N*	*D N*	...	...	...	...	...	...
Lycopodium selago L.	*sp*	*D N*	*D N*	*D N*	*N*	*N*	*N*	...	*N*	*N*
Ophioglossum vulgatum L.	*sp*	*D*	*D N*	*D N*	...	...	...	...	...	*D*
Pilularia globulifera L.	*Msp*	...	...	...	...	...	*N*	...	...	...
Polypodium vulgare L.	*sp*	*D N*	*D N*	*N*	*N*	*D N*	*D N*	*D N*	*D N*	*D N*
Pteridium aquilinum (L.) Kuhn	*sp*	...	...	...	...	...	...	*N*	*N*	*N*
Selaginella selaginoides (L.) Link.	*sp*	*D N*	*D N*	*N*	...	...	...	...	...	...
BRYOPHYTA										
Sphagnum sp.	*sp*	*D*	*D*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*	*D N*
ALGAE										
Chara sp.	*oosp*	←——*D N*——→ (I–III)			...	*N*	*N*	*D*	...	...
Nitella sp.	*oosp*	←——*N*——→ (I–III)			...	...	...	...	...	...
Pediastrum sp.		←——*D N*——→ (I–III)			...	...	...	...	...	...

of juniper as indicated by a pronounced peak in its pollen curve then conditions must also have permitted the growth of tree species of *Betula*. The somewhat reduced juniper values of Zone II are due to the increased proportion of *Betula* pollen and do not necessarily imply a decline in the abundance of juniper. The decrease in Zone III, however, is a real one as it coincides with the decrease in the tree pollen frequency. Pollen diagrams from East Prussia, Tyrol and Denmark all show the decline of *Juniperus* in the middle of Zone III, i.e. the coldest part of it, and a sudden rise to its absolute maximum at the boundary of Zone III to Zone IV (Iversen 1954). This pattern is repeated at Llyn Dwythwch and at Nant Ffrancon but the recovery is delayed until Zone IV, probably because of the effects of altitude and oceanicity. The value of *Juniperus* as an indicator of the behaviour of birch is increased by the fact that its pollen, unlike that of *Betula*, is not carried far by the wind (Iversen 1947; van der Hammen 1951) and hence is a reliable index of its presence close to the site.

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Hippophaë rhamnoides *L.*

In Britain Late-glacial records of *Hippophaë* are relatively few and come from Kentmere and Skelsmergh, Westmorland (Walker 1955 *a*), Seamer and Flixton, Yorkshire (Godwin & Walker, in Clark (1954)), Windermere, Westmorland (Godwin & Willis 1959), Malham Tarn Moss, W. R. Yorkshire (Pigott & Pigott 1959), Aby Grange, Lincolnshire (Suggate & West 1959), Mapastown, Co. Louth (Mitchell 1953) and Garscadden Mains, Glasgow (Donner 1957). Although until recent years the pollen of *Hippophaë* was confused with that of *Helianthemum* the stellate hairs of leaves and stems of the former are quite distinctive and are often preserved. No macroscopic remains of this plant were recorded from Irish sites by Jessen (1949) and the more recent pollen record (Mitchell 1953), the first from Ireland, comes from near the east coast. Faegri (1943) warned against ignoring the possibility of long distance transport when endeavouring to explain finds of quite isolated *Hippophaë* pollen in sediments of a timberless epoch and this seems to be appropriate in the case of the Irish find. Of the Scottish sites examined by Donner (1957) only Garscadden Mains, near Glasgow, yielded pollen of *Hippophaë* and this site was very close to Late-glacial sea level and to the contemporary shoreline. It is perhaps premature to speculate on the former distribution of this species but the evidence so far available suggests that it was restricted to England, Wales and southern Scotland, its northernmost station being at sea level. At the present day *Hippophaë* has a disjunct distribution in Scandinavia, including both coastal and mountain habitats where trees are lacking. It is quite intolerant of shade and cannot grow under trees (Degerbøl & Iversen 1945). Even so, it fails to reach the tree line in the Alps and does not flower in the sub-alpine zone (Gams 1943). In northern Norway it reaches the tree line (600 m) but is sterile above 400 m (Nordhagen 1921). A partial explanation of its sterility at the higher altitudes is probably its intolerance of more than a thin and transient snow cover (chianophobous) (Gams 1943). Iversen (1954) characterizes it as a pioneer plant of unstable, fresh soil, deficient in humus and this accounts for its occurrence in the Late-glacial zones.

Saussurea alpina (*L.*) *D.C.*

The pollen grains of this arctic-alpine are described for the first time from a British Late-glacial site and have been recorded only from Zones II and III on Zealand (Iversen 1954) and from Zone III in the Tyrol (Zagwijn 1952). The photographs in plate 23 illustrate the tricolporate grain, which measures $44\,\mu$ in length and $39\cdot6\,\mu$ in equatorial diameter, and possesses a tectate wall composed of anastomosing columellae (seen in optical section in photograph *h*) which grade smaller towards the margin of the furrow, with shallow texturate echinae mounted upon it. At the present day in Scandanavia it occurs in the boreal conifer forest belt as well as above the tree line (Iversen 1954). In the central Alps, where it favours humic rendzina soils in grassland and also north-facing scree slopes on shales and serpentine, its altitudinal range is from 1600 to 3000 m (Braun-Blanquet 1935).

Conclusions

The Late-glacial flora of the Caernarvonshire mountains is shown to have included amongst those plants identified at specific level types whose present distributions are arctic-alpine (*Betula nana*, *Saussurea alpina*), oceanic northern (*Armeria maritima*, *Plantago* *maritima*, *Isoetes echinospora*), and sub-arctic and sub-alpine (*Juniperus communis*, *Cryptogramma crispa*, *Lycopodium annotinum*, *L. selago*, *Ophioglossum vulgatum*, *Polemonium caeruleum*). The oceanic element is emphasized by the presence of *Empetrum nigrum*, *Littorella uniflora*, *Myriophyllum alterniflorum*, and *Polypodium vulgare*, while moderately thermophilous plants include *Poterium sanguisorba*, *Typha latifolia* and *Valeriana officinalis*.

The existence of parallel vegetation changes extending to considerable detail at two closely comparable sites greatly reinforces the validity of the general conclusions that can be drawn. Differences detected in the behaviour of certain species at the two sites fall into a pattern which is consistent with their different altitudinal position. For example, all the arctic-alpine and sub-arctic species listed above are represented with higher pollen frequencies at Llyn Dwythwch and the relatively thermophilous *Filipendula ulmaria* is more strongly represented at Nant Ffrancon. The higher percentages of *Betula* at Nant Ffrancon, which closely approach those recorded in lowland Anglesey, and the recovery of fruits of *B. pubescens* from the Allerød layer there indicate the presence around that site of tree birches forming 'park-tundra' in Zone II. It is suggested that the rather low percentages of *Betula* at Llyn Dwythwch do not necessarily indicate its growth at that altitude but may reflect over a small distance the vegetation of the Llanberis valley. The absence at Llyn Dwythwch of a pronounced peak in the *Juniperus* curve supports this view. The phenomenon of juniper preceding the expansion of birch recurs in Zone IV. This time a pronounced peak does occur in the *Juniperus* curve at Llyn Dwythwch showing that the Post-glacial climatic amelioration had already exceeded that of the Allerød oscillation and that birch forest was able to grow up to the altitude of this site at least. Observations on the Late-glacial distribution of *Betula* and *Juniperus* in Britain and Ireland are in accord with this local altitudinal differentiation between 'park-tundra' and treeless vegetation.

The changing proportion of *Betula nana* through the Late-glacial Period, reflecting in inverse relation to the tree birch the Allerød climatic oscillation, is demonstrated for the first time in Britain although it has already been detected by Schütrumpf in Holstein (Godwin 1956, p. 192).

The low intensity of competition indicated by the abundance of dwarf pteridophytes was probably a factor of importance for the calcicolous species *Plantago media*, *Polemonium caeruleum*, *Poterium sanguisorba* and *Helianthemum* sp. which are no longer present in the Caernarvonshire mountains. The production of fresh soils by the comminution of parent rock by the passage of ice and by frost action in the period immediately following the retreat of the Welsh ice undoubtedly provided a suitable habitat for these plants. The subjection of soil parent material formed at this time to leaching throughout the Post-glacial Period and the slow rate of weathering of the local Ordovician and Cambrian strata which has been inadequate for the replenishment of essential minerals has led to the extinction locally of some exacting species and to the restriction of others to outcrops of basic volcanic rocks of the Bedded Pyroclastic Series (Williams 1930). The disappearance of the more eutrophic elements of the aquatic flora, such as *Typha latifolia*, from the mountain lakes is attributable to the same cause. Additional hazards to the survival of Late-glacial plants during the Post-glacial Period were the encroachment of forest and ombrogenous peat formation. However, almost continuous zone by zone records are presented for *Empetrum nigrum*, *Filipendula ulmaria*, *Succisa pratensis* and for the genera

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Artemisia, *Potentilla*, *Ranunculus* and *Rumex* throughout the Late- and Post-glacial Periods. Slightly less complete, but nevertheless convincing, records are given for the persistence of *Ophioglossum vulgatum*, *Lycopodium selago*, *Cryptogramma crispa* and *Thalictrum*. *Cryptogramma crispa*, *Lycopodium annotinum* and *Saussurea alpina* are new British Late-glacial records.

The large increases in the representation of *Cryptogramma crispa*, *Lycopodium selago* and *Saussurea alpina* at the end of Zone III reflect floristic changes that illustrate in a remarkable way the incidence of environmental factors, namely late snow lie and possibly intensified frost action.

The distribution of Late-glacial sites in relation to moraines

An account of the distribution of cwm (corrie) moraines in Caernarvonshire has been given (Seddon 1957) in which, with few exceptions, the moraines listed are very fresh in appearance. They have steep slopes and are crescentic in form, either simple or composed of confluent mounds with intervening troughs. The terminal moraines which impound Llyn Dwythwch and Llyn Idwal are massive and subdued in form and are clearly of earlier origin.

The deposits described from Cwm Idwal are situated in a trough between the mounds of a fresh moraine which constricts the lake at a point about one-third of its length from the back of the cwm. The similar deposits in Cwm Cynghorion are situated in a small basin behind a simple crescentic moraine. The Nant Ffrancon lake site lies outside the young moraines which are found in the corries on its west side. Llyn Dwythwch occupies the floor of a large cwm which has four subsidiary cwms at higher levels in the mountainsides containing it. Fresh moraines occur in two of these subsidiary cwms and hence the deposits in the lake, like those at Nant Ffrancon, lay outside the limit of the late cwm glaciation.

The stratigraphy of the sites examined shows that only Post-glacial deposits occur inside the fresh moraines and that outside them Late-glacial deposits are found. The two Late-glacial sites described are lakes which by reason of their situation received meltwater from the glaciers which deposited the fresh moraines. The upper clay layer of the Late-glacial sequence, here attaining great thickness and exhibiting crude lamination, therefore appears to be contemporary with the formation of these moraines. The last cwm glaciation of the district is thus referred to Zone III of the pollen-analytical sequence, the post-Allerød climatic retrogression.

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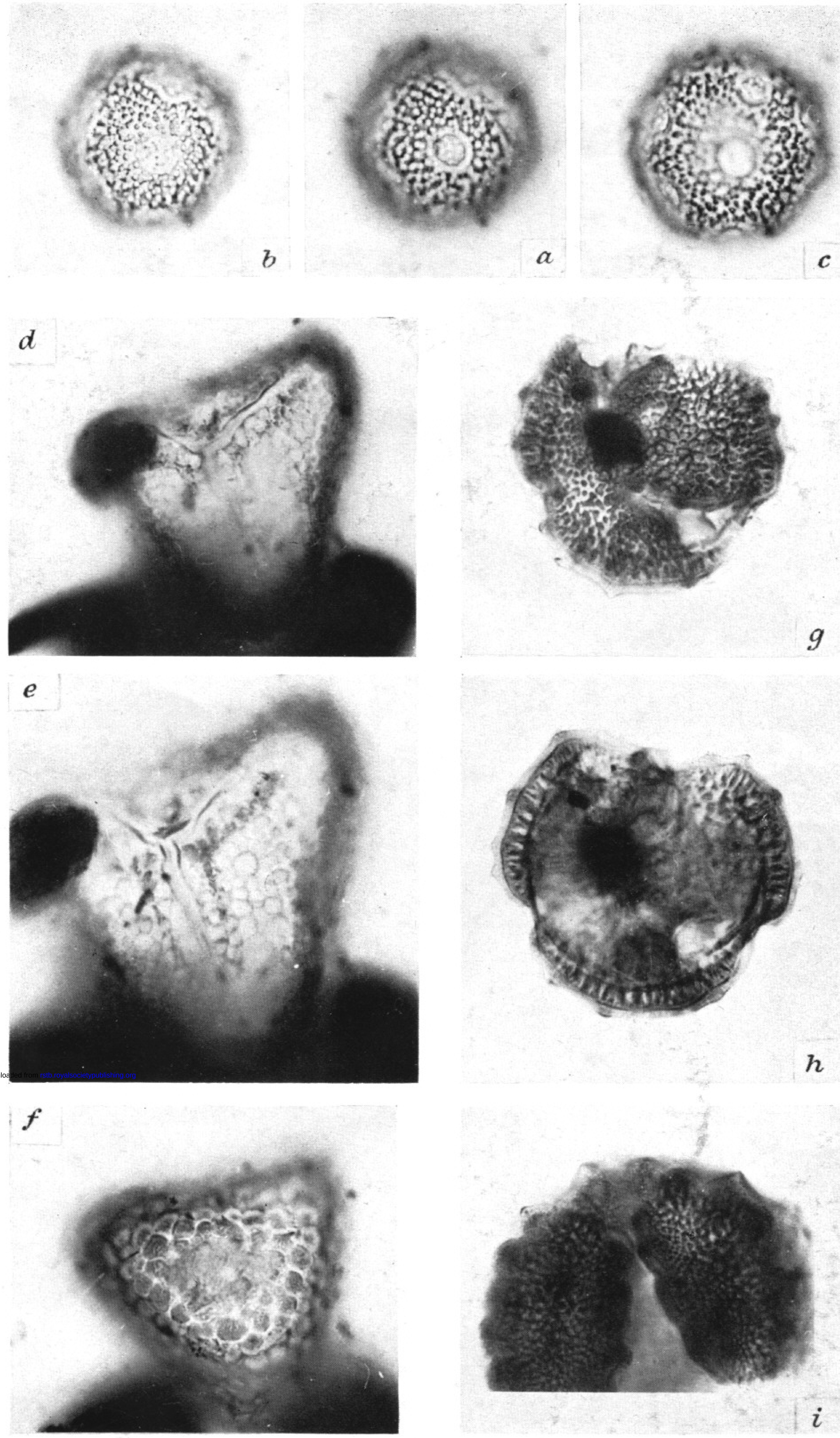

FIGURE 10. (*a*), (*b*), (*c*) Pollen grain of the genus *Silene* from Nant Ffrancon, 855 cm (Zone I) magn. × 1000: in (*a*) small bright points around margin of focused area are spinulae projecting from surface of outer wall, dark points within focused area are perforations in the outer wall, bright spots within focused area are columellae supporting the outer wall; in (*b*) at a lower level of focus below the outer wall or tectum only the columellae are visible.

(*d*), (*e*), (*f*) Spore of *Cryptogramma crispa* from Llyn Dwythwch, 720 cm (Zone III) magn. × 500: (*d*) and (*e*) show the tri-radiate scar, (*f*) shows reverse side of spore.

(*g*), (*h*), (*i*) Pollen grain of *Saussurea alpina* from Nant Ffrancon, 765 cm (Zone (III) magn. × 1000; (*g*) and (*h*) are in polar view showing the wall surface and optical section respectively; (*i*) shows equatorial view of one furrow.