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A SYNOPSIS OF THE DACTYLORCHIDS OF THE BRITISH ISLES

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Introduction

In accepting the invitation so kindly proffered me by the Rübel Institute to give some account for continental botanists of recent work on the British dactylorchids, I find myself limited by the lack of that personal knowledge of the dactylorchid floras of central and southern Europe which would have allowed me to have attempted an integrative rather than a purely local summary. In so protean a group, literature compilation does not assist one greatly towards a comprehension of the variation pattern, and herbarium specimens are of little assistance when so many of the phenotypic characters of importance are destroyed even with the most careful of pressing. In any case, type descriptions and the study of small numbers of preserved plants can give little appreciation of the phenotypic variability of breeding populations, and it is these, the breeding populations, which must be taken as the units of variation in any attempt to compare the dactylorchid floras of different geographical regions. It is clear that such comparisons should be based upon the biometrical study of adequate population samples of living plants, if any advance is to be made over the orthodox taxonomic approach exemplified by the monographical treatments of CAMUS (1928–29), von Soó (1930–40) and others.

This account, therefore, is mainly restricted to the plants occurring in the British Isles and those continental races with which I have some personal familiarity. While the keys have been constructed so as to cover the taxa cur-

rently recognised in Britain, they may be expected to lead to the identification of most of the north-western European species, and may provide some guide for the detection of infraspecific units at present recorded only from Britain but almost certainly occurring also in neighbouring parts of the Continent. The keys do not of course take into account the northern Scandinavian endemic *Eumaculatae* and *Majales*, or the central European and North African taxa of the subsection *Sesquipedales* Vermeulen.

Nomenclature

In general, the nomenclature of VERMEULEN (1947) has been adopted, with minor modifications. The main one involves the re-uniting of the generic subsections *Majales* (Pugsl.) Vermln., *Angustifoliae* Vermln. and *Subsesquipedales* (Pugsl.) Vermln. in the subsection *Majales* (Pugsl.). The reasons for this change have been given elsewhere (HESLOP-HARRISON, 1954); the principal one is simply that the tetraploid marsh orchids intergrade morphologically to such an extent that it is difficult to point to variational discontinuities upon which species limits may be based, let alone to justify the recognition of taxa of higher rank.

The primary division of the genus *Dactylorchis* (Klinge) Vermln. is into the sections *Iberanthus* (Schlechter) Vermln., *Sambucinae* (Parl.) Vermln. and *Maculatae* (Parl.) Vermln. The section *Iberanthus* contains a single species, the stoloniferous *Dactylorchis iberica* (Bieb.) Vermln. The section *Sambucinae* is composed of three species of which the most widespread is *D. sambucina*, which occurs throughout central and western Continental Europe, extending in Scandinavia north to 61° N. latitude, but not occurring in the British Isles. The palmate orchids proper form the section *Maculatae*, the Britannic forms of which are the topic of this paper. The nomenclature of these may be summarised as follows.

DACTYLORCHIS (Klinge) Vermeulen (1947)

Sect. *Maculatae* (Parl.) Vermln.

I. Subsect. *INCARNATAE* Vermln. (*Latifoliae verae* Pugsl. 1935)

Dactylorchis incarnata (L.) Vermln.

Orchis incarnata L. 1755 sec. Vermln.; *O. latifolia* L. 1753 sec. Pugsl.; *O. strictifolia* Opiz (1825); *O. angustifolia* Wimm. (1829), (non *O. angustifolia* Lois. apud Reichb. 1830); *O. lanceata* Dietr. (1833).

subsp. ***incarnata***

D. incarnata subsp. *lanceata* (Dietr.) Vermln.

subsp. ***cruenta*** (Müll.) Vermln.

Orchis cruenta Müll. (1782); *O. incarnatus* subsp. *cruentus* Asch. and Graebn. (1907).

subsp. ***coccinea*** (Pugsl.) H.-Harr. f.

O. latifolia var. *coccinea* Pugsl. (1935); *O. strictifolia* subsp. *coccinea* Clapham (1952).

- subsp. **pulchella** (Druce) H.-Harr. f.
O. incarnata var. *pulchella* Druce (1918); *O. incarnata* var. *pulchrrior* Druce (1927); *O. latifolia* var. *pulchella* (Druce) Pugsl. (1935).
subsp. **gemmana** (Pugsl.) H.-Harr. f.
O. latifolia var. *gemmana* Pugsl. (1935).
subsp. **ochroleuca** (Boll) H.-Harr. f.
Orchis incarnata β *ochroleuca* (Wüstnei) Boll (1860); *O. incarnatus* race *ochroleucus* Asch. and Graebn. (1907); *O. latifolia* var. *ochroleuca* (Boll) Pugsl. (1935); *O. strictifolia* var. *ochroleuca* (Boll) Hylander (1942).

II. Subsect. EUMACULATAE Vermln. (Maculatae E.G. and A.Camus, 1929).

Dactylorchis maculata (L.) Vermln.

Orchis maculata L. (1753)

[subsp. **maculata**

Dactylorchis maculata subsp. *typica* Vermln.; not British: see Heslop-Harrison, 1951]

subsp. **ericetorum** (Linton) Vermln.

Orchis maculata var. *praecox* Webster (1886); *O. maculata* subsp. *ericetorum* Linton (1900); *O. elodes* Grisebach (1846)?

Dactylorchis fuchsii (Druce) Vermln.

Orchis maculata var. *trilobata* de Bréb. (1837); *O. maculata* var. *meyeri* Reichb. f. (1851); *O. maculata* var. *obscura* Neuman (1909); *O. fuchsii* Druce (1914).

subsp. **fuchsii**

Dactylorchis fuchsii subsp. *typica* Vermln.

subsp. **hebridensis** (Wilm.) H.-Harr. f.

Orchis hebridensis Wilmott (1939); *O. fuchsii* var. *hebridensis* (Wilm.) H.-Harr. p. (1940); *O. maculata* subsp. *cornubiensis* Pugsl. (1940) *Dactylorchis maculata* subsp. *hebridensis* Vermln.; *Orchis fuchsii* subsp. *hebridensis* (Wilm.) Clapham (1952).

subsp. **okellyi** (Druce) Vermln.

Orchis maculata var. *okellyi* Druce (1909); *Orchis okellyi* Druce (1914).

III. Subsect. MAJALES (Pugsley) H.-Harr. f.

Dactylorchis majalis (Reichb. p.) Vermln.

Orchis latifolia Sturm (1799), Fries (1842) et auct. mult., non *O. latifolia* Linnaeus.

[subsp. **majalis**

Not British.]

subsp. **occidentalis** (Pugsl.) H.-Harr. f.

Orchis majalis var. *occidentalis* Pugsl. (1935); *O. occidentalis* (Pugsl.) Wilm. (1938); *Dactylorchis occidentalis* (Wilm.) Vermln.; *Orchis kerryensis* Wilm. (1936); *Dactylorchis kerryensis* (Wilm.) Vermln.

Dactylorchis traunsteineri (Saut.) Vermln. (1949).

Orchis traunsteineri Saut. ex Reichb. p. (1830); *O. majalis* subsp. *traunsteinerioides* Pugsl. (1936); *O. traunsteinerioides* Pugsl. (1940); *Dactylorchis traunsteinerioides* (Pugsl.) Vermln.

Dactylorchis praetermissa (Druce) Vermln.

Orchis praetermissa Druce (1913); *O. pardalina* Pugsl. (1935)

Dactylorchis purpurella (T. and T.A. Stephenson) Vermln.

Orchis purpurella T. and T.A. Stephenson (1920).

General Aspects of Variation in the Genus

As first demonstrated by DARWIN (1862) and MÜLLER (1883), the floral mechanism of the dactylorchids acts as an effective agent to promote cross-pollination and to exclude the possibility of self-pollination, even of one flower from another of the same inflorescence. Although MARTENS (1926) has suggested that self-pollination may occur in a Belgian form of *D. maculata*, no evidence that this is in any sense a common occurrence has come to light in an extensive investigation of the British taxa, and HAGERUP's observations on Faroese *D. maculata* (1951) show that self-pollination cannot be general even where pollinating insects are scarce.

Guarded against self-pollination by the elaboration of their floral mechanisms, the dactylorchids have not apparently developed genetical incompatibility systems. In artificial self-pollination tests in which pollinia of freshly opened flowers were transferred to the stigmatic surface of the same flowers, normal seed set has been obtained with all of the British taxa.

In the last two decades practically all of the European representatives of the genus have been investigated cytologically. The base chromosome number is $x = 20$, and the bulk of the species are diploid, $2n = 40$, and tetraploid, $2n = 80$ (RICHARDSON, 1935; HAGERUP, 1938; HEUSSER, 1938; VERMEULEN, 1938 and HESLOP-HARRISON, 1951, 1953 a and b). The hexaploid number, $2n = 120$, has been reported by VERMEULEN for an Estonian plant referred to *D. traunsteineri*, but it is not yet established whether this number is characteristic of entire populations. Other populations of *D. traunsteineri* are tetraploid (HESLOP-HARRISON, 1953a) and it is possible that the plant examined by VERMEULEN was simply an aberrant individual, perhaps the result of superfertilisation of the type described by HAGERUP (1944) as occurring in *D. maculata*.

Of the generic subsections discussed in this paper, the Incarnatae are characterised by the possession of a uniform chromosome number of $2n = 40$, the Eumaculatae comprise two morphologically differentiated groups, one with a chromosome number of $2n = 40$ and the other with $2n = 80$, and the great majority of chromosome counts in the Majales have given the number $2n = 80$.

All of the Britannic forms of the Incarnatae so far tested are inter-fertile to the extent that cross-pollinations produce a normal seed set. Artificial hybrids between the different forms have not yet been brought to flower, so that the fertility of the F_1 remains to be established. Nevertheless, there is little reason to believe that intrinsic sterility barriers of any magnitude exist within the subsection.

Within the two chromosome series of the Eumaculatae, the morphological characteristics of which are discussed below, there is again no evidence of the existence of sterility barriers. The two groups themselves are, however, partially isolated genetically as is to be expected from their possession of different chromosome numbers. The hybrid between the Britannic representatives of the subsection, the diploid *D. fuchsii* and the tetraploid *D. maculata* subsp. *ericetorum*, "*Orchis* X *transiens*" (DRUCE, 1915), does not appear to be anything like so common in the British Isles as some authors have asserted. Mixed colonies certainly do occur in habitats intermediate ecologically between those normally preferred by the two species, and while triploid plants, presumably of hybrid origin, do occasionally occur in these, it is by no means the case that a complete series of intergrades is always to be found.

The triploid hybrid when it occurs shows high pollen sterility, and studies of its meiosis promise to be of considerable interest, as throwing light on the derivation of the tetraploid group. The various forms of the latter show few of the characteristics of strict autotetraploids, having high fertility and very regular meiosis.

The third subsection, Majales, constitutes the taxonomically difficult group of marsh orchids, containing numerous ill-differentiated or intergrading ecological and geographical races, all in the British Isles with a chromosome number of $2n = 80$. The meiotic behaviour of triploid hybrids between the diploid *D. fuchsii* and two of the British tetraploid marsh orchid species, *D. praetermissa* and *D. purpurella*, has been interpreted as indicating that both of the latter species may be of amphidiploid origin, a form related to *D. fuchsii* having been one of the diploid progenitors (Heslop-Harrison, 1953b). Evidence has also come to hand that *D. traunsteineri*, recently confirmed as a British plant (Heslop-Harrison, 1953a), may have had a similar origin.

If it is permissible to judge from morphological affinities, the most likely source of the other parents which have participated in the hybridisations from which these amphidiploid marsh orchid species have arisen would appear to be the subsection Incarnatae. If this is so, there is an obvious explanation for the nature of the variability of the group. The whole system may have arisen polytopically over a period of time from recurrent hybridisations between different ecological or geographical races of the parental species, the newly originating amphidiploids being reproductively isolated from their progenitors immediately upon the doubling of the chromosome complements which restored fertility, but being all themselves interfertile. Subsequent migration and conjunction of range would provide the oppor-

tunity for hybridisation, with the consequent local blurring and obscuration of such minor morphological differentiae as may have originally given them distinction.

The interfertility of the various British tetraploid marsh orchids, at least to the extent of producing a viable F_1 , has been demonstrated in experimental crossings; again the fertility of the F_1 itself remains to be demonstrated. In experimental work yet to be published, it has been found that on the diploid level, *D. fuchsii* crosses only with some difficulty with the forms so far tested of the Incarnatae. Artificial cross-pollination in both directions produces a relatively low and variable seed set, and when fertilisation is successful, the embryos formed vary considerably in size. This apparent partial inviability or weakness of hybrid embryos is of some interest, since it cannot be due to the usual cause of such phenomena—disharmony of the zygote with the endosperm—since endosperm is not, of course, formed in this genus.

In contrast, good seed is normally produced in artificial crossings in both directions between the tetraploid marsh orchids and the diploid *D. fuchsii* and Incarnatae. The triploid seeds originating from a cross between *D. purpurella* and *D. fuchsii* have been germinated in culture to give vigorous protocorms. Flowering individuals of these hybrids have not been obtained in cultivation, but triploid hybrids of the same presumed parentage are commonly found in mixed colonies in nature, and cytological examination of the course of microsporogenesis in these has been made the basis of the deductions concerning the genesis of the tetraploid marsh orchids mentioned above. The course of megasporogenesis in these triploid hybrids is currently under investigation. The meiotic events appear to be very different on the female side in comparison with the male, and the possibility seems to exist that the partial seed-fertility which these plants show may arise from nuclear restitution followed by the parthenogenetic development of some triploid embryos.

These fertility/sterility inter-relationships discovered in experiment relate directly to the pattern of hybridisation observed in nature. In a previous paper (HESLOP-HARRISON, 1949b) some indication has been given of the relative frequencies of hybridisation between different Irish dactylorchid taxa. Extending consideration to other British forms and incorporating more recent knowledge, this may be summarised as follows:

(a) Between Eumaculatae and Incarnatae. Hybrids are rare, and no extensive hybrid swarms are known. Hybrids of the putative parentage *D. fuchsii* \times *D. incarnata* so far examined have proved sterile, and meiotic studies have not so far been possible.

(b) Between Eumaculatae and Majales. This is the commonest parentage of the extensive hybrid swarms which so complicate the identification of dactylorchids in almost every part of the British Isles. In southern England, hybrid colonies of *D. fuchsii* \times *D. praetermissa* and *D. maculata* \times *D. praetermissa* are commonly found where colonies of the different species adjoin or overlap, particularly in disturbed habitats. In northern England, Scotland and parts of Ireland, similar hybrid swarms occur with *D. purpurella* replacing *D. praetermissa* as the marsh orchid parent, and in south-western Ireland, with *D. majalis*. As stated above, the reproductive behaviour of the triploid hybrids between Eumaculatae and Majales is under investigation.

(c) Between Incarnatae and Majales. Although hybrid swarms do not apparently arise frequently from hybridisations between these subsections in nature, individual hybrids are to be found not uncommonly where the parents occur together. Hybrids between *D. majalis* itself and members of the *Incarnatae* have not, however, so far been observed, although opportunities for crossing would appear to be available in the south-western Irish range of *D. majalis*, particularly with the coastal subsp. *coccinea* of *D. incarnata*, which is plentiful in that region.

(d) Within Majales. The British forms of this subsection are largely vicarious, but where the ranges are contiguous or overlap, there is evidence of extensive hybridisation, producing in some cases the appearance of complete intergradation, as seen for example in *D. majalis* and *D. purpurella* in the west of Ireland and in Scotland. In England, some highly variable colonies of *D. praetermissa* appear to show the influence of former hybridisation with *D. traunsteineri*. In all cases, intermediate forms between the various species of the Majales show normal meiosis and high pollen and seed fertility.

From the following accounts of the British dactylorchid taxa, the occurrence of two somewhat different types of variation in the genus will be apparent. In general terms, it may be said that within the British Isles the Eumaculatae show mainly geographical variation, this being clear enough in *D. fuchsii* to have resulted in the segregation of taxonomic subspecies. Such local ecological variation as is to be found in this species concerns the vegetative organisation, and much certainly arises from direct plastic response during growth to variation in habitat conditions, particularly availability of soil moisture. In *D. incarnata*, in contrast, variation largely concerns the floral characteristics, and is ecologically correlated to some extent. At least within the British Isles, geographical variation is less significant in this group than in *D. fuchsii*. This matter has been discussed elsewhere (Heslop-Harrison, 1953c) and is considered again below.

A putative scheme may be set out to summarise the foregoing characteristics of the variation of the genus in the British Isles as in fig. 1. This indicates the cytological affinities of the taxa, the types of variation encountered in the different subsections and the extent of hybridisation.

Synopsis of the Species

In the operation of the various keys which follow, it is desirable that the characteristics of a reasonably large sample of individuals of the form under examination be taken into account. Many of the diagnostic features show great variability within local populations (as will be apparent from the illustrations of floral parts, Plates I—IV), and anomalous individuals can nearly always be found which in one or more characteristics depart sufficiently from the average to prevent their identification by the use of keys.

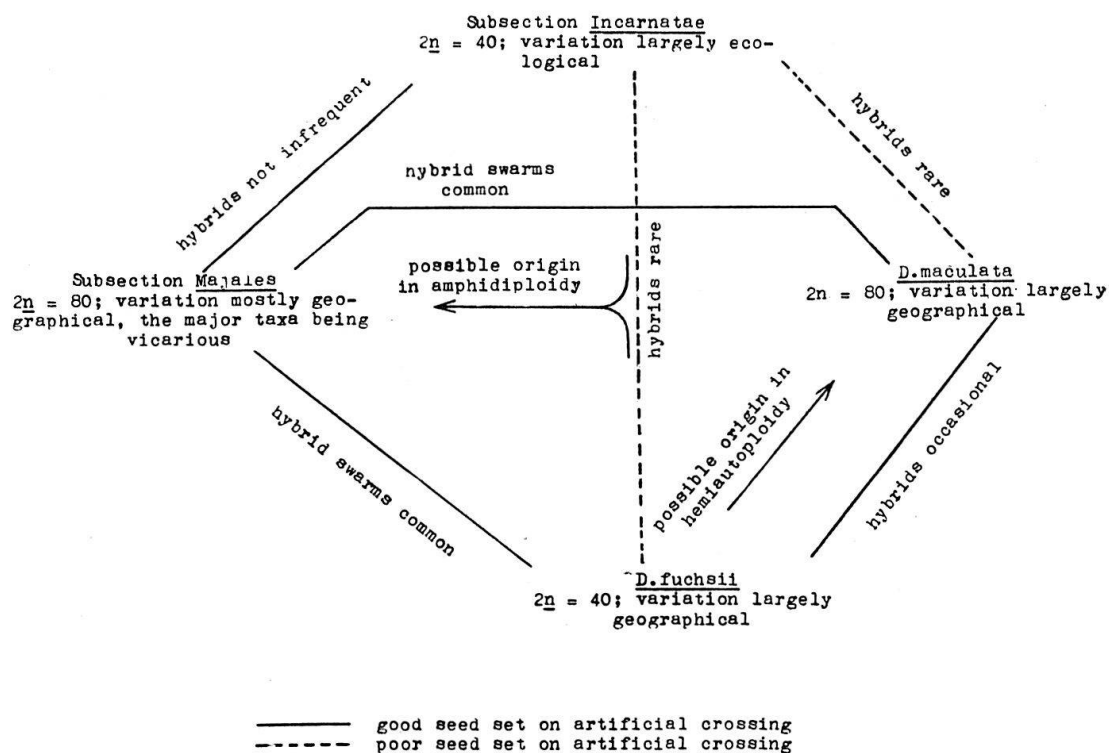


Fig. 1. Putative scheme of inter-relationships in the British dactylorchids.

Hybrid individuals, and naturally also hybrid colonies, will always give trouble in identification. Within the subsection *Majales*, the free formation of fertile hybrids intermediate between the recognised taxa means that some colonies always remain taxonomically indeterminate. In the case of many of the crossings, including some which lead to the formation of hybrid swarms, an assessment of pollen fertility usually provides a ready test of the status

of doubtful individuals. This can be applied to determine hybrids between the diploid and tetraploid *Eumaculatae*, between subsections *Incarnatae* and *Eumaculatae*, between *Incarnatae* and *Majales*, and between *Eumaculatae* and *Majales*.

The technique of observing pollen fertility differs from that normally applicable to plants in which grains are free, because of the production of the pollen in pollinia. As a result of the co-operation of the dysploid nuclei within the massulae of the pollinium, the abortion of micronuclei which, in plants with loose pollen, would normally follow so highly irregular a meiosis as that which occurs in many triploid dactylorchid hybrids, is delayed until after anthesis (HESLOP-HARRISON, 1953b). The simple method of counting empty and malformed pollen grains cannot therefore be applied. Instead, the irregularity of nuclear size and number in the cells of the massula can itself be used as an indication of the course of the preceding meiotic divisions. The pollinia should be dissected from a young flower preferably before the opening of the tepals but after they have begun to colour. A few massulae may then be scraped off onto a slide and the cells loosened by three or four minutes hydrolysis in 10% hydrochloric acid at a temperature of 60—70° C. The acid is then withdrawn and replaced by a drop of aceto-carmin or aceto-orcin (saturated solutions of the stains in 45% acetic acid). After a few minutes gentle warming, the cells of the massulae should be spread out by light pressure with a cover-slip, and the preparation examined under the low powers of the microscope. In a normal fertile individual, two nuclei, tube and generative, differing slightly in size and staining power, will be seen in each cell. Where meiosis and the ensuing pollen mitosis has been irregular, the nuclei in the separated cells of the massulae will be found to vary greatly in size and number.

Dactylorchis (Klinge) Vermln., Section *Maculatae*:

Key to subsections present in central and north-western Europe.

1. Stem solid throughout most of its length; upper non-sheathing bract-like leaves two or more in number (except in the northern part of the range); lower bracts relatively narrow (3 mm or less); flower spur slender (up to 2 mm) chromosome numbers $2n = 40$ and $2n = 80$ *Eumaculatae*

Stem usually hollow throughout most of its length (cavity narrow in some species of subsection *Majales*); 0, 1 or 2 non-sheathing, bract-like leaves on the upper part of the stem; spur usually stout (> 2 mm); lower bracts relatively wide (> 3 mm).

. 2.

2. Stem cavity wide (usually exceeding $\frac{1}{2}$ total diameter); leaves yellow-green, erect, narrowing almost from the base; leaf tip markedly hooded (cucullate); flowers relatively small, labellum generally less than 8 mm in width, its sides often reflexed laterally; chromosome number $2n = 40$ *Incarnatae*

Stem cavity medium or small (often less than $\frac{1}{2}$ total diameter); leaves dark green, often spreading, broadest above the base, ovate (linear in *D. traunsteineri*), apex not or only slightly hooded; flowers mostly large (smaller in *D. purpurella*); labellum generally considerably greater than 8 mm in width (c. 8 mm in *D. purpurella*), its sides \pm reflexed laterally (*D. majalis*, *D. traunsteineri* etc.) or not at all (*D. purpurella*, *D. praetermissa*); chromosome number, $2n = 80$ Majales.

Subsection *Incarnatae*

This subsection is reasonably well differentiated from others in the genus by a number of morphological features, but within the limits established by these differentiae there is a considerable amount of variation. The continuous or reticulate nature of much of this has made subdivision into species difficult, and many authors have treated the subsection simply as one large polytypic species, defining within it subspecific taxa of various ranks and degrees of differentiation (ASCHERSON and GRAEBNER, 1907; CAMUS, 1928—29).

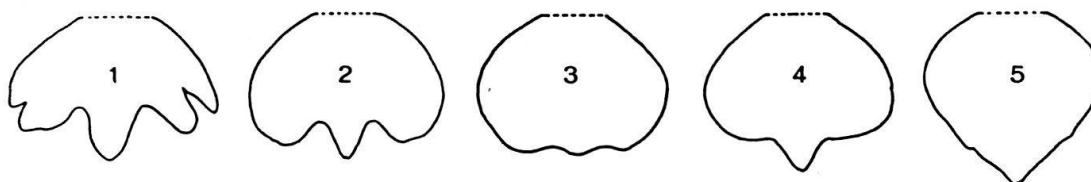


Fig. 2. Labellum shapes in *D. incarnata*.

Within the British Isles, the vegetative organisation of plants of this subsection (all placed here in the taxonomic species, *D. incarnata*) is on the whole rather constant. Much of the variation in vegetative parts is directly conditioned by environmental influences; plant stature can, for example, be altered within fairly wide limits from year to year in cultivation by governing the amount of soil moisture available. Certain habit features are, however, peculiar to particular races and may be genetically determined, in that they cannot be entirely eliminated by alteration of the conditions of cultivation of transplanted adult plants. The characteristic form of stabilised coastal duneland, subsp. *coccinea*, which is usually somewhat dwarf in stature, will normally develop to a greater size in cultivation when protected from the effects of grazing and trampling, but transplanted individuals still tend to retain the recurved leaf posture which is a feature of the plant in nature.

The floral variation of *D. incarnata* in Britain is more striking, and it is this which has attracted most taxonomic attention. The flower colour range includes pure white, yellowish-white (approaching Séguy Colour Standard 270, Séguy, 1936), flesh-pink (Séguy tints 18, 19 and 20; matched well also by the illustration given for *Orchis incarnata* by FISCHER and NELSON, 1931),

magenta (Séguy tints 58 and 59 and more intense), the deepest tints being ruby-red to maroon (somewhat deeper than Séguy 51). There is in addition considerable variation in labellum size, shape and patterning. The range of shape and patterning is illustrated in figs. 2 and 3. The shapes and patterns in these figures are not in any sense intended to represent modal types, but merely illustrate convenient reference points in what is a continuous variation range. They have been adopted as arbitrary standards in scoring the variation in these features, and distributions obtained by scoring some characteristic populations are given below in Table I.

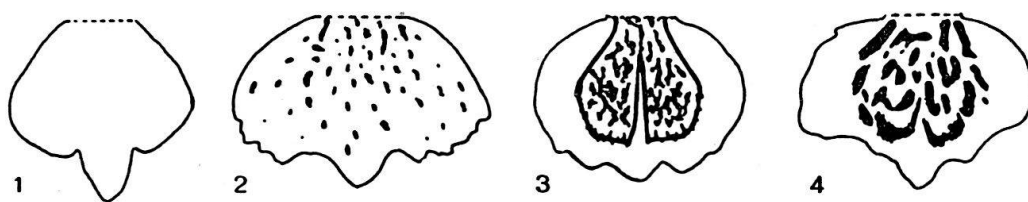


Fig. 3. Labellum patterns in *D. incarnata*.

Attempts to give recognition to the internal diversity of *D. incarnata* by taxonomic subdivision have, as already stated, not been outstandingly successful, due to the intergrading or reticulate nature of much of the variation. Little justice is done to the actual variation pattern within the species by concentration upon individual variants. For this reason, no attempt has been made here to apply to the British forms the nomenclature of VERMEULEN (1949), who has described and named nineteen varieties and forms of the species from Holland. While some of these are evidently represented by populations of appreciable size, the bulk appear to be based upon small numbers of selected individuals characterised by one or more distinctive morphological features. Some of the labellum shape and pattern variants named by VERMEULEN are to be found together in almost any breeding population, and they represent no doubt simply extreme types which arise from time to time in the normal course of genetical segregation and recombination.

A more fruitful approach is perhaps to be found in the study of the characteristics of the breeding populations themselves. Difficulties arise here also, however, from the reticulate form of the variation. This is exemplified by the situation in the British Isles. Intraspecific taxa have been established by DRUCE (1918), PUGSLEY (1935) and others to embrace what have appeared to be distinct enough local forms, and these have been based often enough upon more than one diagnostic feature. The same character combinations are frequently found to recur in colonies remote from the original type area, and to this extent some of these intraspecific taxa may be looked upon as

giving a reasonably objective picture of part of the variation. But the systems of character correlation upon which this type of taxonomic subdivision is based are not by any means universal. They break down in two ways: through the existence of populations of low variability which possess character combinations unlike those found in the more widely ranging varieties which happen to have gained taxonomic recognition, and through the existence of populations of high intrinsic variability, within which individuals show apparently random combinations of characters.

Part of the infraspecific variation of *D. incarnata* is, however, ecologically based. The collective species has a fairly wide ecological tolerance range, and within this range, the more extreme types of habitat are commonly found to be colonised mainly by populations which show a relatively narrow variation range and which are often characterised by distinctive morphological features. Today, the polymorphic colonies, at least in the British Isles, are mostly restricted to areas where there has been an extensive history of human interference with habitats: they are, for example, to be found in the severely modified marshes and fens of East Anglia.

It is therefore perhaps most satisfactory to base a taxonomic subdivision upon the definition of a number of reasonably well differentiated habitat races, representing, as it were, the specialised "radiations" of the species which today show relative homogeneity, recognising at the same time that polymorphic colonies exist within which all of the phenotypic characteristics of the ecological races may appear together, intergrading, or in atypical combinations.

In the British Isles, the bulk of the habitat races can conveniently be placed in six groups which appear to have sufficient distinction to justify taxonomic recognition as subspecies, and the key which follows is intended to allow the identification of these. As with others in this paper, it is essential to realise that this key is intended for application to populations and not to individuals. Polymorphic populations cannot, as populations, be justifiably assigned to these subspecies.

1. Anthocyanin pigmentation totally absent from the plant; flowers creamy, or yellowish-white; labellum mostly shape grade 1 (fig. 2). subsp. *ochroleuca*
 Anthocyanin pigment present in the flowers; labellum shapes mainly grades 2, 3, 4 and 5 2
2. Flower colour flesh-pink 3
 Flower colour purple, magenta, ruby- or crimson-red (to maroon on drying) 4
3. Labellum small (< 8 mm in width, < 7 mm in length), pattern mostly grade 3 (fig. 3); leaves usually 4 or 5 in number; overall stature up to 40 cm. subsp. *incarnata*

Labellum large (> 9 mm in width, > 7 mm in length), pattern mostly grades 1 and 2; leaves 6 or more in number; stature often greatly exceeding 40 cm.

- subsp. *gemmana*
- 4. Flower colour magenta or purple, labellum shape mostly grades 4 and 5 5
 Flower colour ruby- or crimson-red, labellum shape mostly grades 2 and 3; leaves often relatively broad and recurved subsp. *coccinea*
- 5. Leaves without spots, blotches or fields of colour subsp. *pulchella*
 Leaves of some individuals with spots, blotches or zones of reddish or purplish pigment, mostly on both upper and lower surfaces subsp. *cruenta*

subsp. *incarnata*

This, the type form of the species, is in Britain characteristic of marshy soils with high mineral content and base status, tolerating a soil-*pH* range of 6.0—8.0. In the southern counties of England it is plentiful in the water meadows which adjoin many of the streams and rivers which drain the chalk, and in parts of East Anglia, colonies of fairly uniform facies are to be found in river-side sedge meadow and in areas subject to inundation where fen peat has been cut back to the level of the mineral soil. The form is probably less common in the north and west of the British Isles, but it is nevertheless widespread, occurring in marshes generally where there is active movement of soil water. In southern England, the flowering period commences in May, reaching a peak in early June. In the northern part of the range colonies continue flowering into early July. Some biometrical data for a sample from a characteristic southern English population are given in Table I. Labella from homologous flowers of a sample of 27 individuals are illustrated in Plate I A.

subsp. *coccinea*

Populations referable to this subspecies are characteristically found in moist hollows in stabilised coastal duneland, usually on sandy humus 5—10 cms. deep, with a *pH* at tuber depth ranging from 6.5—8.5. The associated flora often includes such characteristic species as *Carex arenaria*, *Salix repens* and the duneland form of *Epipactis palustris*. The subspecies is common along the western seaboard of the British Isles, occurring in suitable localities from Devon to the Orkneys. East coast colonies are somewhat fewer. In Ireland colonies referable to this subspecies occur inland, particularly about the lakes of the central limestone plain.

In exposed habitats and under the pressure of grazing, the habit becomes very dwarf, and plants may flower vigorously at a height of less than 5 cms. The flowering peak is a fortnight or so later than for subsp. *incarnata* at similar latitudes. Some biometrical data for a characteristic sample are given in Table I, and flower dissections are illustrated in Plate I B.

subsp. *ochroleuca*

Homogeneous colonies referable to this subspecies are rare in the British Isles, being known only from East Anglia and South Wales. In East Anglia, plants of the typical *ochroleuca* facies occur in dense reed-swamp dominated by *Phragmites communis* and *Cladium mariscus*, on thick fen peat, pH 7.4—8.0. Biometrical data for a Norfolk colony are recorded in Table I. There is little doubt of the identity of this form with the "*Orchis ochroleuca*" of WÜSTNEI (see synonymy, and NANNFELDT, 1944) which has a wide range in continental Europe in similar habitats.

subsp. *gemmana*

Colonies placed in this taxon occur in the Broads district of Norfolk and in western Ireland. In the former area, the habitat is river-side reed-swamp and sedge meadow, usually on saturated peat, pH 6.4—7.0, the associated vegetation being mainly dominated by *Phragmites communis* and the larger sedges. The form is particularly robust, individuals achieving a stature of 80 cm, and leaf lengths up to 30 cm. As will be seen from the biometrical data recorded in Table I, the average labellum and spur size, leaf dimensions and leaf number considerably exceed those found in most other subspecies of *D. incarnata*. In these characteristics the form resembles southern European dactylorchids placed by VERMEULEN in the subsection Sesquipedales, but various qualitative features and the possession of a chromosome number of $2n = 40$ suggest that it is correctly placed under *D. incarnata*. Labella are illustrated in Plate I C.

subsp. *pulchella*

This subspecies is here used as a taxonomic repository for a variable series of populations of *D. incarnata* all of which are characterised by magenta or purplish flower colour, but which intergrade in other morphological features to a degree preventing further taxonomic subdivision in the present state of knowledge. Labella of population samples of two extreme types are illustrated in Plate I D and E, and biometrical data from these are given in Table I. The Hampshire sample is from the New Forest, the type area of DRUCE's *Orchis incarnata* var. *pulchella* (Druce, 1918) upon which this subspecies is based. In this district, the plant occurs in bogs usually accompanied by *Schoenus nigricans* on peat with a pH c. 5.5. Plants of similar facies occur plentifully in the same type of habitat in Surrey and Dorset. This form, apart from the magenta-purple flower colour, is characterised by a somewhat pointed labellum (mostly shape grades 4 and 5, fig. 2) bearing an irregular

Table I *Dactylorhiza incarnata*. Biometrical data from samples of 50 individuals from some representative British populations

Locality		sub-species	Characters listed below							
			A	B	C	D	E	F		
Water meadow, Hampshire	I	<i>incarnata</i>	5.3±0.08	6.4±0.09	7.3±0.07	2.5±0.02	28.5±0.7	4.8±0.07		
Dune flat, Co. Donegal	II	<i>coccinea</i>	6.2±0.07	7.7±0.13	7.5±0.10	2.7±0.05	18.6±0.4	5.0±0.10		
Reed-swamp, Co. Norfolk	III	<i>gemmana</i>	7.7±0.16	9.7±0.12	8.4±0.07	3.5±0.06	47.8±1.3	6.1±0.08		
Cladium fen, Co. Norfolk	IV	<i>ochroleuca</i>	6.6±0.08	8.8±0.14	8.4±0.09	2.9±0.04	45.4±1.2	4.8±0.08		
Schoenus bog Hampshire	V	<i>pulchella</i>	6.4±0.07	7.5±0.12	7.2±0.06	3.4±0.05	24.6±0.8	4.7±0.11		
Sedge meadow, Co. Donegal	VI	<i>pulchella</i>	5.6±0.07	6.0±0.07	7.3±0.07	2.5±0.04	26.8±0.9	3.9±0.08		
Samples (as above)		Labellum								
		Shape grades					Pattern grades			
1	2	3	4	5	1	2	3	4		
I	—	8	86	6	—	2	11	82	5	
II	—	—	56	40	4	—	—	86	14	
III	2	14	46	34	4	4	96	—	—	
IV	63	31	6	—	—	100	—	—	—	
V	—	—	12	36	52	—	—	7	93	
VI	—	—	23	52	25	46	54	—	—	
A Labellum length, mouth of spur to tip (mm)										
B Labellum width at broadest point (mm)										
C Spur length (mm)										
D Spur width 1 mm from mouth (mm)										
E Overall stature, excluding tubers (cm)										
F Number of expanded foliage leaves per plant, excluding lower scale-like sheathing leaves.										
Labellum shape and pattern: distributions showing % in each class scored by reference to the standards of figs. 2 and 3.										

pattern of lines and bars (pattern grade 4, fig. 3). The Donegal colony occupies an area of mildly acid bog-land with ground-water pH c. 5.0, associated vegetation including much *Sphagnum palustre* and *S. papillosum*. Compared with the New Forest sample, it will be seen that the labellum is somewhat smaller, and while showing a similar shape range, it is either concolorous or patterned with fine dots.

Populations corresponding with these, or intermediate between them, are scattered throughout the British Isles, showing apparently little or no geographical regularity, but distributed ecologically so as to suggest that some sort of ecocline relationship may exist. It is probable that populations of this same complex may have formed the basis of HAUSSKNECHT's *Orchis incarnata* var. *serotina* (SCHULTZE, 1894) described by VON SOÓ (1930—40) as a *Sphagnum*-bog ecotype of the species.

Flowering begins in southern English *pulchella* populations in late May, but in western Ireland, where plants occur thinly scattered over areas of blanket bog, individuals may be found flowering as late as early August.

subsp. *cruenta*

A few populations of *D. incarnata* otherwise referable to subsp. *pulchella* are characterised by the occurrence of individuals which show a fine pinpoint dotting of the leaves, similar to that found in *D. purpurella*. These populations link the subsp. *pulchella* with the present one, which is often maintained as a separate species, *D. cruenta*, because of the very distinctive appearance of plants in which the anthocyanin pigmentation of the vegetative parts is developed to its fullest extent. In these, the upper and lower surfaces of the leaves may be practically entirely suffused with reddish or purplish pigment which extends into the upper part of the stem and the inflorescence (HESLOP-HARRISON, 1950). In the British Isles, plants of this extreme type seem to be restricted to the neighbourhood of the lakes of the western part of the Irish limestone plain, in Cos. Clare, Galway and Mayo. These colonies occur in highly calcareous *Schoenus nigricans* and *Cladium mariscus* fen, broadly similar to the type of habitat in which subsp. *cruenta* occurs in Scandinavia. The connections between the Scandinavian and Irish subsp. *cruenta* and that of the Central European mountains has been discussed elsewhere (HESLOP-HARRISON, 1950; see also PUGSLEY, 1935; GSELL, 1935, and WILMOTT, 1938).

Subsection *Eumaculatae*

VERMEULEN (1947) includes four species in this subsection, *D. maculata* (L.) Vermln., *D. fuchsii* (Druce) Vermln., *D. foliosa* (Soland.) Vermln. and

D. maurusia (Emberger and Maire) Vermln. *D. foliosa* is endemic to Madeira, although it has been introduced successfully as a garden plant in Britain. The status of the North African *D. maurusia* is dubious; in some respects the plant seems to form a connecting link between this subsection and the Incarnatae.

The Eumaculatae of central and north-western Europe are distinguished from all Incarnatae and most Majales by the possession of a solid stem. Hollow-stemmed forms agreeing in other features do, however, occur in northern Spain and A. and D. LÖVE (1948) have described a subspecies *islandica* of *D. maculata* from Iceland in which the stem is hollow.

In Europe, the important line of subdivision in the Eumaculatae is between the two chromosome groups, the diploid and the tetraploid, represented respectively by the polytypic species *D. fuchsii* and *D. maculata*. In superficial characters these species show a good deal of resemblance, and in some parts of the European range, particularly towards the north, the convergence is such that the presence of two entities has not generally been appreciated. Certain morphological features do, however, practically always provide the means for discriminating the two cytotypes, in particular the shape of the labellum. Fig. 4, reproduced from an earlier paper concerned with the discrimination of the cytotypes in Scandinavia (HESLOP-HARRISON, 1951) illustrates characteristic labellum shapes and also the derivation of a simple shape index which has proved efficient in biometrical discrimination of

populations of the two. The index is the ratio $\frac{2A}{B+C}$ (HESLOP-HARRISON, 1948).

The species may be keyed out as follows:

1. Labellum markedly three-lobed, the lobes sub-equal in width, the central one extending beyond the laterals, so that the shape-index (fig. 4) lies mostly between 1.2—1.6; lowest expanded leaf broad, obovate, blunt or only slightly pointed at the apex; upper bract-like (non-sheathing) leaves 2—7 in number *D. fuchsii*
 Labellum three-lobed, the lateral lobes large, often crenulate, the central lobe small, rarely as long as the laterals, so that the shape-index lies between 0.8—1.2; lowest leaf lanceolate, acute; upper bract-like leaves 1—3 in number *D. maculata*

The two species are differentiated also in their ecological tolerance, apparently throughout their European ranges. The various forms of *D. fuchsii* occur mainly upon basic or mildly acid soils, pH range 5.0—8.0, in open woodlands, meadows, chalk downs, drained fen peat and occasionally on sand-dunes. *D. maculata* is more characteristic of acid peaty soils, pH range 4.0—5.5, occurring in heaths, moors, acid pastures and in woodlands on base-poor soils.

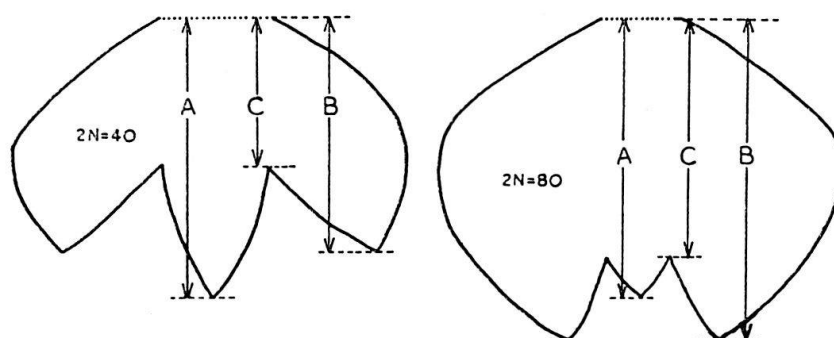


Fig. 4. Labellum shapes in the two cytotypes of the Eumaculatae, showing dimensions used in the derivation of the labellum shape index, which has the value $\frac{2A}{B+C}$. Left, *D. fuchsii*; Right, *D. maculata*.

As in the Incarnatae, much of the vegetative variation is susceptible to direct environmental control, but the bulk of the floral variation is undoubtedly genetic. Colour polymorphism of the type seen in some *D. incarnata* populations is not found in this subsection, and variation in such features as labellum shape and size, flower colour and patterning, leaf-marking and the like, is of a continuous nature suggesting polygenic control.

D. fuchsii

Although the presence of two major entities within the Linnean *Orchis maculata* had long been recognised (at least since de BRÉBISSE, 1836), DRUCE (1914) appears to have been the first author to distinguish as a taxonomic species an undoubted form of the diploid section of the aggregate. Populations of a similar facies to those found in Berkshire, the type area of Druce's species, occur in suitable habitats throughout England and Wales except in western Devon and Cornwall, throughout most of the Scottish mainland, and throughout most of Ireland except in some western localities. Although there is considerable variation in size and habit throughout this distributional area, some of which is clearly correlated with ecological conditions, there is substantial homogeneity in floral characteristics. The flower colour range is from white through pale lilac and rose to magenta (Séguy tints 2—5, 7). Some impression of the range of variation in labellum size, shape and patterning can be gained from Plate II. Biometrical data for two typical colonies are given in Table II.

In the Britannic area, two groups of populations show sufficient distinction to warrant recognition as taxonomic subspecies within *D. fuchsii*, and both are restricted to the western seaboard. These constitute the subspecies *okellyi* and *hebridensis*, a brief account of which has already been given in this

Table II *Dactylorchis fuchsii* and *D. maculata*

Biometrical data from samples of 50 individuals from some representative British populations

Taxon and locality	Characters listed below					
	I	II	III	IV	V	VI
<i>D. fuchsii</i>						
subsp. <i>fuchsii</i> water-meadow, Suffolk	9.3±0.15	1.55±0.023	6.0±0.09	1.32±0.037	46.8±1.12	7.9±0.12
subsp. <i>fuchsii</i> chalk down, Hampshire	9.0±0.13	1.47±0.015	5.9±0.11	1.50±0.037	23.5±0.67	7.5±0.21
subsp. <i>hebridensis</i> , coastal meadow, Co. Galway	12.3±0.18	1.39±0.016	7.8±0.11	1.72±0.041	30.9±0.93	6.5±0.18
subsp. <i>okellyi</i> limestone pavement, Co. Clare	9.7±0.11	1.38±0.017	6.0±0.07	1.51±0.036	17.1±0.43	6.7±0.13
<i>D. maculata</i>						
subsp. <i>erictorum</i> , heath land, Hampshire	9.5±0.13	1.09±0.008	5.6±0.09	1.00±0.022	23.3±0.50	6.7±0.11
subsp. <i>erictorum</i> , mountain pasture, Ross-shire	8.3±0.17	1.06±0.010	4.9±0.12	0.99±0.028	22.7±0.62	5.6±0.15
I Labellum width at broadest point (mm) II Labellum shape index, derived as in fig. 4 III Spur length (mm) IV Spur width (mm) V Overall stature, excluding tubers VI Number of expanded foliage leaves per plant, excluding basal leaf-scales.						

shallow, highly calcareous soils overlying limestone. There is clearly some association between occurrence in this type of habitat and a shift to lower intensities of flower pigmentation in both diploid and tetraploid forms of *D. maculata*. In the limestone district of north Co. Clare in Ireland, the tetra-

ploid *D. maculata* subsp. *ericetorum* shows an unusual abundance of white-flowered individuals, and in Continental Europe, such white-flowered races of *D. maculata* as Krockner's "*Orchis candidissima*" (Krockner 1814) are recorded from districts where limestones predominate.

D. maculata

This, the tetraploid section of the *Eumaculatae*, is represented in north-western Europe by a number of local races some of which have in the past been considered distinct enough to merit segregation as separate taxonomic species. In view of the great intrinsic variation of most populations and the intergradation which neighbouring colonies tend to show, this would seem not to be warranted, and a taxonomic treatment based upon the recognition of a number of subspecies appears more appropriate. A biometrical comparison of some Swedish and British populations (HESLOP-HARRISON, 1951) has shown that the southern Swedish lowland form of the species, corresponding with subsp. *maculata*, has no exact counterpart in the British Isles, and the separation of the British race as subsp. *ericetorum* appears therefore justified. The two subspecies are distinguished by a considerable difference in average flower spur dimensions, 8.0×1.8 mm in subsp. *maculata*, and 6.5×1.0 mm in subsp. *ericetorum*. At high altitudes in central Scandinavia, a race comparable with subsp. *ericetorum* exists, and some populations of Germany, northern France and the Low Countries are closely similar. The relationship between subsp. *ericetorum* and GRISEBACH's *Orchis elodes* (Grisebach, 1846), the type area of which is in northern Holland, requires investigation, since Grisebach's very full description of his species (quoted by Godfery, 1921) suggests that the same race may have been involved.

D. maculata subsp. *ericetorum* occurs throughout the British Isles, attaining its greatest abundance in the west and north on peaty, base-poor soils overlying siliceous rocks. Like other races of the species, subsp. *ericetorum* shows an extraordinary range of floral variability, particularly in the size, shape, colour and patterning of the labellum (Plate IID). Although occasional isolated colonies may be found which exhibit only part of the total form range of the subspecies, the majority reveal great polymorphism. The span of variation is, however, fairly constant throughout the British Isles, and there is less sign of the type of regional variation which has led to the taxonomic subdivision of *D. fuchsii* within this area. The dwarf character of montane and maritime races (e.g., *Orchis maculata* var. *praecox* of WEBSTER, 1886, described from Welsh mountain pastures) appears to be mainly due to direct environmental modification, and certainly these cannot be separated from

colonies occurring in more favourable habitats on the basis of floral characteristics. As mentioned above, a race with a paler average flower colour exists in Co. Clare; this has been confused with *D. fuchsii* subsp. *okellyi* in the same area (PRAEGER, 1934) but it has not gained taxonomic recognition in its own right. Populations in the Inner Hebrides which reach a flowering peak in late July and early August, a month or so later than those of the mainland at similar latitudes, show certain unusual floral characteristics (HESLOP-HARRISON, 1948) and require further investigation.

Subsection Majales

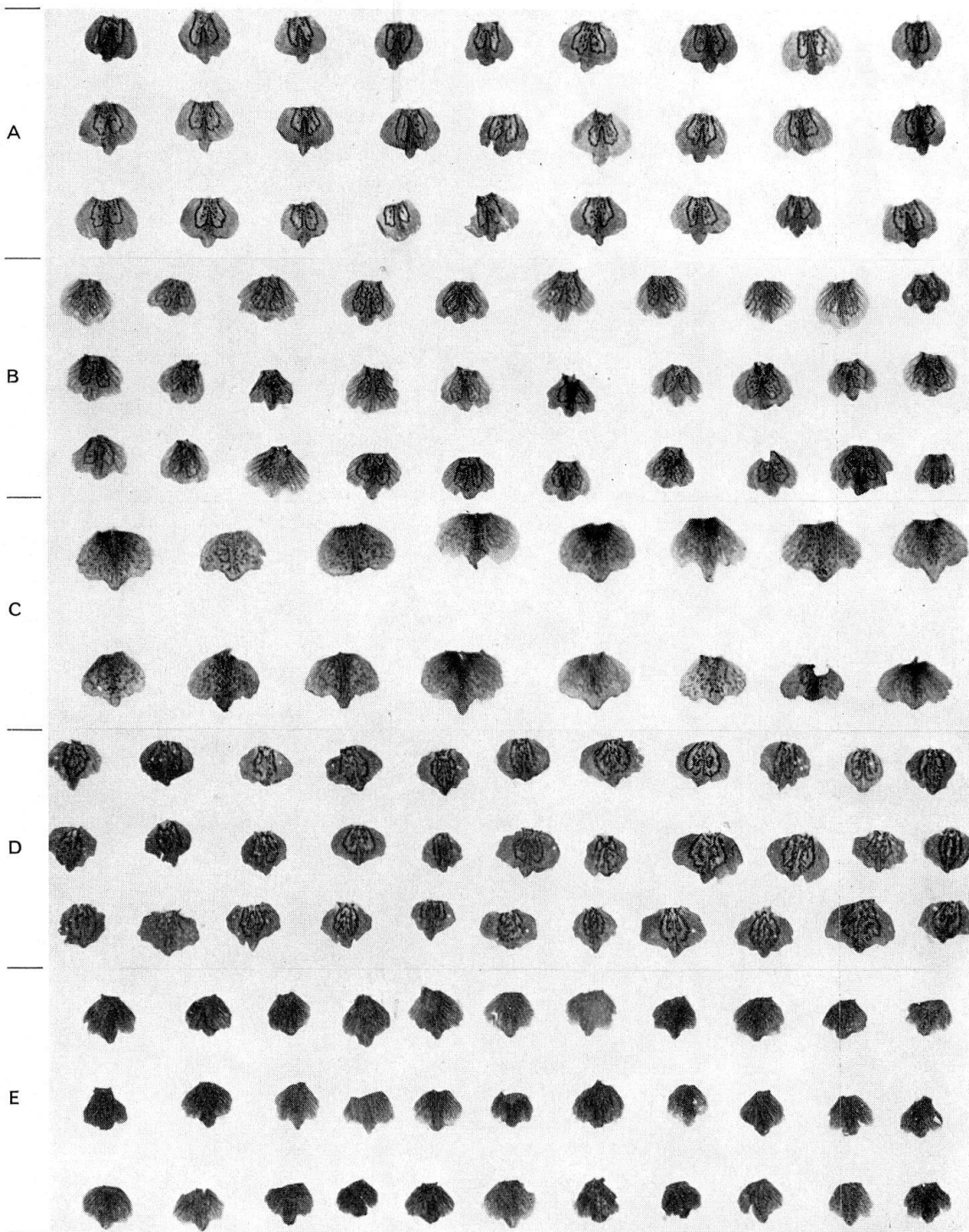
As already indicated, the present-day complexity of this subsection may be attributable to the polytopic origin of its components and their subsequent intergradation through hybridisation. Naturally, in dealing with the flux of poorly differentiated populations which exists in central and north-western Europe, there has been much difference of opinion among systematists as to where lines of demarcation are to be drawn, and it is not surprising that an extensive synonymy has developed.

In Continental Europe, upwards of thirty forms have been named as species which, from their described characteristics, would appear to belong in this subsection as here constituted. The degrees of differentiation and affinities of these cannot be adequately judged from the literature or from the small numbers of preserved plants accessible in herbaria. Confusion has been as rife in the British Isles, where ten or more specific names have been applied. For the purpose of the present account, four major entities are recognised and treated as taxonomic species, although it is appreciated that the degree of differentiation of some of their populations from others is so low that it would be equally justifiable to reduce all to subspecies of a single polymorphic species, *D. majalis*, which is in effect the treatment adopted by CLAPHAM (1952).

The four species may be keyed out as follows:

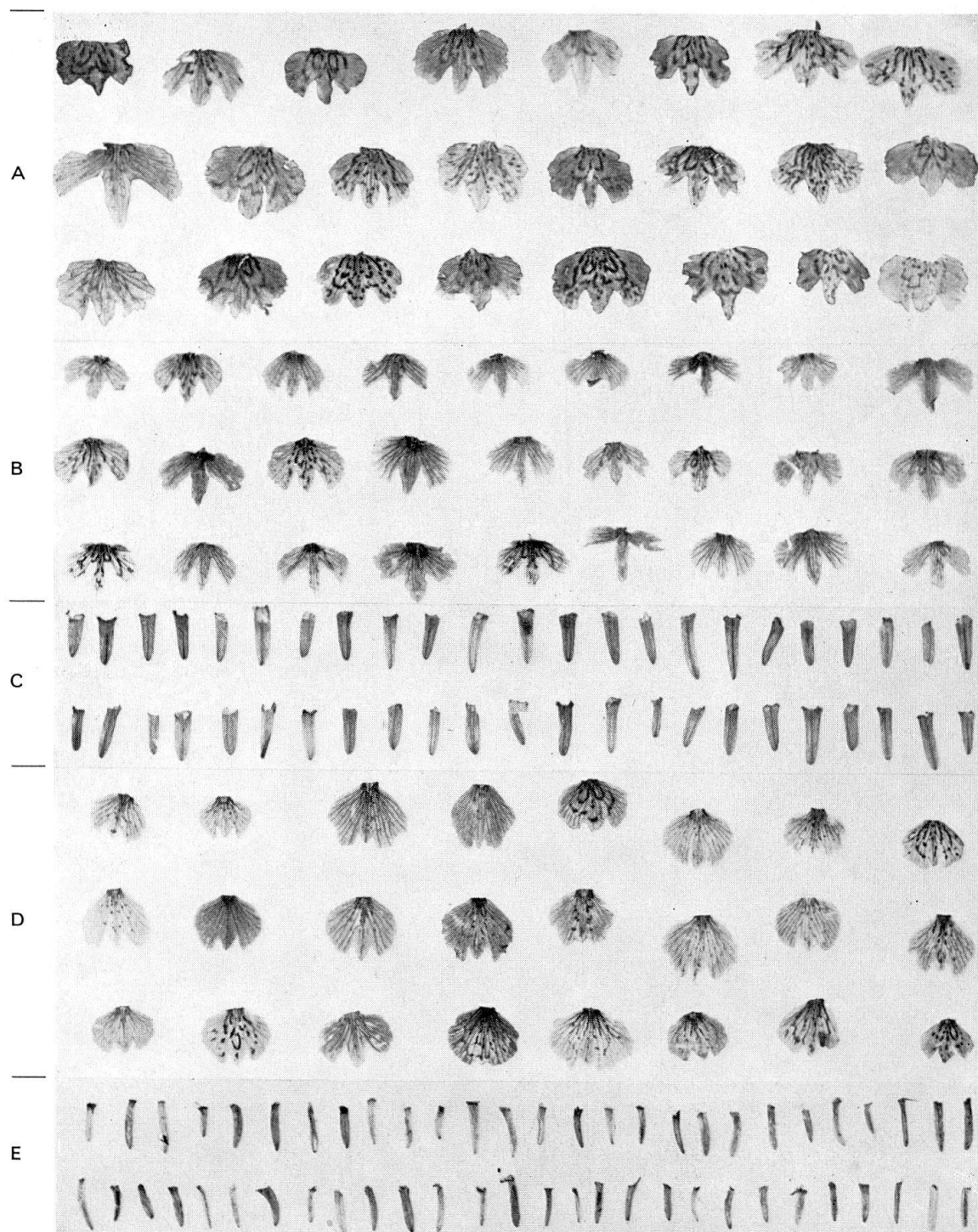
1. Leaves very narrow (mostly less than 1.5 cm in width) lanceolate or linear lanceolate; few in number (usually 3 or four, more rarely 5); often marked with small transverse purple or brownish bars, never with rings or blotches; inflorescence often lax, few-flowered; labellum deltoid or obcordate *D. traunsteineri*
 Lower leaves usually broad (> 1.5 cm) ovate or lanceolate, generally six or more in number, unspotted, marked with fine pin-point dotting, or with ring-spots, or heavy bars and blotches; inflorescence usually many-flowered and dense; labellum elliptical, diamond-shaped or three-lobed with angular incised lateral lobes 2
2. Labellum subentire, ovate or diamond-shaped, small (< 8 mm in width and length), dark, rich reddish-purple in colour, marked with irregular pattern of heavy lines and bars; leaves unspotted or marked with a pattern of pin-point dotting mostly towards the apex *D. purpurella*

Plate I. Labellum mounts from homologous flowers
from population samples of *D. incarnata*, $\times 1$



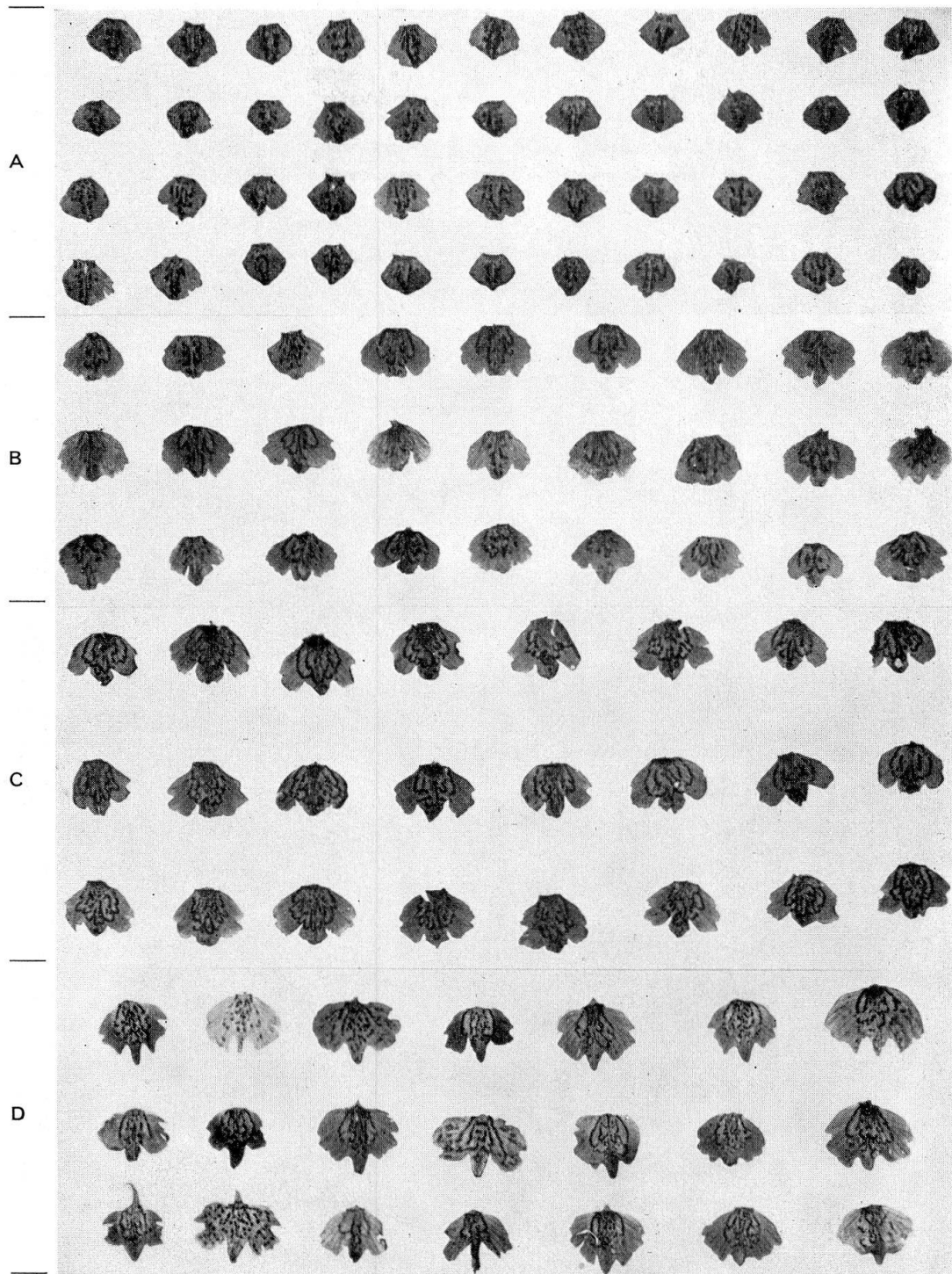
- A. subsp. *incarnata* (Hampshire)
- B. subsp. *coccinea* (Co. Donegal)
- C. subsp. *gemmana* (Norfolk)
- D. subsp. *pulchella* (New Forest, Hampshire)
- E. subsp. *pulchella* (Co. Donegal)

Plate II. Flower dissections of *Eumaculatae*.
 Labella from homologous flowers, $\times 1$



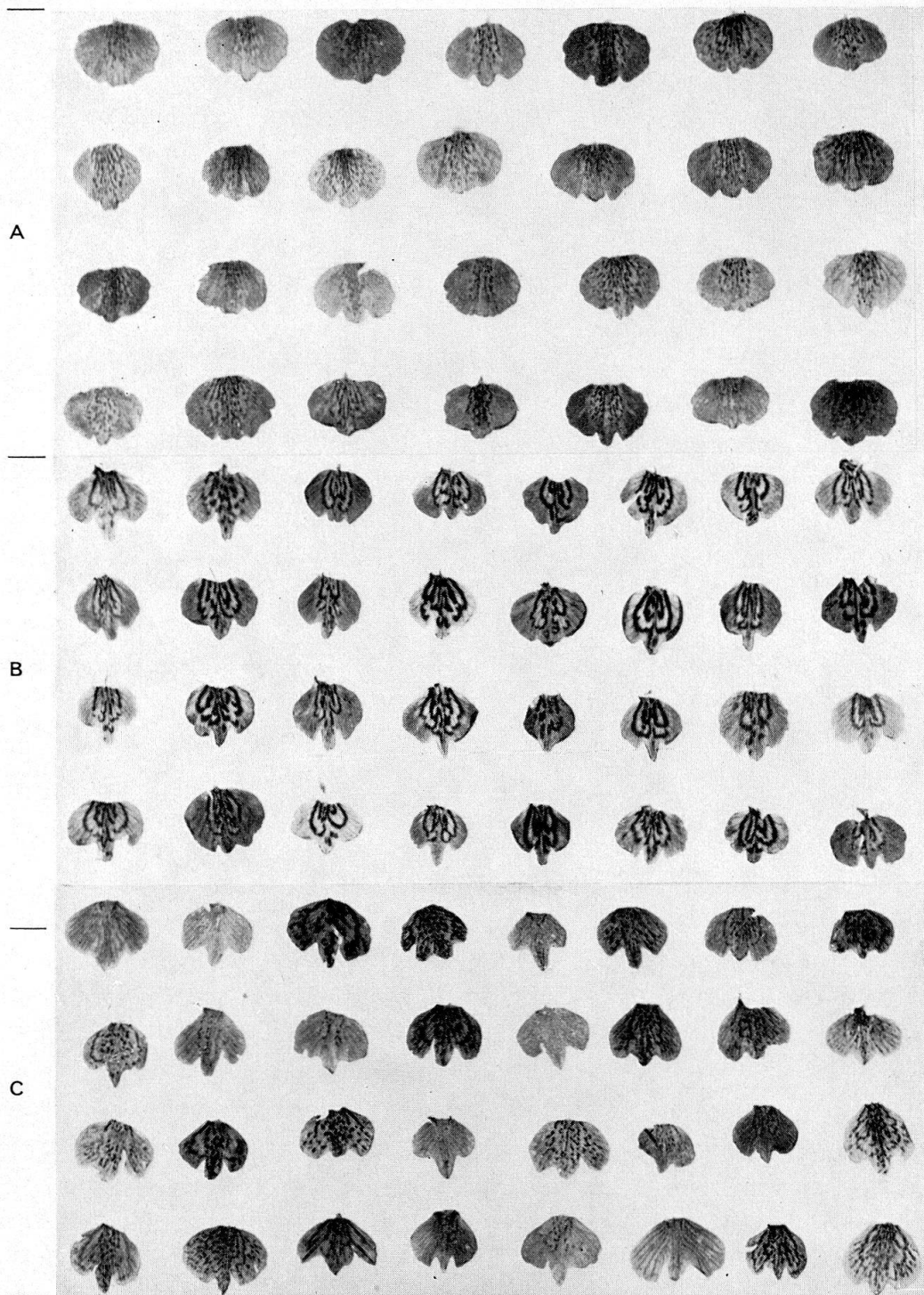
- A. 24 plants of *D. fuchsii* subsp. *hebridensis* from Co. Galway;
 B. 27 plants of *D. fuchsii* subsp. *fuchsii* from Co. Westmeath;
 D. 24 plants of *D. maculata* subsp. *ericetorum* from Co. Donegal.
 Labellum spurs from homologous flowers:
 C. 46 plants of *D. fuchsii* subsp. *fuchsii* from the same locality as A above;
 E. 55 plants of *D. maculata* subsp. *ericetorum* from the same locality as D.

Plate III. Subsection *Majales*: labella from homologous flowers from population samples to show intergradation between *D. purpurella* and *D. majalis* subsp. *occidentalis*, $\times 1$



- A. 44 plants of *D. purpurella* from a colony in Co. Waterford. These correspond closely with the Stephensons' "Form A";
- B. 27 plants of *D. purpurella* from a colony in Anglesea. These approach the Stephensons' "Form B";
- C. 24 plants of form linking *D. purpurella* and *D. majalis* subsp. *occidentalis* from a colony in Co. Mayo, on the margin of the distributional area of the latter;
- D. 21 plants of *D. majalis* subsp. *occidentalis* from the type area of this taxon, in Co. Clare.

Plate IV. Subsection *Majales*: labella from homologous flowers from population samples, $\times 1$



- A. 28 plants of *D. praetermissa* from a colony of typical facies in Hampshire;
- B. A sample of 32 plants from the leaf-marked portion of a colony of *D. praetermissa* in south Devon. Plants of this type correspond with Pugsley's "*Orchis pardalina*" (= *D. praetermissa* var. *junialis*), and they made up some 75% of the individuals of this colony. In a large sample examined cytologically, all were found to possess $2n = 80$ chromosomes, and all showed normal fertility.
- C. 32 plants of *D. traunsteineri* from Co. Westmeath.

Labellum not diamond shaped, usually > 10 mm in width and 8 mm in length; light pink, lilac, magenta or rosy-purple in colour, marked with a pattern of dots or regularly disposed bars or lines; leaves unspotted, or marked with ring-spots or heavy bars and blotches 3

3. Labellum elliptical, obscurely three-lobed, with rounded lateral and short, blunt central lobes, flat when fresh, or margins curved forward; leaves unmarked, or with rather regular ring-spots *D. praetermissa*
Labellum angular, three-lobed, lateral lobes notched or incised, slightly reflexed when fresh, median lobe triangular, somewhat pointed; leaves unmarked, or with spots, bars, blotches or occasionally heavy ring markings *D. majalis*

Of these four species, three, *D. praetermissa*, *D. purpurella* and *D. majalis*, are fairly widely ranging in the British Isles, having distributions which are largely mutually exclusive. The taxonomic problem of the fourth has only recently been clarified (Heslop-Harrison, 1953b) in Britain, and its distribution is at present inadequately known.

A scheme showing some of the directions of variation within the British Majales is given in fig. 6.

D. praetermissa

This species, described first by Druce in 1914, is the common marsh orchid of the south and east of England, occurring plentifully throughout its range on base rich soils in fens, marshes, water meadows, and even occasionally on drier chalk-downs and in disturbed habitats in quarries and industrial spoil heaps. *D. praetermissa* is absent from the north of England and from Scotland and Ireland.

Two features of *D. praetermissa*, otherwise a distinct enough entity, merit attention. The first concerns the incidence of anthocyanin pigmentation of the leaves in its populations, and the other its intergradation in parts of southern England with *D. traunsteineri*, discussed further under that species.

Whilst DRUCE's type description was based upon plants lacking leaf marking entirely, practically all populations of the species contain individuals in which anthocyanin pigmentation of the leaves is present. Characteristically, this pigment is deposited in the cells of the upper epidermis in a pattern of ring-shaped spots (fig. 5) but this is by no means the only form of patterning. The proportion of leaf-marked individuals varies between colonies, and there is evidence of some degree of geographical regularity in this. In some Sussex colonies, heavily marked individuals represent up to 20% of the total. In certain westerly localities, notably in south Devon, leaf-marked individuals equal or exceed the unspotted in number. Since in these populations intermediates, although present, are not numerous, the result is a bimodal distribution. The "anthocyanin-high" mode of this distribution has, until recent years, formed the basis of most of the interpretations of the Lin-

naean *Orchis latifolia* by British authors (T. and T.A.STEPHENSON, 1921; GODFERY and T. and T.A.STEPHENSON, 1924). More recently, PUGSLEY (1935), following his application of the name *Orchis latifolia* to the plant pre-

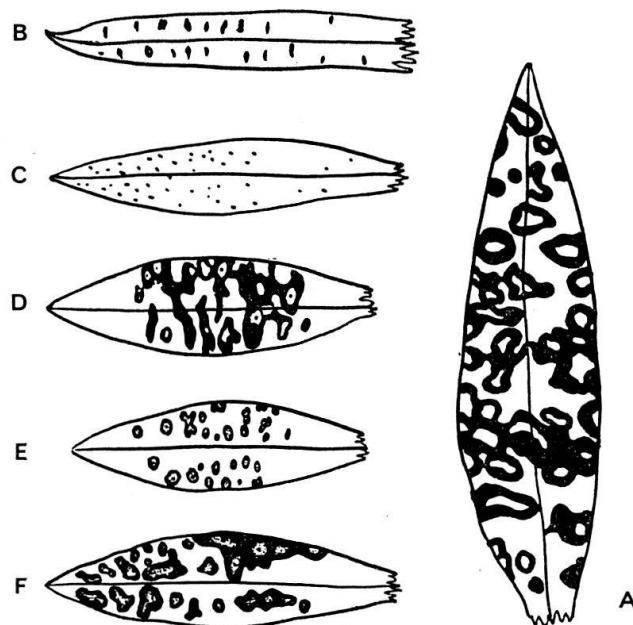


Fig. 5. Leaf marking in British Majales

A. *D. praetermissa* var. *junialis* ($\times \frac{3}{8}$)

B. *D. traunsteineri* ($\times \frac{3}{8}$)

C. *D. purpurella* ($\times \frac{1}{2}$)

D, E, F, *D. majalis*; D from Dingle, Co. Kerry; E from Macroom, Co. Cork; F from Ballyvaughan, Co. Clare (all $\times \frac{1}{2}$).

viously widely known as *O. incarnata*, has named the leaf-marked element in *D. praetermissa* populations as *Orchis pardalina*, quoting in synonymy VERMEULEN's *O. latifolia* var. *junialis* (Vermeulen, 1933). The possibility of a hybrid origin of these leaf-marked individuals has repeatedly been suggested, the parentage *D. praetermissa* and a member of the Eumaculatae usually being indicated (DRUCE, 1923; CLAPHAM, TUTIN and WARBURG, 1952). The breeding behaviour is, however, entirely regular (HESLOP-HARRISON, 1953c), and there seems no reason to believe that these plants are anything but normal segregates of populations otherwise referable to *D. praetermissa*. If separate taxonomic recognition is required for them, then the name *D. praetermissa* var. *junialis* (Vermeulen, 1949) is available.

D. purpurella

This species was described by T. and T.A.STEPHENSON (1920) from Wales, and most tetraploid marsh orchid populations of England and Wales north

marked plants, and through these *D. purpurella* grades into *D. majalis*. There are in fact western Scottish and Hebridean populations which are closely similar morphologically to some of those of south-western Ireland referable to *D. majalis* subsp. *occidentalis* (HALL, 1937; CAMPBELL, 1937; J.W.H. HARRISON, 1944). These are, however, distinguished by a later flowering period which reaches a peak in July.

Populations placed under *D. purpurella* occupy a fairly wide ecological range, occurring in marshes, moist meadows, dune pastures and the like, most prolifically on soils of relatively high base status, pH 6.0—7.5, but also occasionally on acid grassland, particularly in maritime localities. The populations occurring in fens are generally of a facies recalling *D. praetermissa*, and clear variation in this direction is to be seen in a great many Scottish populations, especially in the Highlands. This similarity to *D. praetermissa* led DRUCE to place these populations under that species as var. *pulchella* (Druce, 1920), a variety which has since been transferred to *D. purpurella* (Pugsley, 1935).

D. majalis

The tetraploid marsh orchid populations of the west of Ireland appear to provide the closest approach among the Britannic forms to the Saxon plant upon which REICHENBACH's *Orchis majalis* was based (Reichenbach, 1830). This fact was first appreciated by PUGSLEY (1935), who referred populations occurring in Cos. Clare and Galway to REICHENBACH's species as var. *occidentalis*, distinguished by a dwarfer habit and a short spike of dark flowers with a short central lobe to the labellum. While these characteristics may justify segregation at an infraspecific level, PUGSLEY himself was reluctant to treat the Irish race as specifically distinct from continental *D. majalis*, and WILMOTT's segregation of the species "*Orchis occidentalis*" seems therefore undesirable.

As was discovered by HALL (1937), the tetraploid dactylorchid populations of western Ireland form a highly variable complex to which no type description can apply with any degree of adequacy. The intrinsic variability of the colonies is high, and there is variation between colonies which has apparently little geographical or ecological regularity. The flowering period is remarkably protracted, beginning in May and continuing into July, and there is some evidence of chronological variation, the late-flowering plants of a given colony being morphologically dissimilar from those flowering early.

It is possible to define certain directions of variation within the complex, and so to indicate where convergence with other dactylorchid taxa is apparent. In the direction of reduced leaf and flower pigmentation, through the form

named "*Orchis kerryensis*" by WILMOTT (1936), there is an approach to *D. praetermissa*. Plants of this facies, with a tall habit recalling the southern English form, occur in water meadows and fens in Cork and Kerry, and these were indeed recorded as *D. praetermissa* by DRUCE, the author of the species. These plants are characterised by a rounded labellum, matching in shape that of *D. praetermissa*, and similarly marked with a pattern of dots and short bars.

Intergradation of *D. majalis* with *D. purpurella* has been mentioned above in the account of that species. Flower dissections from a sample of an intermediate population on the margin of the area of *D. majalis* are illustrated in Plate IIIC. The connection with the "Form B" of *D. purpurella* (Plate IIIB) is obvious.

D. traunsteineri

Eastern Irish populations now referred to this species were first distinguished by PUGSLEY (1936) and named by him as *Orchis majalis* subsp. *traunsteinerioides*. Several additional Irish stations have subsequently been added, and colonies of similar facies occur in various scattered localities in southern England (HESLOP-HARRISON, 1953a). Other records, from northern England and southern Scotland, remain to be examined now that the status of the plant is better understood, and the map previously published (HESLOP-HARRISON, 1949b) for "*Orchis majalis* subsp. *traunsteinerioides*" should be withdrawn as inaccurate.

In the majority of the Britannic stations so far examined where *D. traunsteineri* exists in a form closely similar to that occurring throughout the Central European mountains, the habitat is of the nature of rich fen, strongly affected by calcareous ground-water, pH 7.0—8.0. This is in accordance with the predilections of the species in the Alps where, according to KELLER (quoted by von Soó, 1930—40) "ist die Art eine Charakterpflanze der mineralstoffreichen Flachmoore".

In eastern Ireland, where the only other tetraploid marsh orchid present is *D. purpurella* which does not enter the same type of habitat, the various *D. traunsteineri* populations are distinct enough in their general aspect and show reasonable homogeneity between themselves (Plate IVC). Such hybridisation as does occur is with *D. incarnata* and *D. fuchsii*, and triploid hybrids arising from crossing with either of these are readily distinguishable. Hybridisation does not appear to have affected appreciably certain English colonies, notably that at Cothill in Berkshire, recorded by PUGSLEY (1946), since these agree well with those in Ireland. Elsewhere, however, there is marked evidence of hybridisation with *D. praetermissa*, and in Norfolk,

colonies exist in which a full range of intermediates links the two entities. Plants morphologically intermediate between the characteristic variation ranges of *D. praetermissa* and *D. traunsteineri* show normal fertility, and it is apparent that there is no inherent sterility barrier between the two species. Ecological isolation is evidently not effective, and it is probable that the remaining "pure" colonies of *D. traunsteineri* in southern England owe their persistence to the chance that immigration of *D. praetermissa* into their immediate vicinity has failed or taken place at a low rate. The Irish colonies are, of course, guarded from introgression by the absence of *D. praetermissa* from that country altogether.

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