

## STUDIES ON WELSH ORCHIDS

### THE VARIATION OF *DACTYLORCHIS PURPURELLA* (T. & T. A. STEPH.) VERMEUL. IN NORTH WALES

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#### ABSTRACT

Among ten spatially isolated populations of *D. purpurella* in North Wales statistically significant differences have been found in most of the phenotypic characters. Highly significant differences exist between populations only short distances apart.

The phenotypic variation follows a reticulate pattern and, as far as these results are concerned, no useful taxonomic subdivisions appear to be possible.

Two groups of correlated characters have been found :

- (a) among three vegetative characters : the number of sheathing leaves, the number of non-sheathing leaves and leaf width ;
- (b) among three floral dimensions : labellum width, labellum length and spur thickness.

#### INTRODUCTION

The marsh orchid now known as *Dactylorchis purpurella* was first described by T. & T. A. Stephenson (1920) from plants found near Aberystwyth, Cardiganshire, v.c. 46. The variability of the species was apparent from the outset, for the Stephensons recognized two forms : dwarf plants with flowers of a vivid reddish-purple colour and a small, almost entire, irregularly diamond-shaped labellum ('form A'); and taller plants with flowers of a rich, dark purple, and a rather larger, more rounded, shallowly trilobed labellum ('form B').

It is clear that while they felt that 'form A' was quite distinct from other marsh orchids, they were not so confident about 'form B.'

In 1921 they visited the Isle of Arran and in several stations saw plants of 'form B' growing with what they accepted as '*Orchis pulchella*' (= *O. praetermissa* var. *pulchella* Druce). The latter differed from their 'form B' only in having unspotted leaves and being somewhat larger. Without declaring the complete identity of these forms the Stephensons (1922) nevertheless realised their very close similarity and suggested that the var. *pulchella* would be better separated from *O. praetermissa* Druce. Eight years later T. Stephenson (1930) still referred to *Orchis purpurella* 'form B' and the var. *pulchella* as distinct forms, although he emphasized the slightness of the differences which separated them. This variety was finally transferred to *O. purpurella* by H. W. Pugsley (1935), but it was clear that even as a variety it had little to distinguish it from the "type" (Hall, 1937).

Further varieties of *O. purpurella* subsequently described by T. Stephenson (1937) are var. *maculosa*, in which the leaves are spotted all over and not merely on either the apical or basal half as normally found; and var. *crassifolia*, in which the plants are much bigger, more leafy and have much larger labella. Variations in other directions were also evident : in the population on which the description of var. *maculosa* was based some of the plants had flowers of the dark crimson-purple typical of the species, but many had rose-coloured flowers; while, in the Orkneys, populations apparently indistinguishable in other respects from *D. purpurella* were found to contain a proportion of heavily leaf-spotted plants (1930).

As Pugsley (1935) pointed out, there was little to separate these from *D. majalis* (Rchb.) Vermln. except their later flowering.

In North Wales *D. purpurella* is frequently found in suitable habitats. Even within

this restricted geographical area it shows a wide range of variation both within populations and between one population and another. The populations vary from those composed almost entirely of small, distinctive plants with short spikes of small, purple flowers (approaching Stephenson's form A), through some in which the majority of individuals are larger, leafier and with broader, more rounded, obscurely trilobed labella (presumably Stephenson's form B), to populations which, in their vegetative features, appear to approach the var. *crassifolia* Steph.

Many of the Anglesey populations are very nearly and sometimes completely lacking in leaf-marking. As these are usually composed of rather large, leafy plants, they have occasionally been recorded as *D. praetermissa* (Druce) Vermeul., a species which has not been found so far in v.c. 52.

In order to obtain some impression of the pattern of variation among these populations a biometric study of ten colonies was made in the flowering seasons in 1957, 1958 and 1959. The results are presented below.

### METHODS

The morphological characters studied are those which have been used in previous work on the dactylorchids (Heslop-Harrison, 1948, *et seq.*), namely : (a) stature; (b) number of leaves per plant; (c) leaf dimensions; (d) leaf marking; (e) labellum dimensions; (f) spur dimensions, and in addition, (g) the number of non-sheathing, bract-like leaves has been included.

To avoid the unnecessary destruction which mass collecting would entail, measurements of all the vegetative characters were made in the field; flower colour, shape of spike and leaf marking were also noted for each plant in the sample. One homologous flower was collected from each plant and kept in a stoppered jar to prevent wilting. As soon as possible afterwards labella and spurs from these flowers were mounted by pasting on thin card. They were then placed under moderate pressure to dry and measurements made within a week to avoid any errors due to shrinking.

### THE POPULATIONS

The localities of the populations shown in Fig. 1 are :

P1. Damp, base-rich meadow at Brithdir, near Dolgellau, Merioneth, v.c. 48.

P2. Dune slack at Mochras, Merioneth, v.c. 48.

P3. Marshy tract fringing the Artro estuary at Mochras, Merioneth. This colony is separated from P2 by over 365 yards, the intervening ground being occupied partly by a sandy ridge and partly by salt marsh. The colonies P2 and P3 have therefore been treated as distinct populations.

P4. Dune slack separated from P3 by only 95 yards of sand dunes. This colony had many plants with unusually large spikes of paler flowers, with rather larger, more trilobed labella. Because of these differences it was treated as a separate population for biometric purposes. It is not suggested that it is isolated from P3 as a breeding unit.

P5. Damp meadow land along the River Cegin, near Bangor, Caernarvonshire, v.c. 49. *Dactylorchis fuchsii* and several hybrids of this species with *D. purpurella* are the only other orchids here.

P6. Cors Erddreiniog, 3 mls. N.N.E. of Llangefni, Anglesey, v.c. 52, is an area of fen where the most abundant marsh orchid is *D. traunsteineri* (Saut.) Vermeul. (Lacey & Roberts, 1958). *D. purpurella* occurs sparsely in the small tracts of damp grassland and sedge-meadow around the main fen area.

P7. Marshy bottom of a disused limestone quarry, on the edge of Malltraeth Marsh, near Llangristiolus, Anglesey, v.c. 52. The orchids grow among grasses and sedges, with a few plants of the hybrid *D. fuchsii* × *D. purpurella*.

P8. Small coastal marsh near Llanfwrog, Anglesey. *D. purpurella* occurs mostly in the patches of grass and sedge meadow fringing the marsh. *D. fuchsii* occurs on the

rather drier parts adjacent to the marsh and here again the hybrid *D. fuchsii*  $\times$  *D. purpurella* is frequent.

P9. Marshy tract along the upper edge of the salt marsh of the Cefni Estuary, Newborough Warren Nature Reserve, Anglesey. Other orchid species growing here are

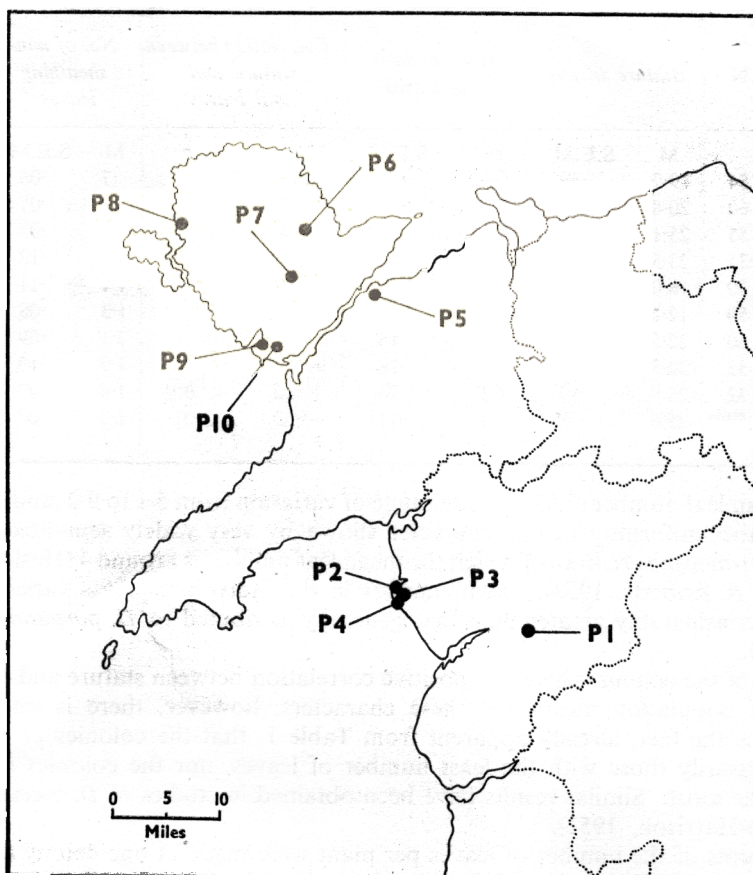


Fig. Localities of the colonies of *D. purpurella* mentioned in the text.

*Epipactis palustris*, *D. incarnata* and *D. fuchsii*. Here also occurs a colony of heavily leaf-spotted plants whose status will be discussed in a later paper.

P10. Dune meadow near Llyn Rhos Ddu, in Newborough Warren Nature Reserve, Anglesey. This colony is over 1¼ ml. from P9, and no *D. purpurella* occurs in the intervening ground. There are no heavily leaf-spotted plants growing here, the only other marsh orchid occurring being *D. incarnata*.

## RESULTS

### Stature

The dwarf habit of *D. purpurella* was emphasized by the Stephensons (1920) and the var. *pulchella* was stated by Pugsley (1935) to be, in general, taller than the "type." In the present account, therefore, stature, measured from soil level to the tip of the flower spike, has been included (Table 1), although it is realized that it is readily influenced by environmental conditions.

### Leaf Number

In counting the number of leaves the non-sheathing, upper leaves were included.



The data (Table 1) show that there is a close correlation between the number of non-sheathing leaves and the number of sheathing leaves. The correlation coefficient ( $r = +.88$  with  $p < .001$ ) indicates that an increase in the mean number of sheathing leaves is usually accompanied by an increase in the mean number of non-sheathing leaves.

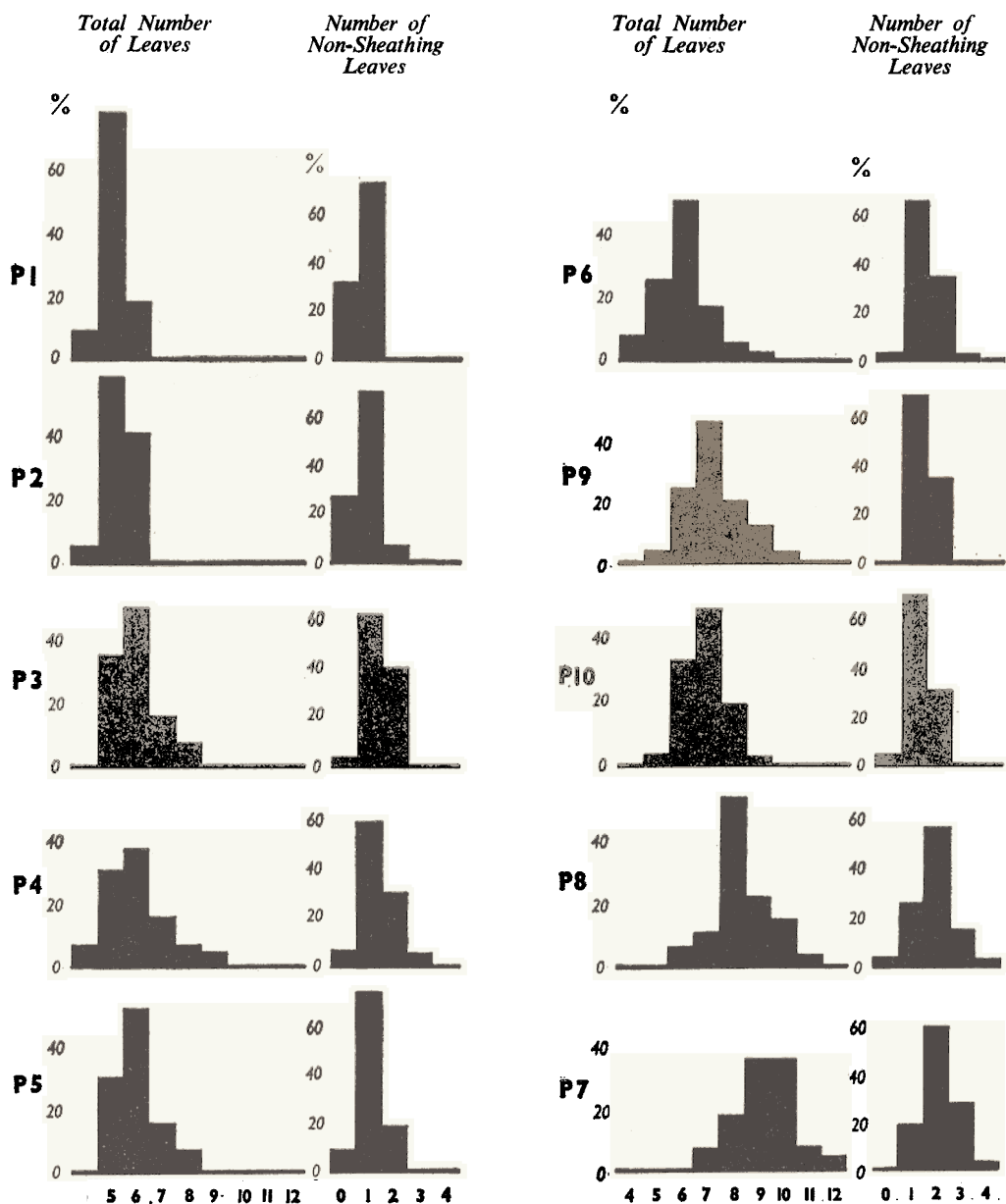


Fig. 2. Frequency distribution of the total number of leaves per plant and the number of non-sheathing leaves per plant in the ten populations.

*Leaf dimensions*

Both leaf measurements given in Table 2 were taken from the second fully expanded leaf from the base of the stem. Length was measured from the tip of the leaf to the opening of the sheath, and width at the widest part, which in the great majority was near or just below the middle.

The extreme variation in leaf width among the *D. purpurella* populations is shown by the fact that individual values range from 1.0 cm in the Merioneth colony, P2, to 5.0 cm in the Anglesey colony, P7. The population means for leaf width fall into four groups which are separated from one another by relatively large and statistically significant differences.

TABLE 2

Population data for leaf dimensions and leaf ratio. Symbols as in Table 1

Populations	N	Length in cm.		Width in cm.		Ratio $\frac{\text{Length}}{\text{Width}}$		Correlation between total leaves and leaf width	
		M	S.E.M.	M	S.E.M.	M	S.E.M.	r	p
P1	54	7.1	.14	1.4	.02	5.1	.13	+ .28	< .05
P2	60	8.5	.17	1.4	.03	6.1	.13	+ .48	< .001
P3	55	9.7	.25	1.8	.07	5.4	.15	+ .66	< .001
P4	31	10.5	.32	1.8	.09	5.8	.24	+ .69	< .001
P5	30	8.6	.21	1.8	.07	4.8	.24	+ .34	.05
P6	50	9.9	.25	1.9	.06	5.2	.21	+ .39	< .01
P7	60	10.2	.22	3.2	.10	3.2	.15	+ .68	< .001
P8	35	9.9	.33	2.3	.09	4.3	.17	+ .48	< .01
P9	32	10.6	.24	1.8	.08	5.9	.22	+ .76	< .001
P10	58	11.1	.23	2.4	.08	4.6	.17	+ .59	< .001

The ratio mean leaf length/mean leaf width shows continuous variation in nine of the colonies, i.e., the values form a series in which the differences between adjacent pairs are very small and not significant. In the Anglesey colony, P7, however, this ratio differs by a large and highly significant amount from all of the others. This feature is very obvious in the field, and coupled with the large number of leaves, gives this population a most distinctive appearance.

The population means for leaf length and leaf width show no correlation, but, as shown in Table 2, there is a significant correlation between leaf number and leaf width within each of the populations. Between the population means for these two characters there is an even higher correlation ( $r = +.91$ ,  $p < .001$ ): it follows that, in general, the population with fewest leaves usually has the narrowest, the one with most leaves also has the broadest.

*Leaf spotting*

Leaf marking in *D. purpurella* usually consists of small, solid, dark spots, approximately .5 to 1 mm diameter. Table 3 shows the incidence of leaf spotting in the populations. It appeared to be entirely absent in only one colony (P7), although two others (P9 and P10) had a very high preponderance of unmarked plants. One colony (P1) showed leaf spotting in 100% of the individuals examined. A peculiar feature in some colonies (P5 and P8) was the occurrence of no more than two or three spots on each of the upper two or three leaves, the lower being entirely unspotted.

TABLE 3

Leaf marking. Percentage incidence in four arbitrary classes :

1. Unmarked.
2. Very few, solid spots of under 1 mm. diameter; 2 to 5 spots on each of the upper two or three leaves only.
3. More numerous, solid spots, of the same size as in Class 2, and occurring on most of the leaves.
4. Somewhat larger, solid spots, of about 1.5 to 1.8 mm. diameter; density as in Class 3.

Population	1	2	3	4
P1			100	
P2	11.7	16.7	68.3	3.3
P3	18.2	10.9	60.0	10.9
P4	19.3	6.5	67.7	6.5
P5	78.6	21.4		
P6	52.0	36.0	10.0	2.0
P7	100			
P8	61.0	39.0		
P9	93.7	6.3		
P10	98.3			

*Labellum dimensions*

Table 4 gives the population data for labellum dimensions. The results of *t* tests between each pair of means show that the differences between many of the populations are highly significant.

TABLE 4

Population data for labellum and spur dimensions. Symbols as in Table 1.

Populations	N	Labellum length in cm.		Labellum width in cm.		Correlation between labellum length and labellum width		Spur length in cm.		Spur width in cm.	
		M	S.E.M.	M	S.E.M.	r	p	M	S.E.M.	M	S.E.M.
P1	50	.63	.006	.79	.006	+ .35	< .01	.77	.007	.32	.004
P2	63	.71	.006	.91	.009	+ .41	.001	.82	.007	.33	.003
P3	77	.71	.006	.93	.009	+ .53	< .001	.81	.008	.33	.003
P4	34	.75	.006	.99	.012	+ .57	< .001	.79	.011	.38	.006
P5	35	.66	.009	.85	.013	+ .14	> .05	.70	.016	.31	.004
P6	35	.71	.009	.93	.014	+ .66	< .001	.77	.015	.33	.006
P7	60	.82	.009	.93	.008	+ .30	.01	.84	.011	.39	.005
P8	50	.72	.006	.99	.011	+ .27	.05	.87	.009	.33	.005
P9	58	.71	.007	.94	.011	+ .18	> .05	.84	.011	.32	.004
P10	95	.72	.005	.97	.005	+ .30	< .01	.79	.007	.37	.003

Correlation between mean labellum length and mean labellum width :  $r = +.67$ ,  $p < .05$

Correlation between mean labellum length and mean spur width :  $r = +.83$ ,  $p = .001$

The relationships of the populations for these two dimensions are shown graphically in Fig. 3. With the exception of the colony P7 it is clear that there is a close correlation between mean labellum length and mean labellum width : for nine of the populations the correlation coefficient is  $+ .93$  ( $p < .001$ ). Even when the colony P7 is included the value of  $r$  is  $+ .67$  and significant with  $p < .05$ .



It is worth noting that the mean labellum dimensions for the Merioneth colony, P1, agree remarkably well both with the measurements given by the Stephensons (1920) for

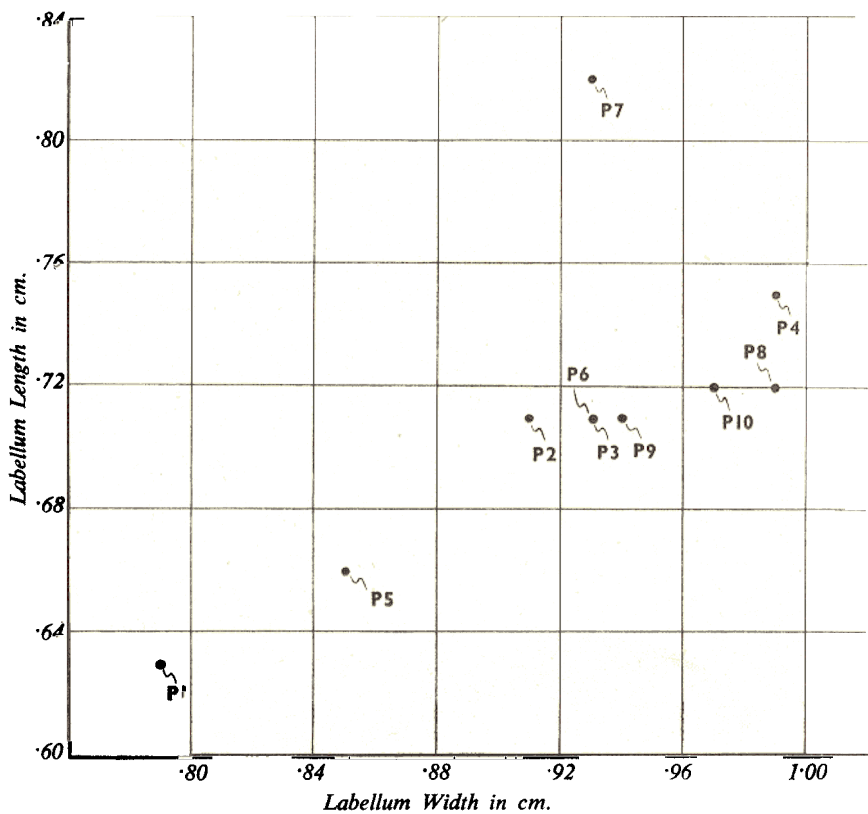


Fig. 3. Relationship of labellum width to labellum length.

their 'form A' (8 mm. × 6 mm.) and with those for an Irish colony of *D. purpurella* given by Heslop-Harrison (1953) : (·79 cm. × ·61 cm.).

Labellum shape

In order to give an impression of the variation in labellum shape in *D. purpurella* an attempt has been made to grade each colony by matching the labella to five shapes which have been taken as standards (Fig. 4), although the diversity is so great as to reduce the precision of any such grading. The results are given in Table 5.

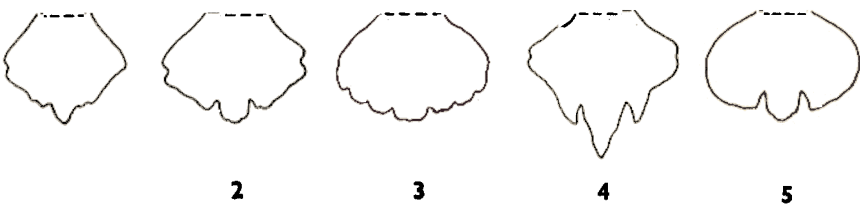


Fig. 4. Five labellum shapes used as standards for grading the *D. purpurella* colonies.

It can be seen that in the colony P1 74% of all individuals conform with grade 1, with only 4% in grade 3. In colony P2, which in vegetative features agrees closely with P1 (see Tables 1 and 2), 35% conform with grade 1 and an equal number with grade 2, while 14% conform with grade 5, a shape which is not present in P1. This colony, P2,



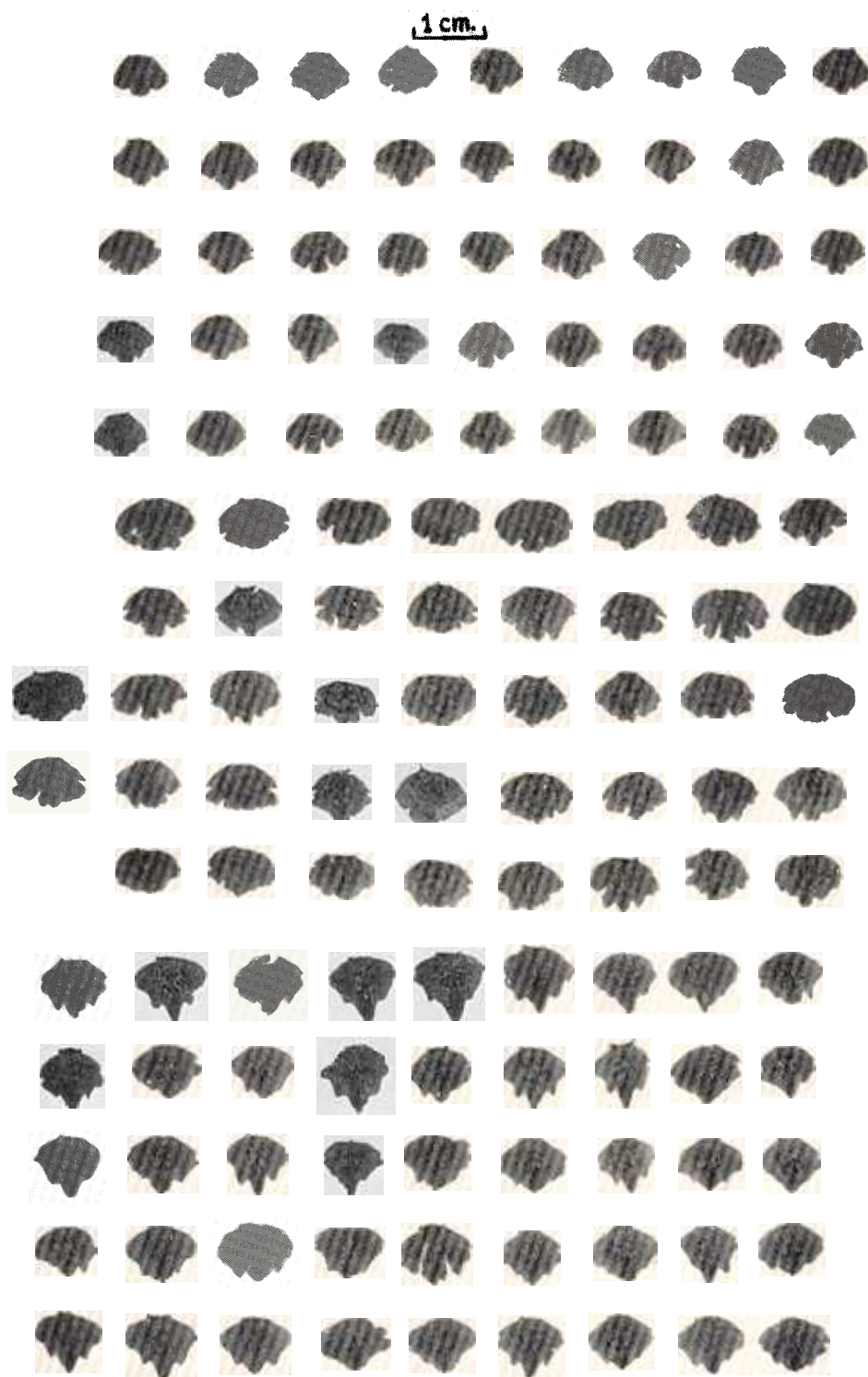


PLATE 1.

Random samples of labella from three populations of *D. purpurella* : top, 50 plants from the Merioneth colony, P1; middle, 45 plants from the Anglesey colony, P8; bottom, 45 plants from the Anglesey colony, P7. All  $\times 1$ .

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also differs significantly in the representation of labellum shape grades from the colony P3, which is only separated from it by 365 yards.

TABLE 5  
Percentage distribution of labellum shapes in the *D. purpurella* colonies

Populations	Labellum shape grades				
	1	2	3	4	5
P1	74	22	4		
P2	35	35	16		14
P3	4	22	35.5		38.5
P4	3.3	23	55.7		18
P5	17	60	23		
P6		21	76	3	
P7		8.3	25	66.7	
P8		11	81	8	
P9	2	16	65	15	2
P10		20	63	6	11

The Caernarvonshire colony, P5, intermediate in labellum dimensions between P1 and most of the Anglesey colonies (P6, P8, P9 and P10), is also seen to hold an intermediate position with regard to labellum shapes, 60% of individuals here conforming to grade 2.

Of the Anglesey colonies four agree very closely in the distribution of the grades, the modal class in all of them being grade 3. The fifth, P7, which differs from all of the others by a large and highly significant amount in labellum length, also differs from all of them in the distribution of labellum shape grades: 66.7% conform with grade 4.

An impression of the variation in size and shape of labellum can be obtained from the random samples from three of the colonies, Plate 1.

Between the smallest, P1, and the largest, P7, there is a 53% difference in mean labellum area.

### *Flower colour and labellum pattern*

Flower colour is one of the most constant and distinctive characters of *D. purpurella*, in the majority of populations being either a deep purple or red-purple. Some populations, however, contain a proportion of much paler flowers, approaching the tints found in *D. maculata* subsp. *ericetorum*: in two of the Merionethshire colonies, P2 and P4, 10% and 7% respectively had flowers of this colour.

The Aberystwyth plants from which the Stephenson described their 'form A' had flowers of a vivid red-purple, while plants of 'form B' from Arran and Ambleside had flowers of a rich, dark purple. In the populations considered here no correlation has been discovered between labellum shape and flower colour: in the distinctive colony P1, where most labellum shapes conform with 'form A,' all flowers were of an intense, deep purple such as is almost uniformly found in the Anglesey colonies P6, P7 and P8. The two shades appear to be equally represented in the Merioneth colony, P3, where only 4% of the plants have labella of grade 1, but in the Anglesey colonies P9 and P10 the flowers are almost entirely of a red-purple colour.

Labellum pattern, which in *D. purpurella* usually consists of rather heavy, intense purple markings in the shape of broken bars, crescents and blotches, is fundamentally the same in all of the colonies, with these exceptions:

(a) in the pale-flowered plants in the colonies P2 and P4 labellum pattern was very indistinct and often lacking;

(b) in the Anglesey colony, P7, labellum pattern in most plants tended to consist of dots rather than the broken bars and crescents usually found.

*Length and shape of flower spike*

The Merioneth colony, P4, in addition to having a proportion of pale-flowered individuals, was also distinguished by the fact that many of them had unusually large flower spikes. Because of this, measurements of the spike length were made in the three Merioneth colonies, P2, P3 and P4. Fig. 5 shows the clear difference between the colony P4 and the other Mochras colonies in this respect.

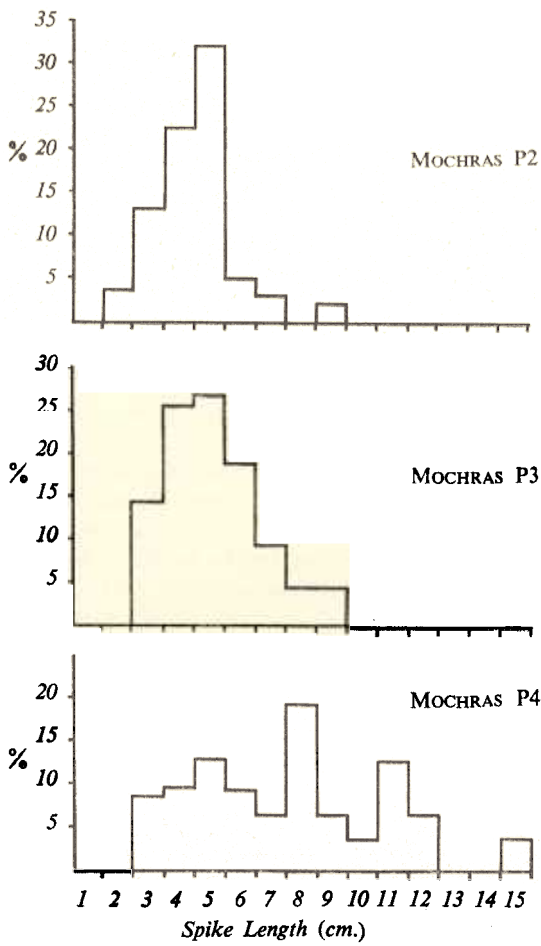


Fig. 5. Frequency distribution of spike length in the three Mochras (Merionethshire) colonies.

The shape of the flower spike deserves some comment, although this was not studied biometrically. In most populations of *D. purpurella* the spike has a more or less flat-topped appearance unique among the British marsh orchids. Two of the populations, P7 and P8, differed appreciably from the others in this character, for in both of them a very large proportion of the plants had distinctly conical spikes, very much like those of *D. praetermissa*. This was a most striking feature of these colonies in the field.

*Spur size*

In order that the data for spur size may be compared with those available for other species of marsh orchids the measurements have been made in the same way. Length of spur was measured from the mouth to the tip, and width about 1 mm from the mouth of the flattened spurs mounted on card (Heslop-Harrison, 1953).

The sample data (Table 4) show the wide variation in spur length that occurs among these populations : individual values vary from .5 cm. to 1.05 cm., a range far greater than is usually given for the species.

The data for spur width show much greater regularity. These fall into two groups : those with means of .31 to .33 cm. and the rest with means of .37 to .39 cm. The difference between these two groups is relatively large and highly significant.

There is no correlation between the population means for spur length and spur width; indeed, spur length seems to vary quite independently of every other character. On the other hand there is a very high correlation between the population means for labellum length and spur width (Table 4).

# CONCLUSIONS

1. For each character the difference between each pair of means was tested for significance by means of a *t*-test. The following groupings have been made as a result, and the populations placed in order of increasing means (Table 6).

TABLE 6  
=  $p < .05$ , \*\* =  $p < .01$ , \*\*\* =  $p < .001$

Character	Grouping
Leaf number	<div>P3</div> <div>P1 * P2 ** P4 * P10 P9 *** P8 ** P7</div> <div>P5</div> <div>P6</div>
Leaf width	<div>P3</div> <div>P1 ** P5 ** P8 P10 *** P7</div> <div>P2</div> <div>P4</div> <div>P6</div> <div>P9</div>
Labellum width	<div>P3</div> <div>P1 *** P5 *** P2 P6 P9 ** P10 P4</div> <div>P7</div> <div>P8</div>
Labellum length	<div>P2</div> <div>P1 ** P5 *** P3 P8 ** P4 *** P7</div> <div>P6 P10</div> <div>P9</div>
Spur length	<div>P5 * P1 P4 P3 P2 P9</div> <div>P6 P10 P7</div> <div>* P8</div>
Spur width	<div>P2</div> <div>P5 P1 P3 *** P10 P4 P7</div> <div>P9 P6</div> <div>P8</div>

In Fig. 6 the inter-relations of the populations with respect to these groups is shown. It is abundantly clear that, as far as these colonies of *D. purpurella* are concerned, none of

the populations can be completely separated from the others; rather, the pattern of variation is, to some extent, reticulate in the sense described by Turrill (1950).

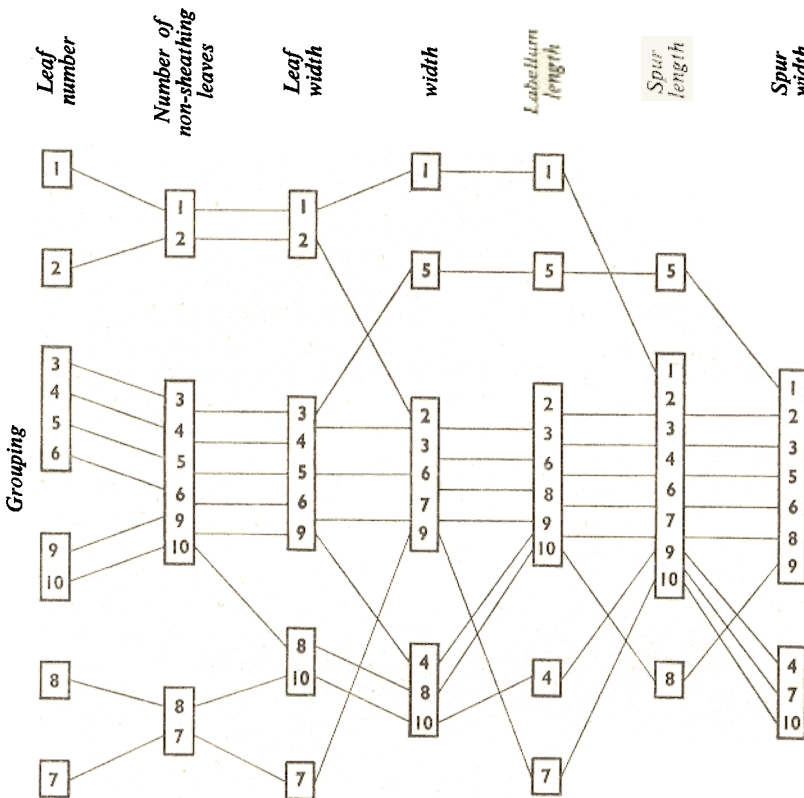


Fig. 6. A simplified representation of character variation in ten populations of *D. purpurella*. The number 1, 2, 3, etc. stand for P1, P2, P3, etc. The thin lines trace the position of each colony in the network.

2. The results indicate that the degree of differentiation of the populations is not in proportion to the distances separating them. For instance, the colonies P3 and P6, separated by 35 miles from each other, agree closely in most vegetative and floral characters with the exception of stature and the incidence of labellum shape grades. On the other hand much bigger differences exist between the three Merioneth colonies, P2, P3 and P4, which are separated from each other by very short distances: P2 and P3 are effectively separated by 365 yards of salt marsh and a sandy ridge; P3 is only separated from P4 by about 95 yards of sand dunes.

In Anglesey the two colonies, P9 and P10, separated by about  $1\frac{1}{2}$  miles, differ appreciably in mean leaf width, labellum width and spur width; the other three colonies, P6, P7 and P8, differ widely from each other in several characters. P6 and P7 are about 5 miles apart and both of them over 11 miles from P8.

3. In the absence of evidence of the persistence of the character combinations found at present in these populations it may be premature to draw any conclusions about the degree of reproductive isolation prevailing among them. It is of interest, however, to note that there is some evidence in the case of the striking Anglesey colony P7: a reference to its resemblance to var. *crassifolia* Steph. occurs in *Rep. Bot. Soc. & E. C.*, 11, 505 (1937). A water-colour drawing of a plant gathered here by members of the B.E.C. Excursion to Anglesey in 1937 shows a plant quite typical of the colony as it is today, so it may not be unreasonable to assume that this colony, at least, has persisted more or less with its present combination of characters for over twenty years.

4. In his description of the var. *crassifolia*, T. Stephenson (1937) gives the following figures : stature 22–25 cm, number of leaves 8 or 9, second leaf from base of stem 12 cm  $\times$  4 cm (in one instance as much as 13 cm  $\times$  4.5 cm), labella mostly 11 mm wide by 8 mm long. In this colony all the plants had unspotted leaves, but the flowers, though larger, were of the same form and colour as the typical species. As far as it is possible to judge from these figures the Anglesey colony, P7, appears to be closely similar to the var. *crassifolia*, from which it seems to differ only in having narrower labella and in possessing an unusual labellum shape. Several plants in this colony were found with as many as 12 leaves, while the length and width of the second leaf were, in some cases, as much as 14.4 cm and 5.0 cm respectively.

5. It is now possible to discuss the 'form A' and 'form B' of the Stephensons. In their original account the Stephensons gave the following figures for their 'form A' plants : stature around 12–15 cm, number of leaves 7, and width of the widest leaf 1.7 cm. A gathering of four plants of 'form A' from Aberystwyth, sent by the Stephensons to the British Museum in 1921, has labella which correspond closely in shape and size with those of the Merionethshire colony, P1, and of Irish colonies of 'form A' (Heslop-Harrison, 1953, 1954). Indeed, the mean labellum dimensions for the Merionethshire plants (.79 cm  $\times$  .63 cm) and those from Co. Donegal (.79 cm  $\times$  .61 cm) show remarkable agreement.

In other respects, however, there is no close agreement between these two colonies and the one described by the Stephensons : their mean stature is 19.7 cm and 20.2 cm; mean leaf number 5.1 and 6.56, and mean leaf width 1.4 cm and 1.99 cm respectively.

It is clear that 'form A' and 'form B' have no significance other than in reference to the size and shape of the labellum. Where the great majority of plants in a colony have labella corresponding to 'form A' the impression gained is of a most distinctive and uniform 'type.' It was this, no doubt, which led the Stephensons to describe their two forms.

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