Notes on the distribution of the Irish Dactylorchids

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The dactylorchids have attracted the attention of many British botanists during the last few decades, and although the work that has been done cannot be said as yet to have resolved the many taxonomic enigmas which the group presents in the British Islands, it has helped to reveal distributional peculiarities which would seem to merit attention in relation to the general problem of the origin of the British flora. The orchidaceous flora of Ireland, long noted for its inclusion of *Neotinea intacta* and *Spiranthes Romanzoffiana,* has been enriched by the addition of certain dactylorchid species and subspecies which are either absent from Great Britain, or which occur only in the extreme west of the Scottish mainland or in the Western Isles. It is the purpose of this short paper to outline the affinities of these plants, and to bring together the facts relating to their distribution as they are at present known. Further field research will probably extend the ranges of some of the forms considered, and there can be little doubt that the application of newer methods of taxonomic investigation will clarify their relationships and perhaps alter our views as to their taxonomic status. Nevertheless sufficient is known about the distribution of the dactylorchids in Britain to make it unlikely that further work will gravely alter the nature of the phytogeographical problems which the western forms present.

The subgenus Dactylorchis Klinge is notorious for its polymorphism and the resultant confusion of its taxonomy. No stability has yet been attained in nomenclature, and this, combined with the difficulty of interpreting herbarium material, makes the tracing of the Continental affinities of the British forms a hazardous process. The most recent Continental treatment of the dactylorchids is that of Vermeulen (1947). Here the subgenus Dactylorchis is elevated to the rank of a genus, which is further divided into three sections, the last of which, Sectio Ma-

culatae (Parl.) Vermln., includes all of the Britannic forms. The case made out for the adoption of the new genus is attractive, and there seems little doubt that it will eventually receive general acceptance. However, the monograph is not yet complete, and the treatment of the British plants so far is not uniformly satis factory. It therefore seems premature to adopt a revision as far-reaching as that which Vermeulen suggests until more of the group is covered.

The following is a list of the Irish dactylorchids considered in the present paper:

ORCHIS L. subgenus D a c t y l o r c h i s Klinge (= DACTYL-
ORCHIS Vermln.)

> *Orchis Fuchsii* Druce (*O. maculata* auct. mult.; *O. maculata* var.
> *Meyeri* Reichb.f.)
> subsp. *O'Kellyi* Druce
> subsp. *hebridensis* (Wilm.) H.-Harr.
> *Orchis ericetorum* (Linton) Marshall (*O. elodes* Griseb.; *O. ma-
> culata* L. sec. Druce.)
> *Orchis latifolia* L. sec. Pugsl. (*O. incarnata* auct. recent.)
> var. *coccinea* Pugsl. (*O. incarnata* f. *atrirubra* Godf.; *O. in-
> carnata* var. *dunensis* Druce).
> var. *cambrica* Pugsl.
> *Orchis cruenta* Müll.
> *Orchis majalis* Reichb. f. (*O. latifolia* auct. mult.)
> subsp. *occidentalis* Pugsl.
> (subsp. *kerryensis* Wilm.)
> subsp. *Traunsteinerioides* Pugsl.
> *Orchis purpurella* Steph.

The facility with which the dactylorchids form hybrids in nature is well known, and is a further permanent source of taxonomic confusion. Under natural conditions, many of the British species are clearly differentiated from each other ecologically, and hybrids between them occur but sporadically in ecotones where the species come into contact. However, over a great part of the British Islands the influence of man in breaking up and modifying natural boundaries has brought about an overlapping or close interdigitation of the dactylorchid species, and in simultaneously providing in disturbed ground habitats where natural competition is mitigated, has allowed the formation of complex

hybrid-swarms. How far this process can be regarded as accounting for the production of the wide-ranging hybrid-swarms of western Ireland and Scotland is problematical. As will be seen below, the fluidity of the populations there suggests rather the amalgamation in relatively recent times of species imperfectly differentiated in former isolation.

The fertility inter-relationships of the Irish subspecies and species is indicated diagrammatically in fig. 1. It should be emphasized that this diagram is based upon the evidence of putative hybrids and hybrid-swarms. The difficulties inherent in the breeding of dactylorchids have so far prevented a systematic exploration of their interfertility by controlled crossings.

DIPLOID SERIES   TETRAPLOID SERIES
2n 40   2n 80
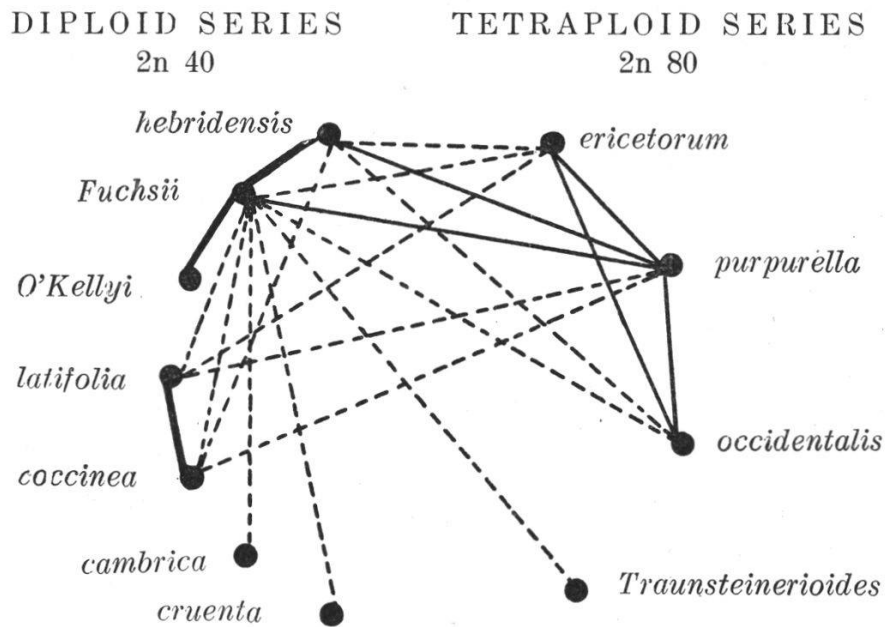
Fig. 1. Hybrid formation among Irish dactylorchids.

━━━━━ links forms showing incomplete differentiation.

──── indicates crossings in which hybrid-swarms are commonly formed.

·········· indicates crossings which occur occasionally, without the formation of hybrid-swarms.

A striking feature is the high fertility which apparently exists between species in different chromosome groups. This is not the place for an extended consideration of this problem, but it may be remarked that the solution may lie in the work of H a g e r u p (1944), who has shown that polyspermaty is of common occurrence among the dactylorchids.

Three of the Irish species are wide-ranging in the country, namely *O. Fuchsii, O. ericetorum* and *O. latifolia*. Their detailed distribution is governed in the main by edaphic and topographical factors. The first two species still remain to be recorded definitely from one or two of the Irish vice-counties, but it seems unlikely that these omissions indicate any real discontinuities in their areas.

O. Fuchsii and *O. ericetorum* are well differentiated ecologically, the former a plant of base-rich soils, pH 5.0—7.5, the latter preferring acid peaty soils, pH 4.2—5.5. Both show a high degree of variability in vegetative and floral characters, and both are capable of plastic modification, particularly of stature, according to the exposure of the habitat. A dwarf ecad of *O. ericetorum* occurs in coastal and montane regions in Ireland similar to that which is widespread in similar situations in Great Britain («*O. praecox*» Webster). Similar habitat-variation occurs in *O. Fuchsii:* in woodland the common form is a lush, broad-leaved plant, up to as much as a metre in height, while the plant of open meadow-land is shorter and more slender.

O. latifolia is a polymorphic in Ireland as it is throughout its western European range. The tall form which is commonly treated as the typical species *(Dactylorchis incarnata* ssp. *lanceata* [Dietrich] Vermln. in Vermeulen's revision) is widespread in saturated fen- and marsh-soils, pH 5.5—8.0. It is replaced in coastal districts by the subspecies *coccinea* Pugsl. *(O. incarnata* var. *dunensis* Druce) a dwarf plant of drier, sandy soils, which occurs in great numbers in dune hollows. An interesting form described by Pugsley in 1935 from Welsh marshes as *O. latifolia* subsp. *cambrica* has proved to have an extensive Irish range (Pugsley, 1936; Harrison, 1949). This plant seems to be closely connected with the *O. incarnata* var. *borealis* of Neuman (Neuman, 1909); unfortunately the data at present available do not allow closer comparison.

The Irish distribution of *O. purpurella* is still imperfectly known, mainly because in the past it has been confounded with the western *majalis* forms. Recent records which can be taken as authentic suggest that it is most frequent in the northern counties (where indeed it is often the commonest dactylorchid of open pasture and meadow-land), thinning out southwards along the

eastern coast but extending as far south as East Cork. On the west coast it extends in quantity as far south as South Galway, where its range overlaps with that of *O. majalis* subsp. *occidentalis* (the consequences of this overlap are discussed further below). South of this it appears to fail, and no authentic records exist from many of the central counties.

The marsh form of *O. purpurella* is a tall-growing plant with erect, unmarked leaves and lilac-purple flower colour which has been recognised taxonomically as var. *pulchella* (Druce) Pugsley. This form has been occasionally misidentified as *O. praetermissa* in Ireland. It now appears certain that *O. praetermissa* in its typical southern English facies does not occur in Ireland. This is a fact of some significance in that it suggests a phytogeographical affinity in this group rather with Scotland and northern England than with southern England, for the two species, *O. praetermissa* and *O. purpurella* are vicarious in Great Britain. *O. praetermissa* is widespread in southern England and in Wales, extending in sporadic colonies as far north as mid-Northumberland in the east and Anglesey in the west. *O. purpurella* possesses a northern range including the whole of Scotland and overlapping in England with that of *O. praetermissa* over a belt roughly 75—150 km in width. The Continental ranges of these two species, so far as they are known, show similar spatial segregation. *O. praetermissa* occurs in northern France, Belgium and Holland, while *O. purpurella* is known with certainty from southern Norway and Sweden, and may also occur in Denmark and northern Germany.

The remaining Irish species and subspecies possess restricted distributions in the British Islands which demand more detailed consideration. In the ensuing accounts, credence has been given only to well established records. In most cases the writer is familiar with the populations in the field, and in all others he has inspected the herbarium material upon which the records concerned have been based. A few historical and ecological notes have been included for the sake of completeness and better comprehension.

O. Fuchsii subsp. *O'Kellyi* Druce (fig. 2).

This plant was first described by D r u c e (1909) from material supplied from Co. Clare by P. B. O'Kelly. It is a highly distinc-

tive form, occurring in great numbers in calcareous soil pockets over the limestone pavement of north Clare. Participants in the Ninth I. P. E. had the opportunity of seeing the plant in July 1949 at the height of its flowering season. The extreme form of the subspecies entirely lacks anthocyanin pigmentation; the flowers are white and fragrant, and the leaves immaculate and slightly glaucous. A few years before D r u c e 's recognition of the Clare plant, E. S. M a r s h a l l had observed a similar race on the limestone at Inchnadamph in Sutherlandshire. For this plant Marshall proposed the name «*O. scotica*» in 1908. This name was not validly published, and the Sutherlandshire race has proved subsequently to be identical with the subsp. *O'Kellyi* of Clare.

In these two western areas the subspecies completely replaces the type on calcareous soils. In *O. Fuchsii* populations elsewhere albino individuals occur at one extreme of the range of colour-variation which agree with the t y p e diagnosis of subsp. *O'Kellyi*, but this fact does not remove the necessity for recognising as a distinct taxonomic entity the race which occurs in Clare and Sutherlandshire. Most Continental authors have ranked *O'Kellyi* as a subspecies or variety of *O. Fuchsii*, or of *O. maculata* L. where that name has been interpreted as covering the diploid section of the aggregate. No Continental races have been identified with subsp. *O'Kellyi*, which therefore stands as a British endemic.

O. Fuchsii subsp. *hebridensis* (Wilm.) H.-Harr. (fig. 3).

The coastal accumulations of calcareous sand in the Hebrides support large colonies of a form of *O. Fuchsii* which is markedly distinct from the type. The plant received recognition in 1939 as *O. hebridensis* Wilm. (W i l m o t t, 1939). Its Hebridean range is now fairly well determined (H a r r i s o n, 1948), and material from Sutherlandshire localities for the subspecies exists in the herbarium of the British Museum. The presence of the subsp. *hebridensis* in Ireland has been reported recently (B r e n a n and S i m p s o n, 1949; H a r r i s o n, 1949; 1950). The Irish habitats are very similar to those favoured by the plant in the west of Scotland; coastal regions where blown sand composed of comminuted molluscan shells has raised the pH of neighbouring peat. It seems probable that the subspecies will prove to have a more
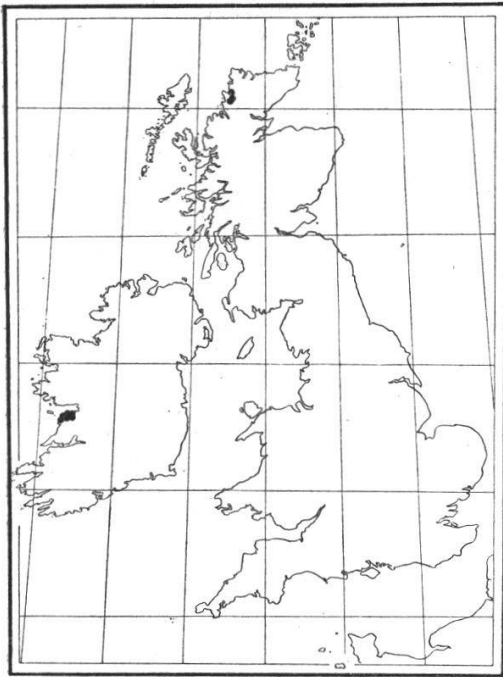
Fig. 2. Distribution of
O. Fuchsii subsp. *O'Kellyi*
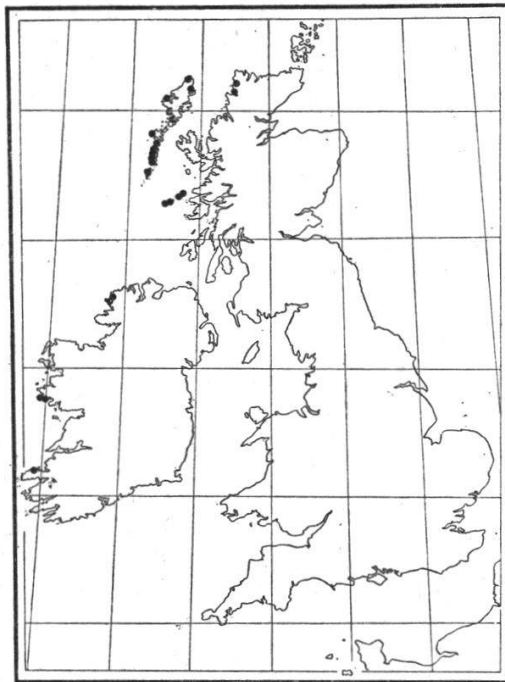
Fig. 3. Distribution of
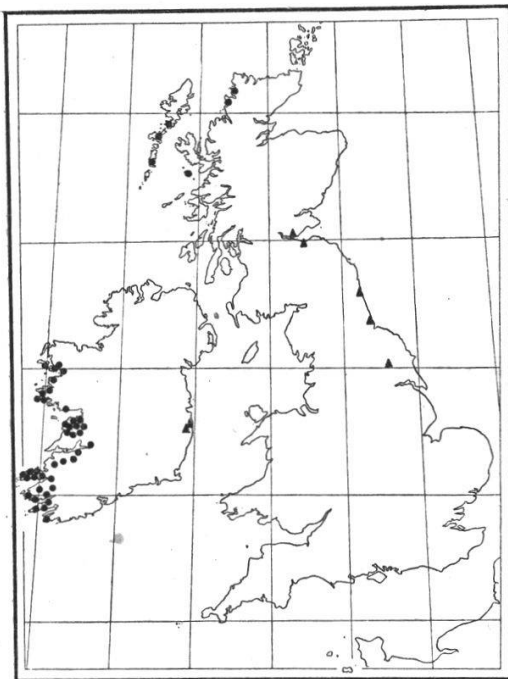*O. Fuchsii* subsp. *hebridensis*

Fig. 4. Distribution of the segregates
of *O. majalis* Reichb.

● subsp. *occidentalis*
(with *kerryensis*)
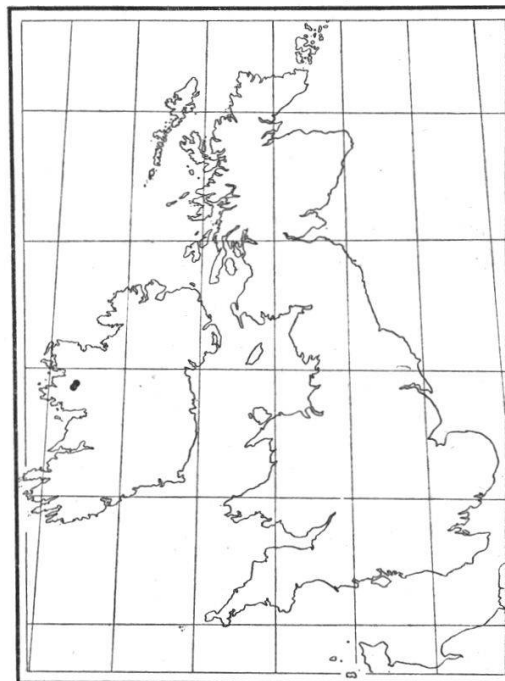▲ subsp. *Traunsteinerioides*.

Fig. 5. Distribution of *O. cruenta*.

extensive range along the western seaboard of Ireland than is in-
dicated in fig. 3.

Vermeulen (1947) suggests that subsp. *hebridensis* may
exist in northern Denmark and southern Norway. His association
of the plant with the tetraploid section of the *maculata* complex
is erroneous; the somatic chromosome number determined from
both Scottish and Irish material is 40.

O. majalis Reichb.

The position of *O. majalis* Reichb., the «*O. latifolia*» of many
Continental authors, in the flora of the British Islands was not
satisfactorily established until 1935, when Pugsley named and
described *O. majalis* subsp. *occidentalis* from several western Irish
localities. In the following year Pugsley recognised a further
Irish subspecies, *O. majalis* subsp. *Traunsteinerioides* (Pugsley,
1936) from material from Co. Wicklow, and Wilmott described
«*O. kerryensis*», another *majalis* form closely connected with the
subsp. *occidentalis*, from Kerry (Wilmott, 1936).

It is unfortunate that the original treatments of the Irish *O.
majalis* failed to take sufficient account of the extreme poly-
morphism of the species. Of the three forms named and described
by 1936, the most distinct is the subsp. *Traunsteinerioides*. This
plant is geographically isolated from the western *majalis* popula-
tions. It is now known to occur in a few stations in northern Eng-
land and southern Scotland, so that the total distribution is as
shown in fig. 4.

The relationship of the two western subspecies, *occidentalis*
and *kerryensis* was investigated in the field by Hall (1937). His
findings suggested that the type descriptions of these two forms
defined the extremes of a highly variable complex of plants, oc-
curring in suitable habitats in a broad coastal belt from west
Cork to west Mayo.

O. majalis subsp. *occidentalis* is now recorded from various
islands in the Inner and Outer Hebrides (Campbell, 1937; J.
W. H. Harrison, 1944), and from west Sutherland (Hall,
1940). The total distribution as at present known is shown in
fig. 4.

O. majalis is one of the most widespread as well as one of the
most polymorphic of the Continental dactylorchids. The range of

the collective species includes practically the whole of western Europe, extending from Portugal into the southern part of the Scandinavian peninsula. The subsp. *baltica* Klinge (*O. latifolia* var. *dunensis* Reichb.) penetrates through central Russia into Siberia and is known from the Caucasus.

O. cruenta Müll.

This is a very recent addition to the list of Irish dactylorchids (H a r r i s o n, 1949 b, 1950 b). It is at present known from the marly shores of Loughs Carra and Mask (fig. 5). A large colony was seen towards the end of the flowering period by members of the I. P. E. during the visit to the shores of Lough Carra near Partry. The Irish form seems to be most closely connected with that described by N e u m a n (1909) from Jämtland in central Sweden under the name *O. cruenta* var. *lanceolata*. The main Continental range of the species is northern, extending from Denmark in the west through Sweden, Finland, the Baltic States and into northern and central Russia. A broad leaved race, corresponding in many respects with the Swedish var. *subelliptica* Neuman, is known from several localities in the Swiss and French Alps.

The nature of the phytogeographical problems which the Irish dactylorchids present will be clear from the preceding accounts and from the accompanying distribution maps. Taking the *O. majalis* subspecies, *occidentalis* and *kerryensis,* as a single taxonomic unit, five of the species and subspecies currently accepted as Irish possess markedly restricted ranges within the country, and of these, four show a western «fringing» distribution in the Britannic area as a whole. Restriction of area may be the result of the operation of factors which are primarily ecological or primarily historical, or it may arise from a complex interaction of both. In a recent paper G o d w i n (1949) has outlined the manner in which the curiously discontinuous distributions of certain components of the British flora may have arisen in post-glacial times as a result of movements and readjustments enforced by continuously changing ecological influences, and has laid emphasis on the importance of competition in this connexion. It seems likely that the distribution of *O. cruenta* can be explained on this basis, a point of view which I have put forward elsewhere (H a r r i-

s o n , 1950 b). Throughout its present European range this species is markedly calcicolous, and one may presume that in late glacial times it occupied a more extensive region in the base rich un-humified soils of that period. The ensuing climatic changes allowed a migration to its present northerly stations, while the development of a strongly competitive lowland marsh flora eliminated it throughout most of its southern range. The remaining southern stations are compensatory in some respect; in the Alps, *O. cruenta* is a plant of high level calcareous marshes (G s e l l , 1935) where competition is reduced; in Ireland it is probable that survival has been possible in the present stations due to the fact that the immigration of many potential competitors was prevented by the early severance of the migratory paths. *O. cruenta* possesses a type of distribution similar to that of *Potentilla fruticosa*, and it seems likely that it has arisen in each case through the same succession of historical causes.

The case of the two subspecies of *O. Fuchsii*, *O'Kellyi* and *hebridensis*, does not appear to be explicable on the basis of area reduction resultant from competition. Here a wide-ranging, successful species, *O. Fuchsii*, is replaced in various western localities by subspecies which are clearly closely allied to the type, but which are nevertheless distinct in the aggregate. Can this be explained on ecological grounds? In favour of an affirmative answer is the fact that in Ireland and Scotland the two subspecies exist under broadly similar hyper-oceanic conditions of climate, and that they occur in each of their stations in similar types of soil: *O'Kellyi* over raw limestone, and *hebridensis* in in stabilised calcareous duneland. The case may be one of direct modification by habitat and climate (one recalls the remarkable modifications which many common species undergo along the Atlantic seaboard of Ireland), or of the selection of morphologically marked ecotypes, again by edaphic and climatic factors.

The features which distinguish the subsp. *O'Kellyi* of north Clare from the neighbouring *O. Fuchsii* populations are striking enough, but nevertheless it does not seem too improbable that they should have arisen through direct modification by habitat. The breeding difficulties already mentioned have so far prevented culture experiments designed to determine the effect of Burren soils upon type *O. Fuchsii*. However, the behaviour of the tetra-

ploid *O. ericetorum* in the Burren district of Clare provides evidence that may be relevant. Despite the calcareous substratum, that species occurs over the entire Burren region in pockets of peat formed over the limestone. But that the race is physiologically abnormal emerges form the fact that comparative analysis reveals a much higher percentage of individuals with totally white, unpatterned flowers and immaculate leaves than is found in the normal moorland populations. This white-flowered *O. ericetorum* race comes into bloom a week or two earlier than the diploid «*O. O'Kellyi*», and its occurrence in the Burren district has led to the suggestion that it, not the *Fuchsii* form, was the original «*O. maculata* var. *immaculata*» of P.B. O'Kelly (P r a e g e r , 1934).

It is less probable that the subsp. *hebridensis* is simply a habitat modification of *O. Fuchsii*. While both in the Hebrides and in Ireland this form is restricted to a particular type of habitat, «typical» *O. Fuchsii* may occupy this same habitat—in many parts of western Ireland the common spotted orchid of the dune meadows is the usual eastern form. In Donegal and Connemara, *hebridensis* colonies show free intergrading with neighbouring *O. Fuchsii*. Further, while in the Outer Hebrides the racial mean is widely different from that of the type *O. Fuchsii* of the mainland, the populations of Coll and Tiree show a slight divergence towards the type species (H a r r i s o n , 1948). It seems likely that the isolated *hebridensis* colonies of the west are the remains of a once continuous population partly differentiated in former isolation, but now, in a few areas, brought back into breeding contact with the main bulk of the species. Distinction is maintained, as in the Hebrides, where isolation continues; elsewhere interbreeding with the more wide-spread eastern form produces a flux of intermediates.

The western Irish *O. majalis* forms seem to provide an example of a similar situation. A difficulty which attended early work on the British marsh orchids was the failure to appreciate that *O. majalis* (*O. latifolia* auct. mult.) was absent from the greater part of the country. It seemed inherently improbable that t h e common marsh orchid of the Continent should be missing from such wide areas of England and Scotland, and the Linnean name «*O. latifolia*» in its *majalis* connotation adhered successively to

O. praetermissa and to *O. purpurella,* and when these were shown to be different from the Continental plant, to some of their hybrids with forms of *O. maculata.* The investigation of the western Irish dactylorchids by P u g s l e y finally revealed a plant which was evidently the authentic Britannic representative of *O. majalis,* in the form which he called subsp. *occidentalis.* As was discovered by H a l l (1937) the plant described later by W i l m o t t under the name «*O. kerryensis*» is not clearly distinguishable from Pugsley's subspecies *occidentalis* either morphologically or geographically. An account of the situation based upon biometrical analysis of population samples is in the course of preparation for publication elsewhere, but the general conclusions from this study can conveniently be summarised here. They are (a) that the early-flowering populations, although highly variable, bear the closest affinity with the principal Continental form of *O. majalis,* and since P u g s l e y 's diagnosis is based upon plants from such a population, they must be recognised as *O. majalis* subsp. *occidentalis:* (b) that Wilmott's description of «*O. kerryensis*» (1936) applies to later flowering, immaculate leaved plants within the variation range of subsp. *occidentalis* (c) that throughout the area of the subsp. *occidentalis* hybridisation with *O. Fuchsii* and *O. ericetorum* occurs rather freely, and (d) that at least towards the northern end of its Irish range, the subsp. *occidentalis* overlaps with *O. purpurella,* and here again hybrid colonies are found.

That crossing should occur between *O. ericetorum* and *O. majalis* subsp. *occidentalis* is not surprising. Both are tetraploids, and although the latter is the earliest flowering of the Irish marsh orchids, reaching a peak in late May, the flowering period of *O. ericetorum* also begins early in the west of Ireland, overlapping with that of the subsp. *occidentalis* by two or three weeks. There is an ecological distinction between the two, *O. ericetorum* being characteristically a plant of peaty soils, and *occidentalis* favouring rich meadowland, but such habitats are frequently juxtaposed in Ireland and the opportunities for crossing are manifold.

The ranges of *O. purpurella* and *O. majalis* subsp. *occidentalis* overlap both in Ireland and Scotland. While the two have similar ecological requirements, they are partly inhibited from crossing by difference in flowering time, since *O. purpurella* reaches a

flowering peak four to six weeks later than *occidentalis*. There seems nevertheless to be some amount of interbreeding in the area of overlap in Ireland, for highly variable colonies with all the marks of hybrid swarms are frequent in Galway. Their flowering continues from late May into mid-July. Exactly similar situations are to be found in the west of Scotland where *O. purpurella* and *O. majalis* subsp. *occidentalis* coexist (P u g s l e y, 1935; H a l l, 1947). Indeed, a process of introgression, involving the «swamping» of isolated *occidentalis* colonies by *O. purpurella* may explain the repeated reports of «off-type» *O. purpurella* (with three-lobed labellum, blotched leaves) from western Scottish localities from which typical early-flowering *occidentalis* is unknown. The parallel between this situation and that outlined above for *O. Fuchsii* and its subspecies *hebridensis* will be clear. In each case we have a race occurring in a series of separate areas isolated in varying degrees. In some, genetical contamination cannot occur because of the absence of close relatives with which crossing is possible, in others a wide-ranging closely related form comes into sufficiently close proximity to allow hybridization to take place. The geographically most isolated populations are the most distinct morphologically; those lying within the area of the potential introgressant seem currently to be losing their identity.

If this interpretation is correct, then it is clear that at least part of the dactylorchid flora of the west of Ireland and the west of Scotland possesses a history different from that elsewhere in the British Islands. In fact, the western dactylorchids must be added to those elements of the Irish and Scottish flora whose present distributions do not accord with a theory of orderly postglacial migration from continental sources v i a England.

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