

THE FLORA OF IRELAND IN ITS EUROPEAN CONTEXT

Journal of Life Sciences, Royal Dublin Society vol. (1983), 143-160.

The Boyle Medal Discourse, 1982

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Abstract

The Irish flora is reviewed in relation to its European distribution. If Pteridophytes, doubtfully native species (including most weeds), apomicts and other critical taxa of uncertain distribution are excluded, the flora amounts to 815 species as against 1172 for Britain. The traditional explanation for this discrepancy (the earlier isolation of Ireland in post-glacial times) is seen to be only partly true; one half of the British species absent from Ireland can be regarded as being excluded by ecological factors. Although many Irish species have a wide distribution outside Ireland, less than half can be regarded as pan-European. 73 Irish species have a more or less Atlantic or Mediterranean-Atlantic distribution; these terms are defined more closely than has been customary and the list of species revised accordingly. The arctic-alpine group is also discussed critically, and seen to contain only 16 species. The 15 Irish species not found in Britain are considered in detail; maps illustrate their unusually large disjunction from their nearest stations on the continent. It is concluded that for most of them the supposition that they survived the last glaciation in Ireland or on land now submerged off its west coast is less unlikely than any alternative explanation.

Most of my working life as a botanist has been devoted either to the study of the flora and vegetation of Ireland or to the writing and editing of *Flora Europaea*. It seems appropriate, therefore, that I should attempt in this lecture to bring the two themes into a closer relationship than is usually accorded to them.

If a botanist from Copenhagen, Hamburg, Brussels or Rouen were to be dropped by helicopter into a Tipperary meadow or on a lake-shore in County Leitrim he would at first find little in the scene that was unfamiliar. All the plants he saw, with perhaps one or two exceptions, would be well known to him, and he would soon deduce that at any rate he was still in northwest Europe. But after a little while he would begin to wonder why this or that species to which he was accustomed in similar habitats at home was apparently absent; and he would soon conclude that the flora of Ireland, though characteristic of northwest Europe, constitutes an impoverished sample of it. We must start, therefore, by asking: how poor, and why?

To answer the first question it is best to enumerate all the plants which are found wild in Ireland, and to compare the list with the corresponding lists from other comparable areas. Under the designation 'wild' I include both natives and naturalised aliens. But to answer the second question properly a distinction must be drawn between the two categories. Richness or poverty in established aliens depends mainly on factors very different from those which determine richness or poverty in natives. For the aliens climate and soil are of some importance, but count for much less than do the accidents of human history - the popularity of gardening, the methods of agriculture and the pattern of international trade. Natives, it is true, may also be dependent on historical as well as ecological factors, but these are mainly the history of ice-sheets, sea-levels

and climatic change. Only in the few instances of recent extinctions from building, drainage, atmospheric pollution or over-collecting does human history play a part.

Naturalised aliens are in some cases important ingredients of the flora: one has only to recall the names of *Rhododendron ponticum* and *Elodea canadensis*. But as in this lecture I am concerned mainly with native species I shall say no more about aliens, except to note that in Ireland, as far as I can judge, their number in relation to native species stands slightly above the European average, though not as high as in Britain, where the coincidence of a love of gardening, a large volume of cosmopolitan trade and a reasonably hospitable climate has allowed an exceptionally large number of foreign species to establish themselves. Unfortunately, it is not as easy as one would wish to distinguish between natives and old-established aliens, particularly among those species which have a tendency to behave as weeds. If a plant grows mainly as a weed of cultivated crops or gardens, but is occasionally seen on river-gravels, sand-dunes or rocky outcrops, is one to conclude that it has spread from the first habitat to the second or vice versa? There is no simple rule; one must weigh up all the available evidence and do one's best, I am convinced, however, that in most of the Floras of the British Isles the number of native species is seriously overstated, partly, I am afraid, on account of a curious form of local patriotism which makes otherwise dispassionate scientists claim for their county or their country as many natives as possible, I may not be entirely free from this failing myself, but in compiling the figures set out below I have tried to discipline myself severely, and have perhaps erred in the other direction, as I have excluded from my lists, whether for Britain or for Ireland, any species about whose native status any serious doubts have been expressed, and all weeds of cultivated ground unless they are reasonably common in other habitats. I have also excluded species believed with fair certainty to be extinct, apomictic microspecies in *Rubus*, *Hieracum*, *Taraxacum*, *Sorbus*, and *Alchemilla*, and a few other critical species of which the delimitation and distribu-

tion are still subject to uncertainty. Finally, I have limited my scope to seed-plants, for the minute spores of Pteridophytes mean that they are governed by very different laws of dispersal than are seed-plants. My figures, therefore, will be considerably smaller than those usually cited for the flora of Ireland, but they form, I hope, a sound basis for comparison. I reckon that, making allowance for the exclusions just mentioned, there are 1190 species native to the British Isles. Of these 375 are found only in Britain, 18 only in Ireland, while 797 are common to both islands. Comparison with other countries on the same basis is not easy, as their national Floras diverge somewhat in their taxonomic concepts and the status of doubtfully native species is harder to assess. But estimates governed by the criteria set out above, which are not, I believe, likely to be seriously inaccurate, yield the following figures:

France	3500
Britain	1172
Belgium	1140
Denmark	1030
Ireland	815

The poverty of the Irish flora is at once apparent, especially if it is realised that the ecological diversity of Ireland is rather greater than that of Belgium and much greater than that of Denmark. But this is even truer of Britain, and the fact that, despite its

Scottish Highlands and its Cornish coast, its native flora only slightly exceeds that of the very much smaller Belgium suggests that some at least of the factors which impoverish the Irish flora impoverish also the British.

The familiar explanation is, of course, insularity. We know that in late-glacial and early post-glacial times the sea-level was low enough for Ireland to have a land connection with Britain and Britain with the Low Countries and northern France. Eventually the rising sea-level severed Ireland from Britain and, some time later, Britain from the Continent. From this it is concluded that of the temperate vegetation which the glacial period had driven to southern latitudes only the advance guard was able to reach Ireland; a later wave got to Britain, but the repopulation of the northern part of the continent continued for some centuries more, stocking it with plants which could have found a niche somewhere in Britain or Ireland had they not been cut off by the sea.

That this is true of the British Isles as a whole is indisputable. But that it constitutes the principal explanation of the difference between the British and the Irish flora is, to my mind, much less certain.

In the first place Britain is much larger than Ireland, and much more varied climatically. No place in Ireland is as dry as Southend, as sunny as Brighton, as warm in summer as Reading, as cold in winter as Braemar, or possesses as wide an annual range of temperature as does Cambridge. On the other hand there is no spot in Ireland that cannot be matched climatically in Britain. Glengarriff is as warm as Falmouth in winter, but no warmer; Maam and the Black Valley at Killarney are wet, but no wetter than parts of Cumbria or Skye; the gales of Malin Head are eclipsed by those of Orkney. In geology also Ireland is less varied: it has nothing to correspond to the inland sands of Surrey or the Breckland, and has virtually no chalk, while its higher mountains are composed of inhospitable siliceous rocks which provide little scope for colonisation by alpine.

These facts alone suggest that if Ireland were still connected to Britain by a land bridge, its flora would probably be much poorer than that of its neighbour.

In Fig. 1 the line AB is drawn from Goole, at the head of the Humber estuary, to Gloucester, at the mouth of the Severn, and then continued southwards to Portland Bill. It delimits an area which I shall henceforth refer to as 'southeast England', though it is larger than that phrase normally implies. All parts of the area so delimited differ from every part of Ireland in climate; they are either drier, or sunnier, or hotter in summer. As many as 74 species native to Britain but not found in Ireland are confined to this area (with occasionally a very few outlying stations just outside it). It is reasonable to regard these plants as ecologically excluded from Ireland; if they cannot migrate to Devon, to Warwickshire or to west Yorkshire they can hardly be expected to have migrated to Ireland, even when there was no sea barrier.

But this is not the only part of Britain in which plants may be found which are ecologically unsuited to Ireland: the same is true of the Highlands of Scotland, or at any rate of their highest summits and some of the lower mountains in the eastern half of the country. The Irish mountains cannot rival the Scottish in altitude, and their warmer winters and lack of reliable snow-cover would not permit the survival of many of the species which flourish on Ben Lawers, Clova or the Cairngorms.



Fig. 1. Great Britain, to illustrate the limits of the districts referred to in the text. South and east of the line AB is 'southeast England'. North and west of the line CD is the 'Celtic fringe'.

If we add to these mountain plants a few others which, though lowland, are found only in the northern quarter of Scotland (such as *Primula scotica*) — and it is hardly reasonable to expect to find in Ireland a plant which in Scotland does not venture south of Inverness — we can add a further 45 species to the list of those excluded from Ireland on ecological grounds alone.

This category of highland plants differs in one respect from those from the southeast: several of them are known from fossil evidence to have grown in Ireland in late-glacial times. *Betula nana* provides the best-known example. The precarious survival in Ireland of minute populations of such species as *Saxifraga nivalis* (which in Britain is nearly, though not completely, confined to the Scottish Highlands) indicates as clearly as do the absentees the generally unfavourable conditions which prevail in Ireland today for plants of this type; and even in the case of species such as *Saxifraga aizoides* and *S. oppositifolia*, which can muster fair-sized populations in northwest Ireland, their enormously greater abundance in Scotland tells the same tale.

Deducting 45 highland and 74 southeastern species from the total of 375 non-Irish plants in Britain, we are left with 256 species of which it can be said that at least part of their range in Britain covers areas with climate and soil comparable to those to be found in Ireland. Can we conclude that all these were kept out of Ireland by its early isolation? Not quite, I think.

In the first place 32 out of the 256 are extremely rare in Britain, with not more than five dots in the Atlas of the B.S.B.I. Many of these are confined to the Lizard and its immediate vicinity, and though the climate of the Lizard can be matched in West Cork, its large exposures of serpentine cannot, and the extremely restricted distribution of these plants is probably the result of soil and climate acting together. Other rarities are in less specialised situations, and we simply do not know why such plants as *Koeleria vallesiana*, *Helianthemum appeninum* and *Ranunculus ophioglossifolius* are as rare as they are. In so far as we understand their ecology there is nothing to prevent them establishing themselves in Ireland, but if they cannot move into the next parish in Britain it is clear that we do not understand it very well. We certainly cannot with any confidence attribute their absence from Ireland to its early isolation; half-a-dozen other explanations are as probable.

This reduces to 224 our list of absentees from Ireland still seeking an explanation. Can it not be assumed that they would be in Ireland if they had not been held back by a barrier? Probably, but the Irish Sea is not the only barrier that demands consideration.

The line CD in Fig. 1 delimits what I call the Celtic fringe of Britain. It approximates to the region where Celtic culture lasted longest and where Celtic blood probably still prevails. And it is also a region in which most of the rocks are Palaeozoic and siliceous, and most of the soils acid and shallow. It is not, I think, entirely fanciful to suggest that this relatively infertile and intractable land, which Romans, Saxons and Normans alike found resistant to easy and rapid colonisation, should also have proved inhospitable to some species of plants. There are at least 38 species of British, but non-Irish, plants which are widespread in most of England, and in some cases also in southeast Scotland, which are not to be found in the Scottish Highlands, in Cornwall, or in Wales except for its southeast and northeast corners. *Gagea luttea*, *Silvaum silaus* and *Campanula glomerata* can serve as examples. If these plants transgress the line CD at all it is only by cautious forays into mid-east Wales or the northern and eastern parts of the Scottish Highlands: nowhere do they come close to the bridge-heads from which an invasion of Ireland must have started - Cornwall, Pembrokeshire, Anglesey and the Llyn peninsula, and southwest Scotland (Islay, Kintyre and Wigtownshire).

We are left, then, with 186 species to which none of these reservations apply, and of which it may be said with reasonable confidence that their absence from Ireland is due, principally if not entirely, to the opening of the Irish Sea before they had completed their northwestward migration. There are probably a few which managed to get across even after the separation from Britain was complete, but although, as will be seen later, I am prepared to admit some long-range dispersal, it is too slow and too uncertain a process to have much effect within the space of 7-8,000 years. We may say, then, that just half the plants which are native to Britain but not to Ireland have been kept out by ecological factors and the other half by its early isolation.

Enough about absences; I must now turn to consider the plants which are in Ireland. Most of these are species of wide geographical range, which implies, of course, great ecological tolerance. A few are truly cosmopolitan, and there are many more which extend to a greater or less extent through the temperate regions of the northern hemisphere. Nevertheless, if we confine our attention to Europe, a close analysis of geographical range reveals some surprising limitations in the area occupied by some of our commonest species. A plant can reasonably be called 'pan-European' if it

extends from Ireland northeastwards as far as Russia north of Leningrad, southeastwards to Turkey, Greece or Bulgaria, and southwards to Spain or Portugal south of the fortieth parallel of latitude. Yet of the 815 species we are considering only some 300 satisfy these criteria; and even if we modify the first requirement so as to include plants which find their northeastern limit in south Finland or Latvia the figure rises only to 380 - still less than half the total. What is most surprising, perhaps, is that of the Irish plants which fail to satisfy the criteria, the greatest number fail because they stop short in the southwest: the corner of Europe where one might expect to find them well represented. This suggests that the wetness of the summer is at least as important as the mildness of the winter in determining the composition of the Irish flora.

Whether pan-European or of more limited range in Europe, there are, of course, many species which extend far into Asia or North America. The Asiatic range does not concern us here, but it should be mentioned in connexion with what will be said later about the so-called 'Hiberno-American' plants, that of the Irish species we are dealing with as many as 191 (between a fifth and a quarter of the total) are found in eastern North America and are believed to be native there. (Almost as many occur as naturalised aliens.) And it is of interest to note that about 60% of these species which straddle the Atlantic have a European range centred mainly on the north and centre, being rare in the Mediterranean region or completely absent from it. Over a third are either pan-European or more or less evenly balanced between north and south in their range. There are only ten species common to Ireland and America which show a southerly tendency in Europe, and as they all extend as far north as Denmark it cannot be regarded as very marked. *Potamogeton crispus*, *Potentilla sterilis* and *Juncus acutiflorus* may be cited as examples.

These facts suggest that the channel of communication (to use a non-committal phrase) between western Europe and North America lay through lands which, even in interglacial times, had a distinctly cool climate.

If we turn next to analyse the European distribution of those Irish plants which cannot be called pan-European we find ourselves in a difficulty. For, granted that they are almost all represented in northwest Europe, within this limitation almost every kind of pattern can be found, and between these various patterns there are no clear discontinuities. Some plants thin out towards the east, others towards the south, the southeast, the northeast or the north; and in some cases the distribution is disconcertingly discontinuous. Nearly 30 years ago Matthews attempted to establish different categories of European range for the British and Irish flora as a whole, but although his work was stimulating and suggestive, I find it impossible to accept it in detail. This is due in part to an increase in our understanding of taxonomy and of detailed distribution; in part to the necessarily arbitrary, but unexplained boundary-lines between his categories, and in part to the wrong assignment of some species. It is impossible, for example, to accept the assignment of *Saxifraga hirsuta* to the alpine element or *Minuartia verna* to the arctic- alpine, while *Linum bienne* which is fairly widespread in western Europe and occurs in the northern part of the Balkan peninsula is ill at ease in the Mediterranean element.

I must, therefore, omit (or at least defer to another occasion) any attempt to classify those Irish plants which have a wide, but not a very wide range in Europe, and which include in this range at least parts of central Europe (Germany, Switzerland, Austria, Czechoslovakia, Poland and Hungary). They include species as common as *Linum*

catharticum, *Lysimachia nemorum* and *Salix aurita*, and others as rare as *Carex depauperata* and *Astragalus danicus*, and comprise in all over 330 species.

There are, however, two types of continental distribution which it would be foolish for a student of the Irish flora to brush aside as indefinable, even if he is forced to use somewhat arbitrary criteria in their definition; for both have been the subject of much comment and speculation because of their undoubted relevance to an interpretation of the recent history of the Irish flora. These are (using the terms in a wide sense for the moment) the Atlantic-Mediterranean and the Arctic-Alpine ranges.

If a line be drawn, as in Fig. 2, so as to cut off southwestern Norway and western Jutland, and then to run through Hamburg, Liège, Paris, Limoges, Toulouse, the Maladeta, Pamplona, Leon, Bragança and Coimbra, it delimits Atlantic Europe. Over most of the area the rainfall is heavy to moderate and well distributed through the year, while the temperature shows a small annual range, with fairly mild winters and fairly cool summers. The area covers the British Isles and Holland, much of Belgium, about half of France, nearly half of Portugal, and smaller fractions of Norway, Denmark, Germany and Spain. A detailed study of their European distribution leads me to conclude that 30 Irish species have a purely Atlantic distribution in this strict sense — or at least, if they deviate across the line to the east it is only on a very small scale. All but seven occur in Britain, and it is not surprising to find that most of these are a good deal commoner in the west of Britain than in the east. I have listed them in Table I in their order of abundance in Ireland in order to draw attention to a rather unexpected fact. One might have supposed that these Atlantic species would form a conspicuous and characteristic element in the flora of Ireland. But in fact only one is ubiquitous; six others may be described as common; 11 are distinctly local and 12 are rare. This suggests that the Atlantic flora of Europe has suffered a good deal from local extinctions and that many of its species have a more or less relict distribution — a point to which I shall return

Table 1. Atlantic species in the Irish flora.

<i>Salix atrocinerea</i>	<i>Carum verticillatum</i>
<i>Cirsium dissectum</i>	<i>Limonium binervosum</i>
<i>Carex binervis</i>	<i>Sisyrinchium bermudiana</i>
<i>Hyacinthoides non-scriptus</i>	<i>Meconopsis cambrica</i>
<i>Sedum anglicum</i>	<i>Allium babingtonii</i>
<i>Ulex gallii</i>	<i>Saxifraga hirsuta</i>
<i>Spergularia rupicola</i>	<i>Spiranthes romanzoffiana</i>
<i>Pinguicula lusitanica</i>	<i>Hypericum canadense</i>
<i>Chamaemelum nobile</i>	<i>Trifolium occidentale</i>
<i>Daboecia cantabrica</i>	<i>Viola lactea</i>
<i>Saxifraga spathularis</i>	<i>Erica mackaiana</i>
<i>Euphrasia tetraquetra</i>	<i>Asparagus officinalis</i>
<i>Eriocaulon aquaticum</i>	<i>Ranunculus tripartitus</i>
<i>Euphorbia hyberna</i>	<i>Erica vagans</i>
<i>Scilla verna</i>	<i>Erica ciliaris</i>



Fig. 2. Western Europe, showing the limits of the strictly Atlantic region (defined by the line AB), and the continental distribution of two Atlantic species found in Ireland but not in Britain. *Saxifraga hirsuta* xxx *Saxifraga spathularis*

Asparagus officinalis implies of course subsp. *prostratus*, which alone is native to Ireland, and I exclude from the circumscription of *Euphorbia hyberna* the Mediterranean subspecies *insularis* and *canuti* (which are often treated as separate species).

It will be noticed that included in Table 1 are four species which are normally relegated to the North American element. But their distribution in Europe is rigidly Atlantic; their North American connexions will be discussed later. So as not to appear too rigid in my definitions I append as a supplement (Table 2) a list of species of

which most of their territory lies in the Atlantic domain, but which deviate from it here and there to an extent which cannot be overlooked. They may be reasonably described as sub-Atlantic. Once more they are listed in their order of approximate abundance in Ireland, and it will be seen that they are, for the most part, much commoner, only 3 of the 12 being rare.

Table 2. Sub-Atlantic species in the Irish flora.

Ulex	
europaeus	Scutellaria minor
Erica cinerea	Carduus tenuiflorus
Scrophularia auriculata	Lepidium heterophyllum
Hypericum elodes	Oenanthe fluviatilis
Ranunculus hederaceus	Wahlenbergia hederacea
Beta vulgaris, subsp. maritima	Cicendia filiformis

The species which I have classified as sub- Atlantic transgress the border of the Atlantic domain by extensions either into the Baltic region or into Eastern France, Switzerland and Germany. But there are others which transgress the border by extensions in to the Mediterranean region, and are best called Mediterranean-Atlantic. They have for so long been the subject of comment and speculation that they demand attention here. Some of them are often referred to simply as Mediterranean, but this is misleading, as they all occur in the Atlantic region as well; even *Neotinea maculata*, which comes nearest to having a purely Mediterranean range outside Ireland, has been recorded from near Santander, apart from its recently discovered station in the Isle of Man. These plants vary greatly however in the extent of their penetration into the Mediterranean region, and in the relative importance of their Atlantic and Mediterranean ranges. At the opposite extreme from *Neotinea* we have *Euphorbia portlandica*, which is not found east of Gibraltar, and is therefore not Mediterranean in the literal geographical interpretation of the word. It is, however, included in the Mediterranean-Atlantic category because the climate of south Portugal and southwest Spain is indisputably of a Mediterranean type. Between these extremes every kind of intermediate is to be found.

The 25 Irish species of Mediterranean- Atlantic range are set out in Table 3.

Table 3. Mediterranean-Atlantic plants in the Irish flora.

Conopodium majus	Juncus acutus
Hypericum androsaemum	Lavatera arborea
Umbilicus rupestris	Erica erigena
Oenanthe crocata	Neotinea maculata
Scirpus cemuus	Arbutus unedo
Desmazeria manna	Vulpia fasciculata
Euphorbia portlandica	Sibthorpia europaea
Halimione portulacoides	Simethis planifolia
Ranunculus omiophyllus	Arthrocnemum perenne
Parentucellia viscosa	Lotus subbiflorus
Rubia peregrina	Otanthus maritimus
Parapholis strigosa	Geranium purpureum

As with the Atlantic list, so here also one may append a few species which transgress the Mediterranean-Atlantic limits but not by very far. There are, perhaps, six which, in this sense, may be called sub-Mediterranean-Atlantic. *Trifolium glomeratum* and *Linum bienne* extend to Serbia and northern Bulgaria, where the climate is of a Central European type; *Polygonum maritimum* and *Euphorbia paralias* extend to the shores of the Black Sea (the former even to the Sea of Azov); *Tuberaria guttata* is scattered through much of eastern France and has an outlying colony in east Central Germany; while *Phleum arenarium* penetrates into the Baltic as far as Gotland. In the rest of their range, however, they are all Mediterranean-Atlantic.

The considerable number of these Atlantic and Mediterranean-Atlantic species in the Irish flora suggests that some of them might find in Ireland their northern limit in Europe. This is in fact true for some 27 species, and, since northwestern Europe possesses an exceptionally mild climate for its latitude, the northern limit in Europe is also the northern limit in the world. The species are listed in Table 4. All but five are restricted or nearly restricted in Europe to the Atlantic-Mediterranean area, but *Mentha pulegium*, *Minuartia recurva*, *Ophrys apifera*, *Orobancha hederæ* and *Pinguicula grandiflora* all extend to Central Europe. It might be possible to add *Rosa arvensis* to the list if it can be shown that it is extinct in Northumberland. In the case of *Tuberaria guttata* it should be explained that there is a 'dead-heat' between Ireland and Germany, as Nordemey (its northern limit in Germany) and Inishturk are on exactly the same latitude.

Table 4. Plants with their northern limit in Ireland.

<i>Allium babingtonii</i>	<i>Minuartia recurva</i>
<i>Arbutus unedo</i>	<i>Ophrys apifera</i>
<i>Chamaemelum nobile</i>	<i>Orobancha hederæ</i>
<i>Daboecia cantabrica</i>	<i>Otanthus maritimus</i>
<i>Erica ciliaris</i>	<i>Pinguicula grandiflora</i>
<i>Erica erigena</i>	<i>Polygonum maritimum</i>
<i>Erica mackaiana</i>	<i>Rubia peregrina</i>
<i>Erica vagans</i>	<i>Saxifraga hirsuta</i>
<i>Euphorbia hyberna</i>	<i>Saxifraga spathularis</i>
<i>Euphorbia paralias</i>	<i>Sibthorpia europæa</i>
<i>Hypericum canadense</i>	<i>Simethis planifolia</i>
<i>Juncus acutus</i>	<i>Sisyrinchium bermudiana</i>
<i>Lavatera arborea</i>	<i>Tuberaria guttata</i>
<i>Mentha pulegium</i>	

We must now turn to consider those plants whose range lies mainly in the far north, or in the high mountains of Europe, or in both. The true arctic-alpines account for most of these, but, if the term is to be used in anything like a precise sense, a number of species which are often called arctic-alpine must be excluded from the list. To merit the description of arctic-alpine a species must be fairly widespread in the arctic and subarctic regions of Europe and must re-appear at high altitudes (at least up to 2500 m) in the Alps (often also in the Pyrenees). But it must be scarce in or absent from the intervening areas, for otherwise it becomes merged in the main mass of northern continental species. I exclude, therefore, any species which is found (other than in small, isolated areas) at low altitudes south of about 54°-55° N (the latitude of Belfast, Newcastle-on-Tyne, Copenhagen and Moscow), and also any which occurs in Central

Europe at altitudes below 800m, except in the immediate neighbourhood of high mountains, where it may be, to use the expressive German word, herabgeschwemmt from the alpine region into the river valleys. (It is rather surprising to learn that plants as characteristic of the high-alpine zone as *Alchemilla alpina*, *Dryas octopetala*, *Saxifraga aizoides* and *S. stellaris* can all be found in the alpine valleys at altitudes below 350m.) On these criteria I exclude from the category of arctic-alpine the following species, which are often listed as such: *Saxifraga nivalis*, *Cardaminopsis petraea*, *Saxifraga hirculus*, *Carex bigelowii*, *Minuartia verna*, *Arctostaphylos uva-ursi*, *Vaccinium vitis-idaea* and *Gentiana verna*. All are arctic, but the first is not found on any of the major mountain ranges of Europe; the next three occur very sparingly, if at all, in the Alps and do not ascend into the alpine zone, nor are they found in the Pyrenees; while the last four, though truly alpine, are also widely distributed in the lowlands of Central Europe, especially in the east. *Gentiana verna* deserves particular mention, as its association with *Dryas octopetala* in the Burren, and often too in the high Alps, makes everyone assume that the distribution and history of the two must be identical. But the gentian is common in the hill country and the plains of central and southern Germany at altitudes well below 800 m, and also in the karst of northwestern Yugoslavia, and its representation in the Arctic is extremely meagre, being confined to a few small areas of arctic Russia. The confusion has been made worse by the fact that both German and Russian Floras cite it as occurring in Scandinavia, which is certainly untrue. Its occurrence, therefore, in western Ireland and northern England is rather anomalous, and is best explained by supposing that it survived the last glaciation there, if not exactly *in situ*, not very far away.

There are, however, 16 genuine arctic- alpiners in the Irish flora; they are listed in Table 5. Most of them are confined to montane habitats in Ireland, but *Draba incana* and *Saxifraga oppositifolia* descend almost to sea- level in Donegal, as does *Dryas* in the Burren and *Rhodiola* on Aran.

Table 5. Arctic-alpine species in Ireland.

<i>Alchemilla alpina</i>	<i>Rhodiola rosea</i>
<i>Arenaria ciliata</i>	<i>Salix herbacea</i>
<i>Draba incana</i>	<i>Saussurea alpina</i>
<i>Dryas octopetala</i>	<i>Saxifraga aizoides</i>
<i>Epilobium alsinefolium</i> .	<i>S. oppositifolia</i>
<i>Oxyria digyna</i>	<i>S. stellaris</i>
<i>Poa alpina</i>	<i>Silene acaulis</i>
<i>Polygonum viviparum</i>	<i>Thalictrum alpinum</i>

The history of these plants is well-known and generally agreed, as several of them are well-preserved as late-glacial fossils in the lowlands of temperate Europe. During the last glaciation they occupied large areas of the north European plain, and, in some cases, the unglaciated regions of the British Isles; as the climate became warmer they retreated before the advancing temperate flora northwards or upwards as opportunity offered, and they survive today, therefore, only at high latitudes or in the mountains. To this generalisation *Dryas* in the Burren provides the only notable exception.

In connexion with the arctic-alpine plants we must notice a few that are alpine but not arctic, or arctic-subarctic but not alpine. There is only one species which belongs

indisputably to the first category: *Minuartia recurva*. Two others may be added with some reservations (*Pinguicula grandiflora* and *Euphrasia salisburgensis*), but, as all three are absent from Britain they may be left over until the problem of the non-British plants in Ireland is considered as a whole. Two species merit the description arctic-subarctic: *Ligusticum scoticum* and *Mertensia maritima*. Both are coastal, and the latter seems to be in retreat northwards; at any rate they find their southern limit in Europe close to 54° N in both Britain and Ireland. *Carex aquatilis* nearly qualifies, but it straggles southwards to 52° N in Kerry, south Wales and (rather doubtfully) north Ukraine. *Saxifraga nivalis* provides another marginal case; it is found only north of 55° N, except for isolated stations in Ireland, Wales and the Riesengebirge (on the borders of Poland and Czechoslovakia at 50° 45' N). *Rubus chamaemorus*, which is sometimes designated arctic-subarctic, is too widespread south of the Baltic in north Germany and north Poland to qualify; it also extends to the Riesengebirge.

These plants must be presumed to be arctic in origin; during the glacial epochs they spread southwards, but not far enough south to find refuges in the Alps, Pyrenees or Carpathians when the temperature began to rise. In Britain and Ireland, however, their history is essentially the same as that of arctic-alpine species. In the early part of this lecture I spent some time in discussing the failure of certain species to spread from Britain to Ireland. I implied that this was the normal path of post-glacial immigration, and I do not think that this can be disputed. But there are 15 species of Irish plants (all, in my opinion, native) which are not found in Britain, and we are forced therefore to ask: if they passed through Britain why are they no longer there, and if they did not, by what path did they reach Ireland? These questions have been debated for over a century, often with passion; but all too often an author has been content to demonstrate to his own satisfaction that a rival's theory is impossible without suggesting a clear alternative or facing such difficulties as may lie in the path of its acceptance. I cannot hope to solve these long-disputed problems, but I shall try to define them more clearly than has been usual, to set out the relevant facts more accurately, and at least in some cases to suggest which theory seems the least improbable — for the sad fact is that for most species all theories seem improbable, and, as in discussing the origins of life on earth, one has to attempt the difficult intellectual feat of balancing one improbability against another.

In Table 6 are set out the names of these 15 species, an indication of the nearest known station for each outside Ireland, and the approximate distance which separates this from the nearest Irish station. Two species which might have been included are omitted, because both are known to have grown in Britain within the last century or so, and although their extinction there is probable it is not certain. These are *Saxifraga rosacea*, not found with certainty in Snowdonia for almost a century, but rumoured to be still there, and *Otanthus maritimus*, widespread on the south coast of England only 150 years ago, but not seen for the past 50 years. As with many sea-shore plants, however, its re-appearance after a long interval is by no means impossible. On the other hand, I have discounted British records for two other species - *Simethis planifolia*, which once grew near Bournemouth, but almost certainly as an introduction, and *Euphrasia salisburgensis*, of which one specimen exists, allegedly collected on the Yorkshire limestone, but it has never been seen there by any living botanist.

Table 6 Irish plants not found in Britain.

	Nearest station outside Ireland	minimum disjunction (km)
<i>Neotinea maculata</i>	Isle of Man (Near Santander, north Spain)	350 (1000)
<i>Simethis planifolia</i>	Brittany	550
<i>Arbutus unedo</i>	Brittany (west France (Charente-Maritime))	550 (950)
<i>Inula salicina</i>	Normandy	700
<i>Daboecia cantabrica</i>	west France (near Angers)	900
<i>Saxifraga spathularis</i>	northwest Spain	900
<i>Pinguicula grandiflora</i>	north Spain (Asturias)	950
<i>Saxifraga hirsuta</i>	north Spain (Asturias)	950
<i>Erica erigena</i>	Near Bordeaux	1100
<i>Erica mackaiana</i>	northwest Spain (east Galicia)	1100
<i>Minuartia recurva</i>	northeast Portugal	1100
<i>Euphrasia salisburgensis</i>	Vosges	1250
<i>Arenaria ciliata</i>	Jura	1350
<i>Hypericum canadense</i>	Newfoundland	3250
<i>Sisyrinchium bermudiana</i>	Newfoundland	3250

I have not included any of the so-called Irish endemics, as I do not believe that any of them deserve more than subspecific status, and in a broad survey of this kind I have to limit myself to species. *Arabis ciliata* is included within the compass of *A. hirsuta* by all recent authors; *Saxifraga hartii* must, I have concluded after seeing the populations *in situ*, be reduced to a subspecies of *S. rosacea*; *Rumex hibernicus* is no more than a well-marked ecotype of *R. acetosa*, perhaps to be ranked as a subspecies; *Salix hibernica* is considered by R.D. Meikie to fall within the considerable range of variability shown by *S. phyllicifolia*; and *Antennaria hibernica* is a figment of Braun-Blanquet's phytosociological enthusiasm.

For two species in Table 6 I have duplicated the data on the nearest station and the minimum disjunction. This is because there is good reason to suppose that *Neotinea maculata* reached the Isle of Man by natural means in post-glacial times, presumably from Ireland, and the disjunction from Spain, therefore, is more relevant in discussing the origin of the Irish populations; while for *Arbutus unedo* it has been suggested that the population at Paimpol in Brittany derives from an introduction, and, although I believe that it is more probably native there, it is as well to indicate the position and distance of the nearest undoubtedly native plants. In accordance with their total geographical range in Europe we can recognise three categories among these species. The last two in Table 6 are primarily North American, and are very scantily represented in Europe; *Minuartia recurva*, *Arenaria ciliata*, *Euphrasia salisburgensis* and *Pinguicula grandiflora* are, broadly speaking, alpine; *Inula salicina* is Central European; the remainder are Atlantic or Mediterranean-Atlantic.

Inula salicina may be dismissed first, as providing a distribution which is completely inexplicable. The Irish plants do not differ from those of the Continent; apart from a calcicole tendency it has no specialised ecological requirements; and it is only

moderately well-adapted to long-range dispersal. It ranges over most of Europe, but becomes scarcer in the extreme south and extreme west; its absence from Britain, therefore, would not be so remarkable if it did not turn up (formerly in some abundance) around Lough Derg in Ireland.

I turn next to the North American species. It is necessary to consider in connexion with them two other species which occur in Britain as well as in Ireland, but nowhere else in Europe. These are *Eriocaulon aquaticum*, known from a few stations in the Inner Hebrides and the extreme westerly point of the Scottish mainland, and *Spiranthes romanzoffiana*, with a similar distribution in Scotland and a more recently discovered station on the edge of Dartmoor. Whatever explanation covers the presence of these mainly American species in Ireland will also be valid for Britain. In the first place let us dismiss any notion that any of them have been introduced by man. For the *Eriocaulon* and the *Spiranthes* this has never received serious consideration, but for the two Irish species it has. This is in part because it was at one time claimed that *Juncus tenuis*, another species centred on North America, was native in Ireland; it is now generally agreed that this is not the case. But the claims of the *Sisyrinchium* and the *Hypericum* are much stronger, and probably would not have been questioned were it not for the fact that each has a close relative of weedy habit which is certainly alien in Europe, and with which the Irish plant has been confused. Having seen *Hypericum majus* in the Vosges (it is naturalised also in Bavaria) I am quite satisfied that it differs from *H. canadense* both in morphology and in ecology, and I accept Ingram's conclusion (set out in *Flora Europaea*) that the same is true for *Sisyrinchium bermudiana* and *S. montanum*.

How, then, do they come to exist as natives on the extreme northwest fringe of Europe? The answer is surely given by a study of Hultén's Amphi-atlantic plants. One does not explain the distribution of a plant by giving it a new name, but the data presented by Hultén show that there are dozens of species which straddle the North Atlantic but are absent from the arctic and subarctic regions of Asia. Some of these have a fairly symmetrical distribution (e.g. *Rhynchospora fusca*), covering approximately equal areas in America and in Europe; others, such as *Carex nigra* are much more widespread in Europe than in America. The four plants which we are considering take their place as those in which the asymmetry is markedly in the other direction. Doubtless their European range was once somewhat greater than it is now, but there is no reason to suppose that it extended very far eastwards. Under what conditions the floras of North America and of northwestern Europe were in contact, nor how long ago, we do not know, but it must have been at any rate before the last glaciation. Some of the amphi-atlantic plants doubtless survived this glaciation further south than Ireland, but as our four species survive today in Labrador or central Newfoundland it is not asking the impossible that they should have survived the last glaciation in some sheltered nook, perhaps on land now submerged by the rise in sea-level, off the coasts of Scotland and Ireland. The fact that *Eriocaulon* is known as a post-glacial, and very probably as an interglacial fossil in Irish deposits provides strong corroborative evidence for this suggestion; as does the fact that the Irish populations differ in chromosome number from at any rate most of the American plants. Certainly this hypothesis seems to me to be much less improbable than the only real alternative - that all have been introduced in the last few thousand years by the transatlantic flight of diligent birds.

Let us next consider the eight species of Atlantic or Mediterranean-Atlantic range. Two points must be emphasised from the start — that they are not a homogeneous group ecologically, and that the essential question is not ‘Why do they grow in Ireland?’ but ‘Why do they not grow in Britain?’ I emphasise this last point to help dispel a widespread illusion that most of these plants, because they grow in Spain, must be considered tender and warmth-loving. For one or two this is partly true, but it is now 80 years since Colgan pointed out that *Daboecia* grows high enough in the Cordillera Cantabrica to be covered with snow for several months in the winter. And my most vivid memory of A.J. Wilmott is his description of his first sight of *Saxifraga spathularis*. It was in August, near the summit of Mount Brandon, and, he said, ‘my hands were so numbed with cold that I had to stub up this delicate southern plant with the toe of my boot.’

To account for the presence of these species in Ireland, in most cases so remote from the nearest continental population, only three explanations are possible. Either their distribution in western Europe was once more continuous than it is now, or it has always been discontinuous. In the latter case the plant must have reached Ireland by long-range dispersal, and wind and birds seem to be the only possible agencies. If the distribution was more continuous at one time, it must have been fragmented either before or after the end of the last glaciation. In the former case the Irish populations must have survived this glaciation in or near their present sites. In the latter case a rapid northward migration up the west coast of Europe (partly, no doubt, on land now submerged) must have been followed by a drastic fragmentation of range during the past 8,000 years or so.

The objections to all three explanations are clear. Geologists tell us that nothing except the hardiest plants of arctic-alpine type could have survived a glacial epoch in Ireland. Only one of the eight species has fruits adapted to dispersal by birds, and only one seeds small enough for long-range transport by wind to seem very plausible. And nobody has suggested the nature of the post-glacial climatic change which would permit the extinction of these plants in Cornwall, and in many cases in Kerry and Brittany, and their survival in Connemara. Nevertheless, for each species one of the hypotheses must be true.

Judging by the behaviour of the plants in cultivation and their natural range in the wild, I believe that perglacial survival must be deemed impossible for *Arbutus* (which is only marginally hardy at Kew), very nearly impossible for *Erica erigena* (which is never killed in cultivation in Britain, but looks unhappy after a severe winter), unlikely but not entirely impossible for *Neotinea* and *Simethis*, but well worth considering as the least improbable hypothesis for the other two heaths and for the two saxifrages. As regards long-range dispersal, it seems on the whole the most likely explanation for *Arbutus*, and possibly also for *Neotinea*, which has, like most orchids, seeds almost of the dimensions of Pteridophyte spores. For *Simethis* alone does differential extinction in post-glacial times seem at all plausible, as the distances involved are not very great, but I do not dismiss the possibility of survival as an alternative. This leaves us with *Erica erigena*, and I confess that for this plant none of the theories seems at all plausible. Its extremely disjunct distribution in Spain (for it is only in Ireland and Portugal that it is at all common, even locally) suggests that either it has some quite unexplained power of long-range dispersal, or else that it underwent a severe fragmentation of area some time ago. And there, I am afraid, I must let the matter rest.

The four remaining species, which I categorised as 'broadly speaking alpine' are rather a mixed bunch. *Minuartia recurva* alone merits the term without qualification, for it extends through most of the major mountains of Central and Southern Europe, from the Serra de Gerez in Portugal, through the Pyrenees and Alps, to Sicily and the Romanian Carpathians. Curiously enough it does not occur in the Cordillera Cantábrica, where so many others of the species in Table 6 are to be found, though it is in some of the other Spanish ranges. What tide brought it to southwest Ireland I do not know, but I think it must have been long before the last glaciation; perhaps in some earlier late-glacial period it was widespread on the low country of north-west Europe. *Euphrasia salisburgensis*, if the Scandinavian *E. lapponica* is regarded as a distinct species, is a fairly orthodox alpine except for its occurrence in quantity on the island of Gotland, where it is as unexpected as it is in Ireland. It grows only in the eastern part of the Pyrenees, and not at all in the Cantabrian range, so that it is unlikely to have reached Ireland from the south. The supposition that it survived the last glaciation in Ireland is fortified by the fact that the Irish populations are held to be varietally, distinct from those in Central Europe (as are also the plants of Gotland). With *Arenaria ciliata* we find ourselves in taxonomic difficulties. The Irish plant, which is found only on Ben Bulbin, but is common there, is generally allowed to be distinct at subspecific rank, but as to which other populations are to be included in the same species every author has different views. It is clear that the arctic-alpine complex, which also includes *A. gothica*, *A. norvegica* and *A. humifusa*, seems to have become fragmented quite a long time ago, and the isolated populations have undergone some differentiation. To me it is inconceivable that the Irish form arrived there since the last glaciation. Finally, *Pinguicula grandiflora* is awkwardly poised between the subatlantic and the alpine. On the one hand it is confined to the mountains - Cantabrian range, Pyrenees, Córbières, Jura and western Alps - but it grows mostly below the alpine zone and finds its eastern limit in Savoy. With this distribution its abundance in southwest Ireland is rather surprising, and as I can see no likely staging posts for its advance northwards, either from the Jura or the Pyrenees, in post-glacial time, I conclude that it too dates from interglacial times as an Irish plant.

The continental distributions of some of these plants are mapped in Figs 2-5, chiefly to give an idea of the large disjunction that separates them from their Irish stations. I would emphasise that although the Atlantic flora of Europe, like most other elements, shows some discontinuities, I have not been able to trace any British species of Atlantic-Mediterranean affinities which is separated from the main population by anything like as wide a gap. This suggests that no ordinary history lies behind the isolation of these plants in Ireland, and emboldens me to believe - no matter how hard the geologists try to terrify us with descriptions of the ice ages - that with a few exceptions they survived the last glaciation in Ireland. As Wilmott once said: 'After all the ice is only a deduction; the plants are there.' In one sense, of course, this only pushes further back in time the problem of when, how and why the disjunction arose. But I am afraid that a much fuller knowledge of interglacial vegetation is needed before we can even begin to answer that question.

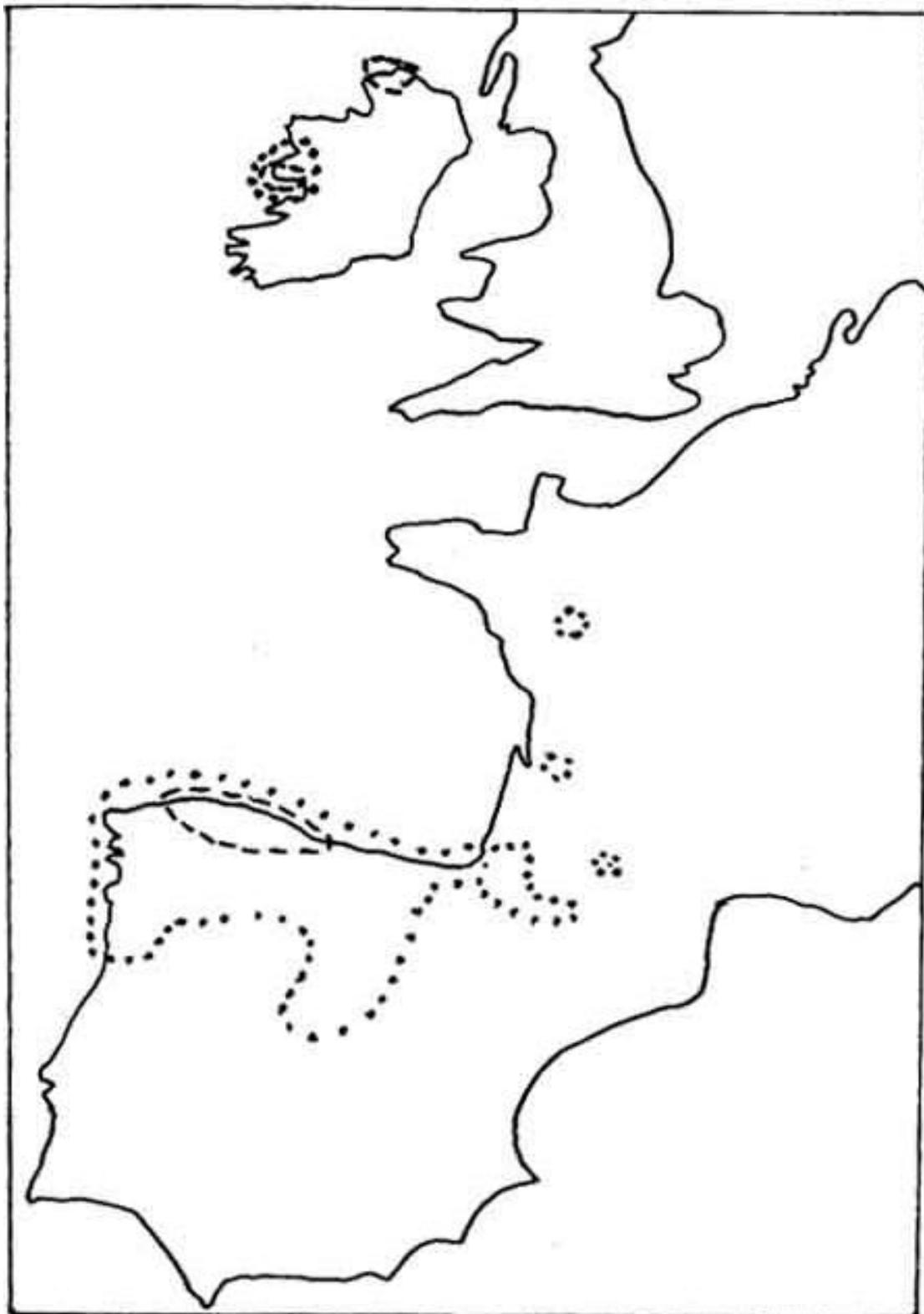


Fig. 3. Western Europe, showing the continental distribution of two Atlantic species found Ireland but not in Britain. *Daboecia cantabrica* --- *Erica mackaiana*

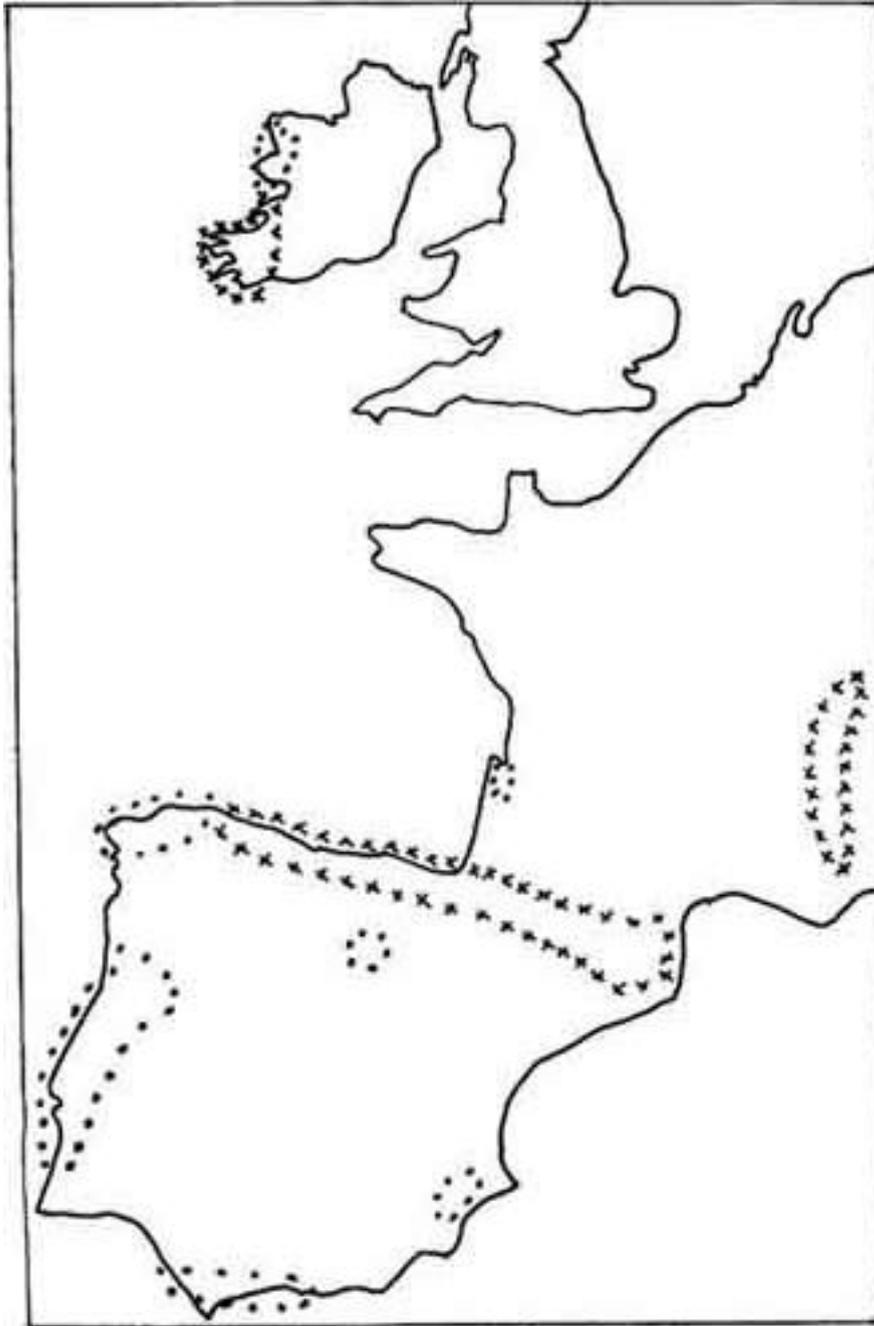


Fig. 4. Western Europe, showing the continental distribution of an Atlantic-Mediterranean and Pyrenean-Alpine species, both found in Ireland but not in Britain. *Erica erigena* xxxxxx *Pinguicula grandiflora*

It is possible that *Pinguicula grandiflora* grows also in southeast Spain, in the Sierra de Cazorla, but the specimens cannot be named with certainty.



Fig. 5. Europe, showing the distribution of two species of alpine type found in Ireland but not in Britain. *Euphrasia salisburgensis* ----- *Minuartia recurva*

My tale is told, and it remains only to adorn it with a moral. This can be simply expressed as *What do they know of Ireland who only Ireland know?*. To understand Irish plants they must be studied abroad as well as at home. Look at *Drosera anglica* on calcareous marl in Gotland, *Daboecia* in shady pine-woods in Portugal, bracken on calcareous screes in the Appenines and *Erica erigena* in a dry, rocky ravine above Málaga, and then come back to Ireland and look on them again with a more far-seeing eye.

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I thought it unsuitable to interrupt with references the text of what is essentially the transcript of a lecture, but I append a bibliography of the writings from which most of my facts and many of my ideas have been derived.

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