

## A reappraisal of the British and Irish dactylorchids, 3. The spotted-orchids

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### ABSTRACT

52 morphological characters were recorded for ten individuals from each of 20 populations of *Dactylorhiza fuchsii* (Druce) Soó and 23 populations of *D. maculata* (L.) Soó. Multivariate analyses of data for both species demonstrate largely continuous morphological variation polarized into two independent trends representing vegetative vigour and degree of pigmentation. Both trends reach greater extremes in *D. fuchsii*. Possible causes of this variation, including environmental modification, are discussed. Univariate, bivariate and multivariate analyses demonstrate considerable overlap between existing and potential infraspecific taxa of both species. Revised diagnostic descriptions are provided for five British and Irish varieties of *D. fuchsii*: var. **fuchsii** (Druce) Bateman & Denholm, **comb. nov.**, var. **hebridensis** (Wilmott) Bateman & Denholm, **comb. nov.**, var. **cornubiensis** (Pugsley) Soó, var. **alpina** (Landwehr) Bateman & Denholm, **comb. et stat. nov.**, and var. **okellyi** (Druce) Bateman & Denholm, **comb. nov.** The morphological distinction of some taxa previously regarded as subspecies has been exaggerated due to insufficient or unrepresentative data and unsubstantiated assumptions regarding their population biology. Their distributions have been confused by a priori identifications of populations based on geographical locations rather than morphological criteria. No justifiable infraspecific taxa can be detected within *D. maculata*. Several long-standing taxonomic and nomenclatural controversies are resolved by detailed study of both the new data and past literature. Solutions to other problems, including the possible conspecificity of *D. fuchsii* and *D. maculata*, require comparable data from Continental spotted-orchid populations.

### INTRODUCTION

The taxonomy and nomenclature of the spotted-orchids have evolved progressively but spasmodically since Linnaeus described *Orchis maculata* L. in 1753. *Dactylorhiza maculata* (L.) Soó (Heath Spotted-orchid) is now more clearly and narrowly delimited, and has been joined in the Subsection *Eumaculatae* Vermeulen by *D. fuchsii* (Druce) Soó (Common Spotted-orchid; Druce 1915) and the exclusively Continental *D. saccifera* (Brongniart) Soó (Brongniart 1832). Senghas (1968) and Landwehr (1975) disagreed with Vermeulen's (1947) surprising inclusion of the Madeiran endemic *D. foliosa* (Solander) Soó in this subsection. Some workers have advocated the amalgamation of *D. fuchsii* with *D. maculata* (e.g. Nelson 1976) and the splitting of *D. saccifera* (e.g. Baumann & Künkele 1982). However, this degree of taxonomic instability at the species level is greatly exceeded by a general lack of consensus over numerous infraspecific taxa, which reflects the difficulty of partitioning largely continuous ranges of morphological variation into satisfactory taxa (Prentice 1986). This problem requires detailed morphological studies capable of identifying and quantifying trends in variation that can be assessed for potential taxonomic value and interpreted in an evolutionary context.

This paper continues our morphometric studies on dactylorchids (Bateman & Denholm 1983,

1985), and concludes our survey of infraspecific morphological variation in British and Irish populations.

#### MATERIALS AND METHODS

20 populations of *D. fuchsii* and 23 of *D. maculata* were sampled between 1982 and 1986, including at least three populations of each of the subspecies listed by Heslop-Harrison (1954) and Clapham (1962). Details of these populations and the sample localities are presented in Tables 1 and 2.

52 morphological characters were recorded for each of ten flowering plants per population (twelve plants of *D. maculata* were measured at Kilmory). Details of these characters (and of ten indices (a–j) derived from them) largely follow Bateman & Denholm (1985), though an additional category ( $5 = \pm$  solid blotch) was introduced for character 11 (type of labellum markings) and mean peripheral bract cell lengths (character 26) represent 30–100 cells, not 10–30 as was erroneously stated previously.

Tables listing mean values and standard deviations for all characters and indices of each study population are available from the authors on request.

Data were analyzed by univariate and multivariate methods using the Genstat computer program (Payne *et al.* 1987). Characters 46–51 were excluded from the multivariate analyses to avoid bias caused by a series of zero values reflecting the absence of a single feature (i.e. leaf markings), and indices were excluded to avoid duplication of their component characters. *D. fuchsii* and *D. maculata* were analyzed separately. After standardization to unit variance, each species yielded two similarity matrices (Gower 1971), the first using population means and the second using data for individual plants. Each matrix was used to link either populations or individuals by their maximum similarities to yield a minimum spanning tree (Gower & Ross 1969) and then compute principal coordinates (Gower 1966), compound vectors incorporating correlated characters of potential diagnostic value. The first two principal coordinates (PC1, PC2) from each analysis were plotted together to assess the degree of morphological separation of potential taxa in these dimensions (see Bateman & Denholm (1983, 1985) for further details of the application of these techniques to dactylochids).

#### MAJOR TRENDS IN MORPHOLOGICAL VARIATION

The multivariate analyses of both populations and individuals demonstrated strikingly similar overall patterns of infraspecific variation in *D. fuchsii* and *D. maculata*. In each of the four analyses (Figs. 1–4), the first two principal coordinates largely represented variation in vegetative vigour and intensity of pigmentation; lower order coordinates consistently accounted for much smaller proportions of the variance than the second and were of little biological or taxonomic significance. For simplicity, we have used our revised classification of *D. fuchsii* into five varieties (shown in the left-hand column of Table 1) throughout this paper.

#### ANALYSES OF POPULATIONS

19 of the 46 characters used for multivariate analysis of *D. fuchsii* populations contributed appreciably to the first two principal coordinates, which together accounted for 50% of the total variance (Table 3). The second coordinate (PC2 on Fig. 1) largely represented characters determined by vegetative and floral anthocyanin pigments, and clearly separated four anthocyanin-low populations from the Burren (var. *okellyi*; PC2 values  $< -0.2$ ) from eight anthocyanin-high populations (vars *hebridensis*, *cornubiensis* and *alpina*; PC2 values  $> 0.1$ ). The eight remaining populations (var. *fuchsii*) had intermediate values for PC2 but were widely dispersed along PC1, which represented characters such as stem, leaf, bract and inflorescence dimensions that determine vegetative vigour. Thus, Oldshore and Polin were the least vigorous and Oaklands and Parham were the most vigorous of the populations studied. Five populations of var. *fuchsii* showed greater overall vigour than all populations of the other varieties.

The superimposed minimum spanning tree resolved variation along these axes into five branches, radiating from the area occupied by less vigorous populations of var. *fuchsii* in the centre of the plot

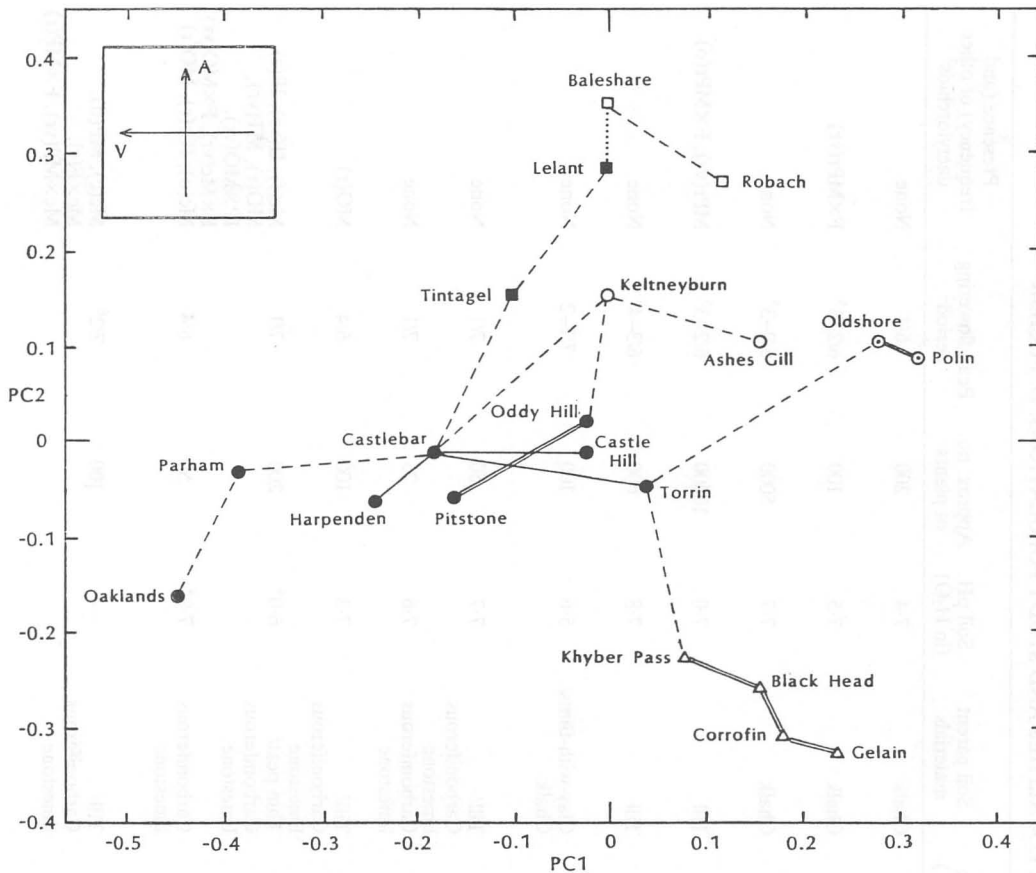


FIGURE 1. Principal coordinates plot of PC1:PC2 with superimposed minimum spanning tree. *D. fuchsii*, population means.

● *var. fuchsii* (● individuals lacking floral anthocyanins; Fig. 3)

□ *var. hebridensis*

■ *var. cornubiensis*

○ *var. alpina* (○ coastal habitats)

△ *var. okellyi* (△ individuals lacking floral anthocyanins; Fig. 3)

Minimum spanning tree links: double line = similarity of populations >95%, single line = 92.6–95%, dashed line = 90–92.5%, dotted line = <90% Inset: Main trends of variation represented on the plot.

V = vegetative vigour

F = floral dimensions

A = anthocyanin pigments.

(Fig. 1). The eight anthocyanin-high populations formed three branches: (i) *var. hebridensis* (Baleshare, Robach) and *var. cornubiensis* (Tintagel, Lelant), (ii) upland populations of *var. alpina* (Keltneyburn, Ashes Gill), and (iii) coastal populations of *var. alpina* (Oldshore, Polin). The strongest links of the tree reflected a combination of geographical and ecological proximity; they occurred between the four populations of *var. okellyi* from the limestone pavements of the Burren, two adjacent populations of *var. alpina* from machair in Sutherland (Oldshore, Polin) and two populations of *var. fuchsii* from chalk soils near the Hertfordshire/Buckinghamshire border (Oddy Hill, Pitstone).

The first two coordinates for *D. maculata* populations incorporated 44% of the total variance, largely encompassed by 21 characters (Table 4). They resembled closely the corresponding

TABLE 1. DETAILS OF SAMPLE LOCALITIES AND STUDY POPULATIONS: *D. FUCHSII*

Taxon <sup>1</sup>	Habitat and locality	Grid reference	Altitude (m O.D.)	Soil parent materials	Soil pH (in H <sub>2</sub> O)	Approx. no. of plants	Peak flowering period <sup>2</sup>	Presence (and frequency) of other dactylorchids <sup>3</sup>
<i>var. fuchsii</i>	Downland, CASTLE HILL, Folkstone, Kent, v.c. 15	61/213.380	125	Chalk	7.4	200	6/4	None
	Downland, ODDY HILL, Wigginton, Herts., v.c. 20	42/934.109	170	Chalk	7.5	100	6/2-3 <sup>5</sup>	F×MPPr(vr)
	PITSTONE Fen, Marsworth, Bucks., v.c. 24	42/938.142	130	Chalk	7.7	5000	6/2-3 <sup>5</sup>	None
	OAKLANDS gravel pits, Colney Heath, Herts., v.c. 20	52/185.082	80	Till	7.0	10000	6/2-3 <sup>5</sup>	MPr(vr), F×MPr(o)
	Willow carr, PARHAM airfield, Suffolk, v.c. 25	62/333.609	35	Till	7.8	600	6/3-4 <sup>5</sup>	None
	Scrubby woodland, HARPENDEN Common, Herts., v.c. 20	52/139.131	120	Clay-with-flints/ Chalk	5.6	100	7/1-2	None
	Marshy meadow, CASTLEBAR, Co. Mayo, v.c. H26	11/165.897	40	Till/ Carboniferous limestone	7.7	50	7/1	None
	Damp meadow, TORRIN, Skye, N. Ebuades, v.c. 104	18/578.201	40	Carboniferous limestone	7.6	25	7/1	None
	<i>var. okellyi</i>	Pavement, BLACK HEAD, Murroogh, Co. Clare, v.c. H9	12/150.116	30	Till/ Carboniferous limestone	7.3	100	6/4
Grassy bank, KHYBER PASS, E. Murroogh, Co. Clare, v.c. H9		12/150.088	80	Thin peat/ Carboniferous limestone	6.0 <sup>4</sup>	200	7/1	Mc(f), II(vr), IP(r), MO(r), MT(vr), IP×MO(vr), F×Mc(vr), F×MO(vr)
Pasture, W. Lough Baile, E. CORROFIN, Co. Clare, v.c. H9		11/324.920	15	Carboniferous limestone	7.9 <sup>4</sup>	50	6/4	Mc(o), ICr(r), MO(r)
Pavement, Lough GELAIN, N. Corrofin, Co. Clare, v.c. H9		11/313.947	35	Till/ Carboniferous limestone	—	100	7/2 <sup>6</sup>	Mc(c), MP(o), Mc×F(r), Mc×MP(vr), F×MP(r)

var. <i>alpina</i>	Pasture, ASHES GILL, Ingleton, Mid- W. Yorks., v.c. 64	34/777.784	290	? Till/mica schist	6-1	200	6/4-7/1	Mc(f), MP(o), F×MP(vr)
	Pasture, KELTNEYBURN, Fortingall, Mid Perth, v.c. 88	27/772.496	165	Till/Cambrian limestone	6-7	350	7/1-2	None
	Machair, OLDSHORE More, W. Sutherland, v.c. 108	29/198.588	5	Blown sand/ Lewisian gneiss	7-7	5000	7/3	None
	Machair, POLIN, Oldshore Beg, W. Sutherland, v.c. 108	29/196.587	5	Blown sand/ Lewisian gneiss	6-9	5000	7/3	None
var. <i>hebridensis</i>	Machair, TEANAMACHAR, BALESHARE, N. Uist, Outer Hebrides, v.c. 110	08/779.618	5	Blown sand/ Lewisian gneiss	7-7	30	7/2	IC(c), MP(f), F×MP(vr)
	Machair, ROBACH, Newtonferry, N. Uist, Outer Hebrides, v.c. 110	08/873.762	5	Blown sand/ Lewisian gneiss	7-9	100	7/1-2	IC(c), MP(f), F×MP(o)
var. <i>cornubiensis</i>	Stable dunes, LELANT, St Ives, W. Cornwall, v.c. 1	10/543.382	30	Blown sand/ Devonian slates	7-7	100	6/3	MPr(o), F×MPr(f)
	Rough grassland, Bossiney cliffs, TINTAGEL, E. Cornwall, v.c. 2	20/065.894	70	Dinantian tuffs/ lavas	5-9	20	6/2-3	None

<sup>1</sup> See 'Classification' for revised nomenclature.

<sup>2</sup> Estimated value. The number before the oblique indicates the month, numbers after the weeks of that month.

<sup>3</sup> F = *D. fuchsii*

Mc = *D. maculata*

II = *D. incarnata* subsp. *incarnata*

IC = *D. incarnata* subsp. *coccinea*

ICr = *D. incarnata* subsp. *cruenta*

IP = *D. incarnata* subsp. *pulchella*

MO = *D. majalis* subsp. *occidentalis*

MP = *D. majalis* subsp. *purpurella*

MPr = *D. majalis* subsp. *praetermissa*

MT = *D. majalis* subsp. *traunsteinerioides*

'c' = common, 'f' = frequent, 'o' = occasional, 'r' = rare, 'vr' = very rare.

<sup>4</sup> Value approximate due to very large amounts of organic matter in sample.

<sup>5</sup> Measured during 1982, a particularly early season.

<sup>6</sup> Measured during 1985, a particularly late season.

TABLE 2. DETAILS OF SAMPLE LOCALITIES AND STUDY POPULATIONS: *D. MACULATA*  
See Table 1 for footnotes and explanation of abbreviations.

Habitat and locality	Grid reference	Altitude (m O.D.)	Soil parent materials	Soil pH (in H <sub>2</sub> O)	Approx. no. of plants	Peak flowering period <sup>2</sup>	Presence (and frequency) of other dactylorhichs <sup>3</sup>
Heath, KYNANCE Cove, Lizard, Cornwall, v.c. 1	10/682.142	70	Peat/serpentinite	5.2	10000	6/2-3	None
Heath, PORLOCK Common, Exmoor, N. Devon, v.c. 4	21/846.462	410	Devonian phyllite	4.5	100	7/4 <sup>6</sup>	None
MATLEY Bog, Denny Lodge, S. Hants., v.c. 11	41/333.073	20	Peat/Barton sands	5.1	1000	6/3-4	None
Bog, N. STEPHILL Bottom, Beaulieu, S. Hants., v.c. 11	41/360.061	20	Peat/Barton sands	4.5 <sup>4</sup>	100	6/3-4	IP(f)
Heath, S. CROCKFORD Bottom, Boldre, S. Hants., v.c. 11	40/349.987	30	Plateau gravels	4.8	500	6/3	None
Bog, THURSLEY Common, Surrey, v.c. 17	41/904.416	55	Peat/Lower greensand	6.0 <sup>4</sup>	50	6/3-4	IP(c)
Streamside marsh, STANMORE Common, Middlesex, v.c. 21	51/159.941	125	Claygate sands	6.6	17	6/4	None
Heath, BRICKETWOOD Common, Herts., v.c. 20	52/128.008	80	Till	5.6	100	6/2 <sup>5</sup>	F(vr), Mc×F(vr)
Pasture, ASHES GILL, Ingleton, Mid-W. Yorks., v.c. 64	34/777.785	280	Thin peat/till/Carboniferous limestone	5.0 <sup>4</sup>	5000	6/4 <sup>6</sup>	F(o), MP(o), Mc×F(r), Mc×MP(vr), F×MP(r)
Streamside marsh, WHITE NOOK, Conistone, Mid-W. Yorks., v.c. 64	34/984.661	205	Peat+alluvium/till/Carboniferous limestone	5.8	80	6/2-3 <sup>5</sup>	F(r), MT(r)
Damp moorland, LLANDEGFAN Common, Anglesey, v.c. 52	23/576.747	90	Till/Mona schists	—	200	7/1	MP(o), Mc×MP(r)

Maritime pavement, POULSALLAGH, W. Lisdoonvarna, Co. Clare, v.c. H9	12/086.018	25	Thin peat/ Carboniferous limestone	6-7	500	6/1	MO(vr), F(vr)
Pavement, BALLYRYAN, W. Lisdoonvarna, Co. Clare, v.c. H9	12/087.018	25	Thin peat/ Carboniferous limestone	6-1	100	6/1	None
Maritime pavement, MURROOGH, Black Head, Co. Clare, v.c. H9	12/143.103	25	Thin peat/ Carboniferous limestone	5-9	50	6/1-2	MO(vr), F(o)
Rough pasture, W. CLIFDEN, W. Galway, v.c. H16	02/651.503	15	Thin peat/Dalradian gneiss	5-6 <sup>4</sup>	500	7/1	MO(o), Mc×MO(vr)
Marsh, above LAWERS Burn, S.W. Kenmore, Mid-Perth, v.c. 88	27/677.411	360	Peat/till/mica schist	5-0	2000	6/4-7/1	None
Rough pasture, GLENCAIRN, S. Boat of Garten, S. Aberdeen, v.c. 92	28/941.163	220	Thin peat/ glaciofluvial sand/ schist	4-4	3000	6/4-7/1	None
Marsh, S. Cran Loch, CULBIN Forest, Nairn, v.c. 96b	28/946.588	8	Peat/blown sand/ glaciofluvial sand	5-9	30	7/1-2	MP(r), Mc×MP(vr)
Heath, N.E. shore Loch CLUANIE, Glen Moriston, Easternness, v.c. 96a	28/174.104	180	Thin peat/granite	5-5	50	7/1	None
Streamside marsh, N.E. ELGOL, Skye, N. Ebudes, v.c. 104	18/536.152	115	Peat/till/doleritic sill	6-1	500	7/1	None
Bog, upper KINLOCH Glen, Rhum, N. Ebudes, v.c. 104	18/369.001	110	Peat/Torridonian sandstone	4-6 <sup>4</sup>	50	7/1	None
Bog, upper KILMORY Glen, Rhum, N. Ebudes, v.c. 104	18/364.010	c.50	Peat/Torridonian sandstone	—	60	7/2-3	None
Machair, HARRIS Bay, Rhum, N. Ebudes, v.c. 104	18/335.958	c.65	Thin peat/raised beach sand/gabbro	5-9	1000	8/1	None

TABLE 3. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES FOR *D. FUCHSII* POPULATION MEANS, LISTED IN ORDER OF DECREASING IMPORTANCE

Principal coordinate	PC1		PC2
Percentage of variance accounted for	27.1		23.1
Variate name, and direction of increase in value of variate in relation to increase in value of vector (e.g. populations with the largest mean values for leaf width and other vigour characters tend to occur towards the left side of PC1 on Fig. 2).	Width of widest leaf	-	Labellum colour, 'y'
	Stem diameter	-	Labellum colour, reflectivity (Y)
	Inflorescence length	-	Presence of leaf markings
	Plant height	-	Stem anthocyanin
	Length of basal bracts	-	Bract anthocyanin
	Length of longest leaf	-	Labellum markings, contrast
	Position of longest leaf up stem	-	Labellum markings, distribution
	Number of non-sheathing leaves	-	Labellum markings, type
	Number of sheathing leaves	-	
	Number of flowers	-	
	Length of floral bracts	-	

TABLE 4. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES FOR *D. MACULATA* POPULATION MEANS, LISTED IN ORDER OF DECREASING IMPORTANCE

Principal coordinate	PC1		PC2
Percentage of variance accounted for	29.2		15.1
Variate name, and direction of increase in value of variate in relation to increase in value of vector.	Stem diameter	-	Bract anthocyanin
	Length of basal bracts	-	Stem anthocyanin
	Length of floral bracts	-	Presence of leaf markings
	Number of flowers	-	Labellum markings, type
	Ovary length	-	Labellum markings, contrast
	Width of widest leaf	-	L.o.p.s <sup>1</sup> , solid markings
	Spur, length	-	Labellum markings, distribution
	Labellum, width	-	
	Plant height	-	
	Inflorescence length	-	
	Length of longest leaf	-	
	Labellum, length to lateral lobe	-	
	Labellum, length to central lobe	-	
	Labellum, length to base of sinus	-	

<sup>1</sup> L.o.p.s = lateral outer perianth segments.

coordinates for *D. fuchsii* populations; PC1 again represented vegetative vigour (though supplemented with some floral dimension characters) and PC2 represented pigmentation. At the extremes of PC1 were the stunted, late-flowering populations from Harris and Porlock, and the especially vigorous populations from marshes at Thursley and Llandegfan (Fig. 2). Separation of populations along PC2 according to degree of pigmentation was less clearly defined than for *D. fuchsii*. The five anthocyanin-low populations from Carboniferous limestone habitats (PC2 values < -0.15) differed considerably in vigour, and consequently formed three separate branches of the minimum spanning tree: Ashes Gill (Yorkshire, hay-meadow), Poulisallagh, Murroogh, Ballyryan (Burren, limestone pavements), and White Nook (Yorkshire, upland pasture). No populations of *D. maculata* were as anthocyanin-rich as the extreme populations of *D. fuchsii*. The Burren populations, and those from New Forest heathlands (Matley, Stephill, Crockford), formed two clusters, but the three populations from the Isle of Rhum (Kilmory, Kinloch, Harris) did not associate closely.



## ANALYSES OF INDIVIDUAL PLANTS

Both principal coordinates plots for individual plants (Figs. 3 & 4) represented more characters but much less of the total variance than the equivalent ordinations of population means (Tables 5 & 6). Characters reflecting floral dimensions made more important contributions to plots for individuals than to those for populations.

Pigmentation replaced vigour as the strongest coordinate (PC1) in the plot of *D. fuchsii* individuals (Fig. 3), which revealed almost complete overlap of the three dark-flowered varieties (vars *hebridensis*, *cornubiensis* and *alpina*) and considerable overlap between them and the supposedly predominantly pale-flowered var. *okellyi*. Var. *fuchsii* again tended to have intermediate values for the pigmentation coordinate (PC1), and included numerous vigorous plants that dominated the positive end of PC2. The apparent discontinuity between anthocyanin-deficient plants (PC1 values  $< -0.15$ ) and the remainder was exaggerated by zero scores for three characters representing a single feature (absence of labellum markings) and was much less evident when the data were re-analyzed without these characters. The anthocyanin-deficient plants were mostly var.

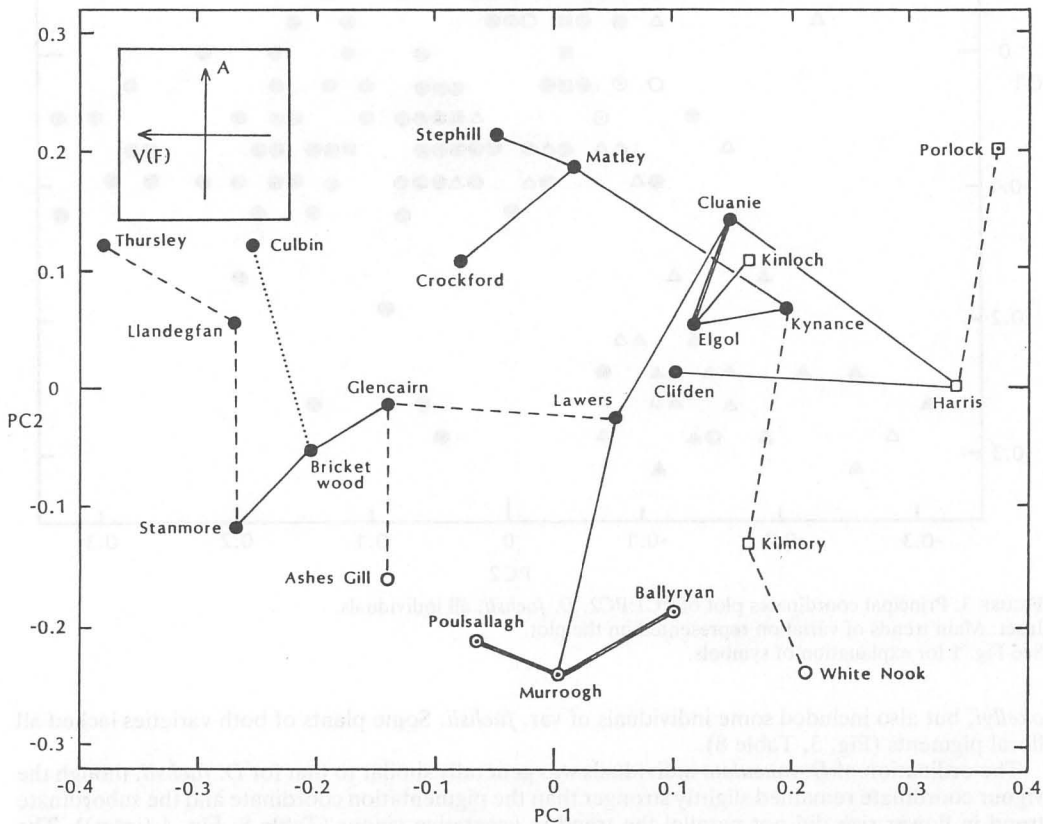


FIGURE 2. Principal coordinates plot of PC1:PC2 with superimposed minimum spanning tree. *D. maculata*, population means.

- Burren
- Other Carboniferous limestone regions (● individuals lacking floral anthocyanins; Fig. 4)
- Rhum
- Porlock
- residuum

See Fig. 1 for strengths of minimum spanning tree links.

Inset: Main trends of variation represented on the plot (see Fig. 1).

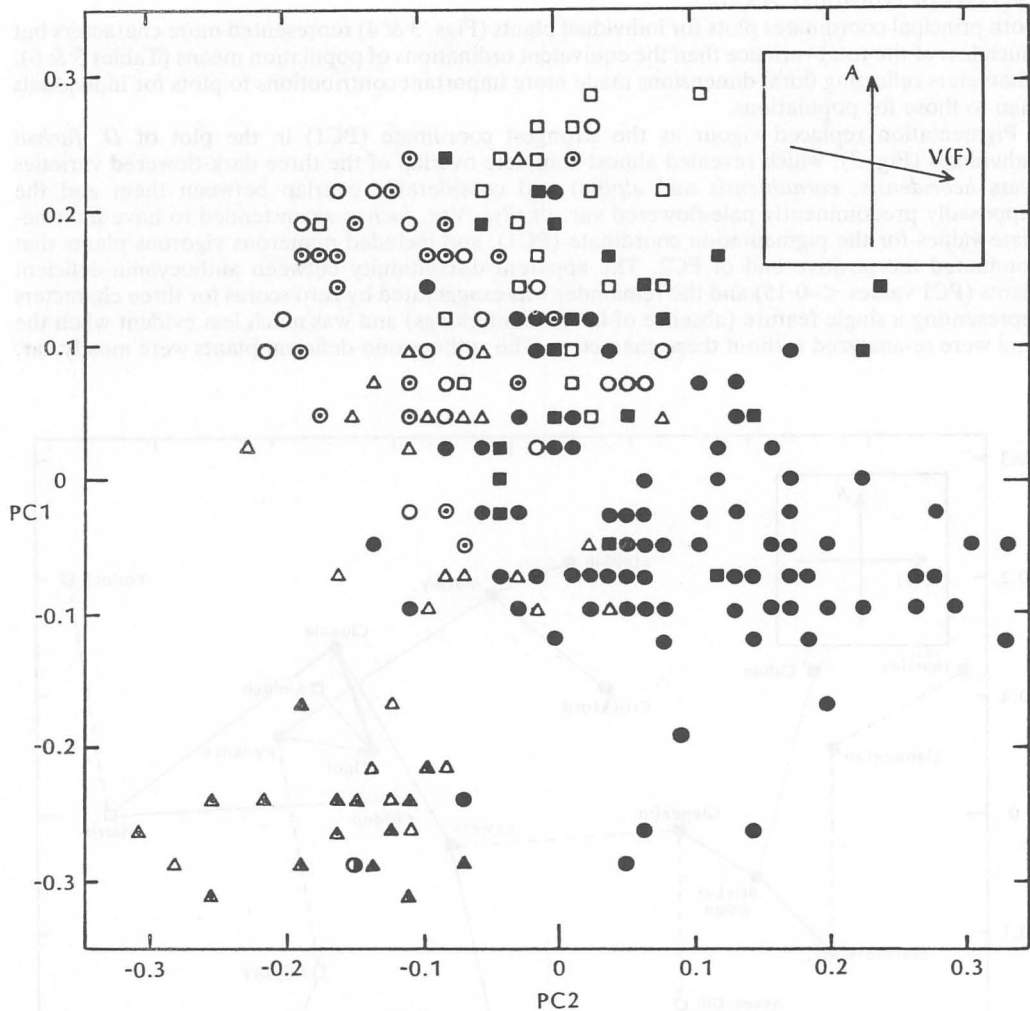


FIGURE 3. Principal coordinates plot of PC1:PC2. *D. fuchsii*, all individuals. Inset: Main trends of variation represented on the plot. See Fig. 1 for explanation of symbols.

*okellyi*, but also included some individuals of var. *fuchsii*. Some plants of both varieties lacked all floral pigments (Fig. 3, Table 8).

The ordination of *D. maculata* individuals was generally similar to that for *D. fuchsii*, though the vigour coordinate remained slightly stronger than the pigmentation coordinate and the subordinate trend in flower size did not parallel the trend in vegetative vigour (Table 8, Fig. 4 (inset)). The morphological extremes on Fig. 4 were anthocyanin-less plants from Carboniferous limestone habitats in the Burren and Yorkshire (bottom), small, late-flowering plants from Porlock and Harris (left) and large, marsh-dwelling plants from Thursley, Llandegfan, Stanmore and Culbin (top right). However, geographically- and/or ecologically-related populations (including those from Rhum) were widely dispersed on the plot, which showed considerable morphological overlap of any potential infraspecific taxa that could be delimited using these criteria.

Thus, variation in both species of spotted-orchid is polarized into two major trends of approximately equal importance: vigour and pigmentation. Each trend represents a group of

consistently correlated characters but the trends themselves are uncorrelated, so that most combinations of intensity of pigmentation and degree of vigour can be encountered within the species as a whole. Extensive intra-population variation further obscures resolution of the populations into clearly delimited intraspecific taxa. *D. fuchsii* achieves greater vigour and more intense pigmentation than *D. maculata*, thus presenting a broader morphological range that offers greater scope for taxonomic subdivision.

#### INTERPRETATION OF VARIATION IN THE SPOTTED-ORCHIDS

The major trends of variation in vigour and pigmentation obscure some interesting subordinate trends, and could represent several causal factors. In this and the following section we examine in greater detail the nature and taxonomic implications of the patterns of variation shown by the spotted-orchids, and speculate on possible underlying mechanisms.

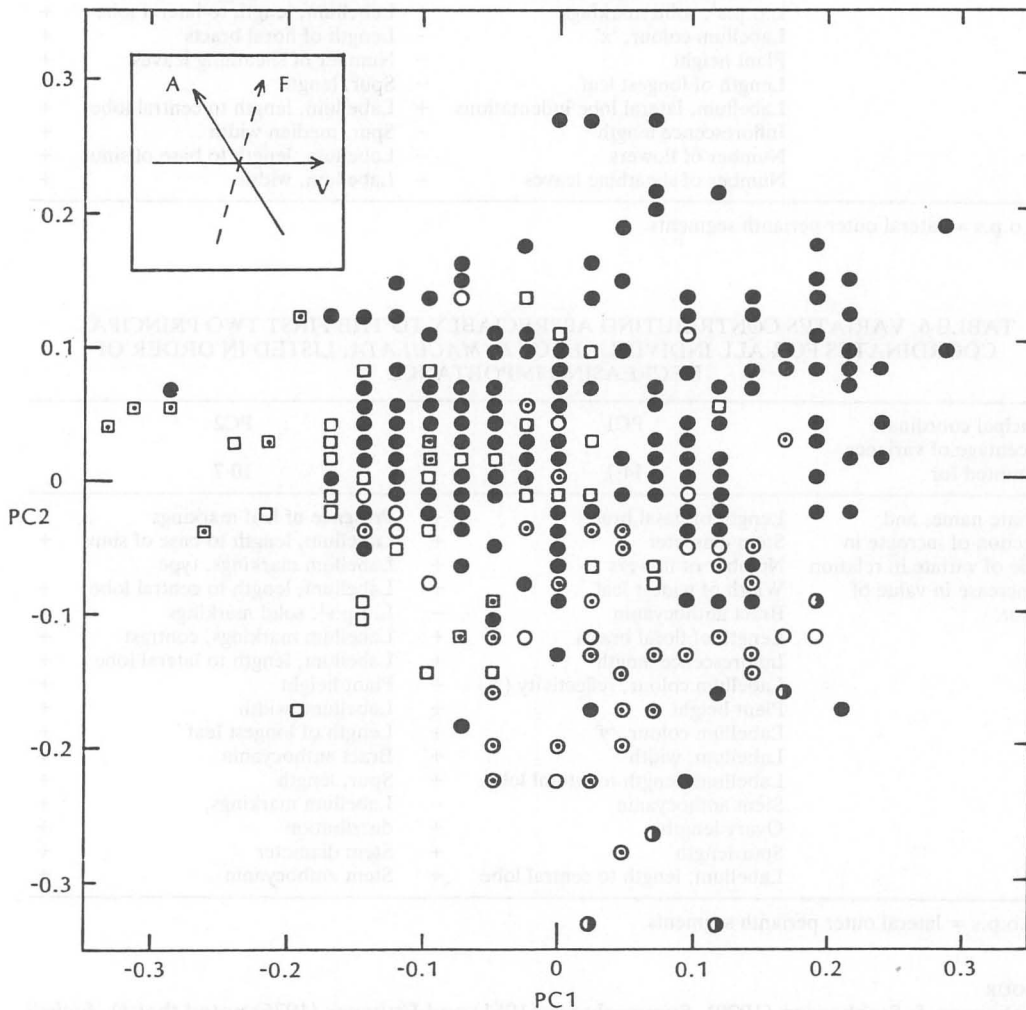


FIGURE 4. Principal coordinates plot of PC1:PC2. *D. maculata*, all individuals.

Inset: Main trends of variation represented on the plot.

See Fig. 2 for explanation of symbols.

TABLE 5. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES FOR ALL INDIVIDUALS OF *D. FUCHSII*, LISTED IN ORDER OF DECREASING IMPORTANCE

Principal coordinate	PC1		PC2	
Percentage of variance accounted for	17.0		13.0	
Variate name, and direction of increase in value of variate in relation to increase in value of vector.	Bract anthocyanin	+	Width of widest leaf	+
	Stem anthocyanin	+	Stem diameter	+
	Labellum colour, reflectivity (Y)	-	Plant height	+
	Labellum colour, 'y'	-	Length of basal bracts	+
	Labellum markings, contrast	+	Inflorescence length	+
	Labellum markings, distribution	+	Length of longest leaf	+
	Presence of leaf markings	+	Number of flowers	+
	Labellum markings, type	+	Position of longest leaf up stem	+
	L.o.p.s <sup>1</sup> , solid markings	+	Labellum, length to lateral lobe	+
	Labellum colour, 'x'	-	Length of floral bracts	+
	Plant height	-	Number of sheathing leaves	+
	Length of longest leaf	-	Spur, length	+
	Labellum, lateral lobe indentations	+	Labellum, length to central lobe	+
	Inflorescence length	-	Spur, median width	+
	Number of flowers	-	Labellum, length to base of sinus	+
	Number of sheathing leaves	-	Labellum, width	+

<sup>1</sup> L.o.p.s = lateral outer perianth segments.

TABLE 6. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES FOR ALL INDIVIDUALS OF *D. MACULATA*, LISTED IN ORDER OF DECREASING IMPORTANCE

Principal coordinate	PC1		PC2	
Percentage of variance accounted for	14.1		10.7	
Variate name, and direction of increase in value of variate in relation to increase in value of vector.	Length of basal bracts	+	Presence of leaf markings	+
	Stem diameter	+	Labellum, length to base of sinus	+
	Number of flowers	+	Labellum markings, type	+
	Width of widest leaf	+	Labellum, length to central lobe	+
	Bract anthocyanin	-	L.o.p.s <sup>1</sup> , solid markings	+
	Length of floral bracts	+	Labellum markings, contrast	+
	Inflorescence length	+	Labellum, length to lateral lobe	+
	Labellum colour, reflectivity (Y)	+	Plant height	+
	Plant height	+	Labellum, width	+
	Labellum colour, 'y'	+	Length of longest leaf	+
	Labellum, width	+	Bract anthocyanin	+
	Labellum, length to lateral lobe	+	Spur, length	+
	Stem anthocyanin	-	Labellum markings, distribution	+
	Ovary length	+	Stem diameter	+
	Spur length	+	Stem anthocyanin	+
	Labellum, length to central lobe	+		

<sup>1</sup> L.o.p.s = lateral outer perianth segments.

## VIGOUR

Stephenson & Stephenson (1920), Summerhayes (1951) and Ettlinger (1976) noted that *D. fuchsii* from clay woodlands tend to be unusually tall and 'leafy'. Harpenden, our only population from a clay wood, had tall (mean height 43 cm) but not especially broad stems (the inflorescence, which was not especially long, was consequently a small proportion (mean value 0.13) of the total stem length)

TABLE 7. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES FOR ALL INDIVIDUALS FROM DARK-FLOWERED POPULATIONS OF *D. FUCHSII*, LISTED IN ORDER OF DECREASING IMPORTANCE

Principal coordinate	PC1	PC2
Percentage of variance accounted for	15.0	11.1
Variate name, and direction of increase in value of variate in relation to increase in value of vector.	Labellum, width	– Labellum, lateral lobe indentations +
	Labellum, length to lateral lobe	– Labellum markings, distribution +
	Labellum, length to central lobe	– Presence of basal leaf –
	Width of widest leaf	– Length anthocyanin –
	Inflorescence length	– Bract anthocyanin +
	Labellum, length to base of sinus	– Leaf colour +
	Spur, median width	– L.o.p.s <sup>1</sup> , position –
	Length of basal bracts	–
	Number of flowers	–
	Spur, width at entrance	–
	Stem diameter	–
	Number of sheathing leaves	–
	Spur, length	–

<sup>1</sup> L.o.p.s = lateral outer perianth segments.

and many long but not particularly broad sheathing leaves that were widely spaced along the stem. These characteristics of lengthening of structures without concomitant increases in width were shared by the population growing in an overgrown meadow at Castlebar, and probably represent a compensation response to low light intensities rather than exceptional vigour per se.

Genuinely vigorous *D. fuchsii* had stems that were unusually broad as well as tall, their leaves were broad as well as long, and they had many (4–6) non-sheathing as well as sheathing leaves. They also had long (>7 cm), many-flowered inflorescences and uppermost sheathing leaves that were broadest well above the base. These increases in overall sizes rather than just lengths of structures were exhibited by the Oaklands and Parham populations from flooded gravel-pits, and those individuals from Pitstone that occupied the marshy floor of the chalk quarry rather than its dry grassy margins. Thus, true vigour in *D. fuchsii* appears to be strongly correlated with high soil moisture content, again suggesting a phenotypic response to environmental (in this case edaphic) factors. Intriguingly, at least some of these marsh-dwelling *D. fuchsii* possessed hollow stems, a feature that is supposedly confined to marsh-orchids.

Two populations of *D. maculata* (Thursley, Llandegfan), collected from amongst tall vegetation in wet habitats, exhibited many of the vigour characteristics shown by the Oaklands and Parham populations of *D. fuchsii*. They had tall, broad stems, long, many-flowered inflorescences, long, broad (though not particularly numerous) leaves widely distributed along the stem and long basal bracts. Three other populations (Culbin, Stanmore, Bricketwood) from *Juncus*-rich marshes showed extreme values for various combinations of these characters, and all five populations possessed rather long spurs.

Populations of both species exhibiting the smallest values for vigour characters grew among short vegetation in exposed coastal (Oldshore and Polin populations of *D. fuchsii*, Harris population of *D. maculata*) or upland (White Nook and Porlock populations of *D. maculata*) habitats, and were probably environmentally dwarfed.

Thus, size variation in vegetative characters may primarily reflect an interaction between the ontogeny of spotted-orchids and environmental factors such as light intensity, soil moisture and exposure (particularly to wind). The resulting effects on the phenotype, which are more readily discerned in *D. fuchsii* than *D. maculata*, obscure any independent geographical trends such as the latitudinal cline in leaf number suggested by Heslop-Harrison (1951).

#### PIGMENTATION

The eight populations of *D. fuchsii* with mean labellum reflectivities below 40% (Fig. 6) also tended to have the lowest standard deviations for this character (all but Tintagel <10%), suggesting that

TABLE 8. GEOGRAPHICAL AND ECOLOGICAL VARIATION IN FREQUENCIES OF ANTHOCYANIN DEFICIENCIES IN *D. FUCHSII* AND *D. MACULATA*

Percentage of plants lacking:		<i>D. FUCHSII</i>				<i>D. MACULATA</i>			
		All populations	Carboniferous limestone: Burren	Carboniferous limestone: Yorks.	Non-Carboniferous limestone	All populations	Carboniferous limestone: Burren	Carboniferous limestone: Yorks.	Non-Carboniferous limestone
Vegetative anthocyanins	Stem anthocyanins	51	70	10	48	64	90	90	56
	Bract anthocyanins	46	68	10	43	39	67	70	31
	Leaf markings	13	43	20	9	15	53	25	8
Floral anthocyanins	L.o.p.s <sup>1</sup> , markings	40	68	40	32	10	10	35	7
	Labellum markings	15	48	0	5	5	0	35	2
	Labellum anthocyanins	12	48	0	3	25	3	35	27
	All floral anthocyanins	8	35	0	2	3	0	30	0
	All floral and vegetative anthocyanins (i.e. albinos)	6	25	0	1	1	0	10	0
	(Total number of plants)	(200)	(40)	(10)	(150)	(232)	(30)	(20)	(182)

<sup>1</sup> L.o.p.s = lateral outer perianth segments.

they constitute a distinct and consistent anthocyanin-high facies of *D. fuchsii*. This was supported by the frequent occurrence of bract and stem anthocyanins in these populations, though leaf and labellum markings were not especially large or bold. However, this group was very heterogenous in other respects, notably labellum size, and included both the largest- and smallest-flowered populations of *D. fuchsii* (Fig. 6). Marked bimodality in labellum dimensions (particularly width) distinguished the large-flowered vars. *hebridensis* and *cornubiensis* from the small-flowered var. *alpina*. As labellum dimensions were only minor contributors to the first two principal coordinates for all *D. fuchsii* individuals (Table 5), this distinction was not apparent in that plot (Fig. 3). When the analysis was repeated using only individuals of dark-flowered populations, PC1 largely separated var. *alpina* from vars *hebridensis* and *cornubiensis* (Fig. 5) using floral dimensions (Table 7). PC2 gave an equal degree of separation of vars. *hebridensis* and *cornubiensis*, but using a more diverse set of unrelated characters that are less easily interpreted (Table 7). Hence, this dark-flowered facies comprised three groups of populations showing approximately equal levels of morphological and ecological differentiation.

Two populations of *D. maculata* (Harris, Rhum; Porlock, Exmoor) resembled the dark-flowered facies of *D. fuchsii* in having mean labellum reflectivities of less than 40%. They were also distinguished by their late flowering (August; Table 2), narrow stems and small number of narrow leaves. However, they were not especially rich in vegetative anthocyanins and do not appear to form a cohesive morphological unit (see 'Classification').

Neither species of spotted-orchid included a distinct pale-flowered facies that could be distinguished by differences in population means for labellum reflectivity, but both included populations with unusually high frequencies of individuals lacking floral and/or vegetative anthocyanins. Anthocyanin-deficient plants of *D. fuchsii* were most frequent in the Carboniferous limestone habitats of the Burren but, contrary to popular belief, comprised a minority of plants in all four study populations (Table 8); these Burren populations even included plants that matched typical individuals of vars *hebridensis*, *cornubiensis* and *alpina* in intensity of floral pigments. Ashes Gill, Yorkshire, the only other study population of *D. fuchsii* from Carboniferous limestone, was attributed to the dark-flowered var. *alpina*. In contrast, *D. maculata* populations with the highest frequencies of plants deficient in vegetative anthocyanins were associated with Carboniferous limestone habitats in both the Burren and Yorkshire (Table 8). Floral pigments were also unusually infrequent in *D. maculata* populations from Yorkshire but, surprisingly, not in those from the Burren; most Burren plants of *D. maculata* possessed diffuse anthocyanins in their labella, albeit at

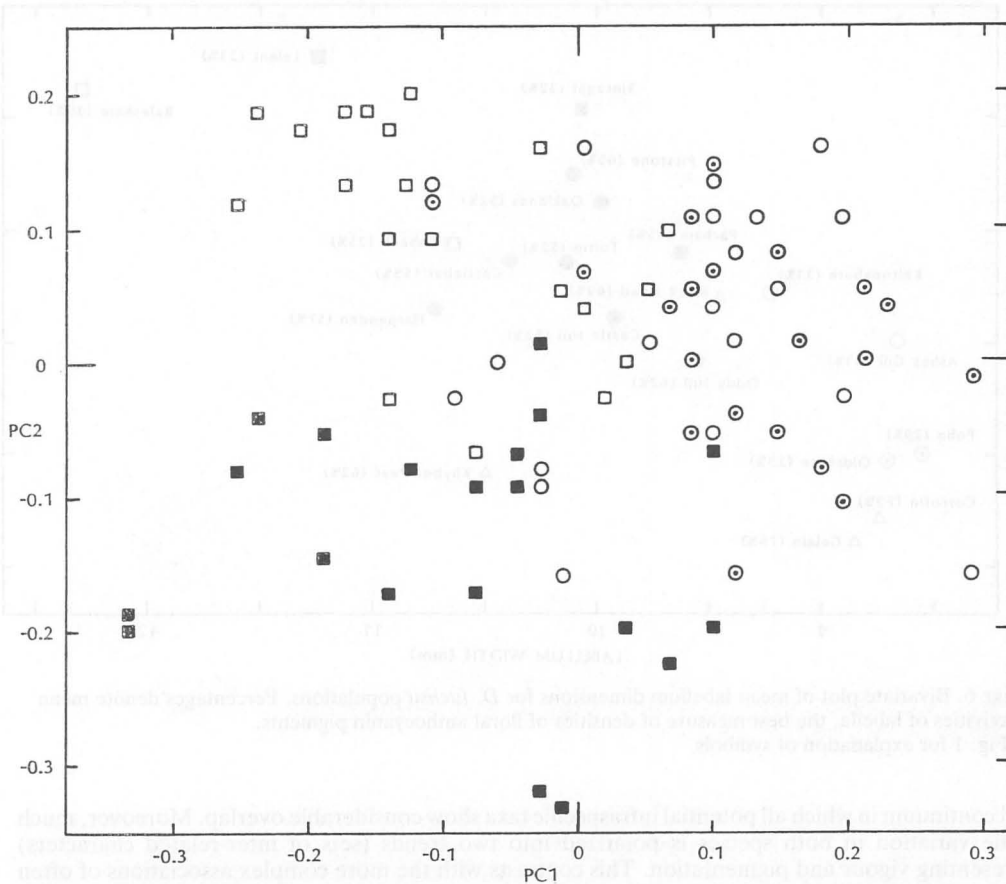


FIGURE 5. Principal coordinates plot of PC1:PC2. *D. fuchsii*, individuals of dark-flowered populations. See Fig. 1 for explanation of symbols.

very low concentrations (over half had reflectivities >70%) and often in very pale hues of red-purple rather than the purple more characteristic of this species. All four anthocyanin-less plants of *D. maculata* that we measured were from Yorkshire (Ashes Gill and White Nook).

Overall, the two species showed similar frequencies of vegetative anthocyanins, but plants lacking all anthocyanins (i.e. true albinos) were more frequent in *D. fuchsii* (Table 8). Labella of *D. fuchsii* more often lacked markings but less often lacked diffuse (i.e. background) anthocyanins than those of *D. maculata*. Approximately 2% of individuals of both species possessed annular leaf markings, a character much more common in marsh-orchids (notably *D. majalis* (Reichenbach) P. F. Hunt & Summerhayes subsp. *occidentalis* (Pugsley) P. D. Sell) but evidently not confined to them (Stephenson & Stephenson 1920; Godfrey 1933; Helsop-Harrison 1948; Wiefelspütz 1976).

#### TAXONOMIC AND EVOLUTIONARY IMPLICATIONS

The delimitation of spotted-orchid taxa and the ranks awarded to them should reflect available knowledge of the nature and causes of their variation: whether the variation is continuous or discontinuous, whether it exhibits geographically- and/or ecologically-related patterns, and to what extent the phenotypic patterns reflect genetic and environmental influences.

Our multivariate analyses demonstrated that each spotted-orchid species constitutes a morpholo-

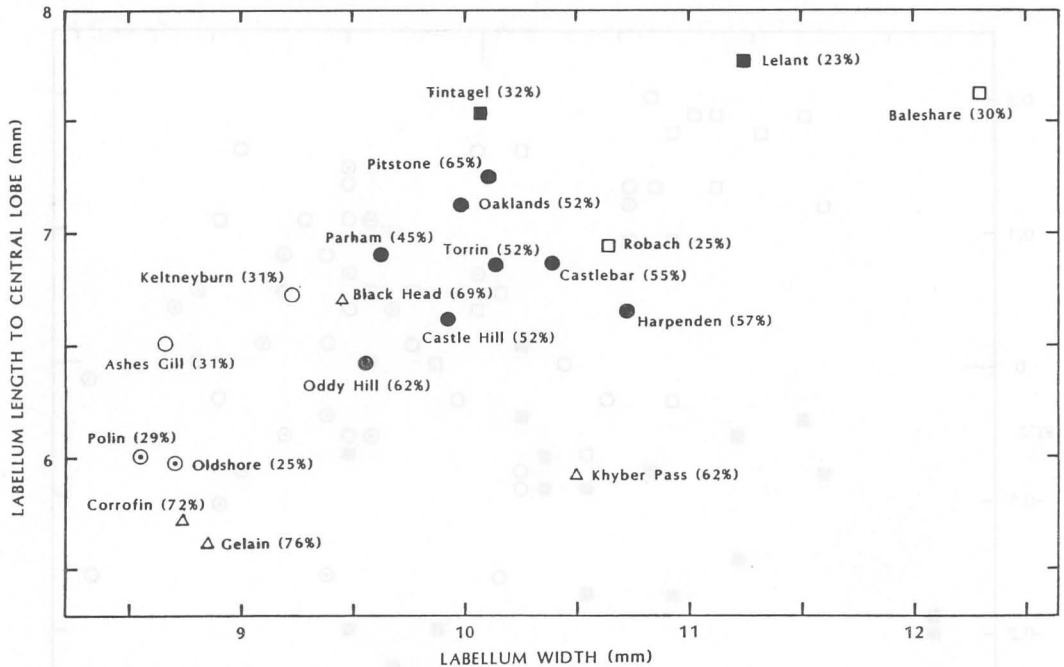


FIGURE 6. Bivariate plot of mean labellum dimensions for *D. fuchsii* populations. Percentages denote mean reflectivities of labella, the best measure of densities of floral anthocyanin pigments. See Fig. 1 for explanation of symbols.

gical continuum in which all potential infraspecific taxa show considerable overlap. Moreover, much of the variation in both species is polarized into two trends (sets of inter-related characters) representing vigour and pigmentation. This contrasts with the more complex associations of often unrelated characters observed in marsh-orchids, whose variation is also continuous but has strong geographical and/or ecological components and can be resolved into subspecies showing only limited morphological overlap (Bateman & Denholm 1983, 1985). Thus, no group of spotted-orchid populations is sufficiently differentiated to merit subspecific status, and those considered worthy of any taxonomic separation have been treated as varieties. We regard the subspecies and the variety as essentially similar concepts; both describe geographically- or ecologically-related groups of populations, but varieties show less morphological differentiation and are separated by fewer, generally less predictive characters. The *D. fuchsii* segregates assigned to this rank are relatively homogeneous and possess distinguishing characters (see 'Classification') that are unlikely to show substantial environmental modification. Var. *fuchsii* remains a comparatively heterogeneous taxon, but further subdivision on the basis of differences in vigour, which may be largely environmentally determined, seems unwise. We have not recognized any infraspecific taxa of *D. maculata*, whose overall range of variation is narrower and even less readily partitioned than that of *D. fuchsii*.

Our treatment of *D. fuchsii* taxa as varieties rather than subspecies contradicts most classifications published during the last 40 years. However, we believe that the taxonomic importance of the two most widely accepted 'subspecies' of *D. fuchsii* (*hebridensis* and *okellyi*) has been inflated by exaggeration of their morphological distinctness, failure to identify optimal diagnostic character states, tautological arguments concerning their identification and speculative assumptions regarding their evolution.

*D. fuchsii* subsp. *hebridensis* was well described from the Hebrides, initially qualitatively by Wilmott (1939) and later quantitatively by Heslop-Harrison (1948, 1952, 1954), but it soon became entrenched as a geographically and ecologically restricted taxon with dark flowers that occupied machair along the western seaboard of the British Isles (Heslop-Harrison 1952, 1954, 1968). Var.



TABLE 9. TREATMENT OF SELECTED INTRASPECIFIC TAXA OF *D. MACULATA* BY

(a) BRITISH AND (b) CONTINENTAL WORKERS

– = taxon not mentioned (0 = taxon not yet described); ✓ = considered to occur in Britain; × = not considered British; abbreviations = taxon considered synonymous with subsp. *maculata* (ma), *elodes* (el), *ericetorum* (er); ? = authors' intentions unclear.

(a)											
Taxon	Druce (1915, 1918, 1924b, 1925)	Bennett (1921)	Stephenson & Stephenson (1921)	Godfery (1921, 1933)	Summerhayes (1951)	Heslop-Harrison (1951, 1954)	Clapham (1952, 1962)	Hunt & Summerhayes (1965)	Ettlinger (1976)	Lang (1980)	Davies <i>et al.</i> (1983)
<i>maculata</i>	✓	–	✓	×	–	×	×	–	–	–	?
<i>ericetorum</i>	ma	✓	?ma	el	✓	✓	✓	✓	✓	✓	✓
<i>elodes</i>	ma	er	×	✓	?er	?er	?er	–	er	er	?
<i>praecox</i>	ma	–	ma	el	–	–	–	–	–	–	–
<i>rhoumensis</i>	0	0	0	0	–	–	✓	✓	✓	–	✓

(b)											
Taxon	Camus & Camus (1929)	Vermeulen (1947)	Soó (1960)	Senghas (1968)	Nelson (1976)	Wiefelspütz (1976)	Landwehr (1977)	Soó (1980)	Sundermann (1980)	Delforge & Tyteca (1984)	
<i>maculata</i>	✓	?	✓	?	er	?	✓	✓	✓	✓	✓
<i>ericetorum</i>	el	✓	✓	el	✓	✓	✓	ma	ma	✓	✓
<i>elodes</i>	✓	?	×	✓	er	×	✓	✓	ma	×	×
<i>praecox</i>	el	el	er	–	–	er	er	–	–	–	–
<i>rhoumensis</i>	0	0	✓	✓	–	–	–	–	–	–	–

*cornubiensis* and coastal populations of var. *alpina*, which were also dark-flowered and conformed to these distributional criteria, were included in *hebridensis* without supporting morphological data (e.g. Perring & Sell 1968) while inland populations of var. *alpina* were excluded. Consequently, *hebridensis* became a morphologically heterogeneous taxon whose individuals could not be identified without knowledge of their geographical location (Heslop-Harrison 1968, p. 23). Its morphological distinction was exaggerated by insufficient knowledge of the broad morphological range encompassed by var. *fuchsii* and failure to recognize the small- and dark-flowered taxon that we have named var. *alpina*.

The recorded (predominantly western) distribution of subsp. *okellyi* resembles that of subsp.

*hebridensis* (Perring & Sell 1968) and also covers a restricted range of habitats, typically limestone pavements. It therefore received the same distributional 'positive feedback' as subsp. *hebridensis*, and progressed from "an indistinct recessive colour race" (Stephenson & Stephenson 1921) to a subspecies exhibiting a typical Atlantic distribution (Heslop-Harrison 1954; Perring & Sell 1968). However, *okellyi* differs from *hebridensis* in having been poorly described in its original diagnosis (Druce 1909), which greatly exaggerated its anthocyanin deficiency. Our data show that flowers from populations of var. *okellyi* in the Burren (its type locality) are not especially pale (their mean labellum reflectivities resemble those of chalk populations of var. *fuchsii* at Oddy Hill and Pitstone), nor are they unusually deficient in bract and stem anthocyanins. Anthocyanin-deficient plants are a subordinate component of most populations of *D. fuchsii* in the Burren, including all four that we studied, and the Burren populations are even less readily distinguished by other supposedly diagnostic characters such as smaller labella and spurs, and narrower stems and leaves. Furthermore, anthocyanin-less *D. fuchsii* from the Burren cannot be distinguished from similar plants growing in other regions and habitats (Fig. 3). Hence, var. *okellyi* is much less differentiated from var. *fuchsii* than has generally been assumed, and differs mainly in the higher frequency of individuals deficient in floral and/or vegetative anthocyanins. It coexists in the Burren with an analogous anthocyanin-low variant of *D. maculata* (see 'Classification').

A third British spotted-orchid subspecies, *D. maculata* subsp. *rhoumensis*, has not received such general acceptance. This enigmatic Rhum endemic reputedly has pale purple flowers, bold labellum markings, blooms in August and is diploid (Heslop-Harrison 1948). Our three study populations from Rhum differed appreciably in morphology and phenology both from each other and from the original diagnosis of *rhoumensis* (see 'Classification'), but not from populations of *D. maculata* elsewhere in the British Isles. We cannot therefore identify any cohesive infraspecific taxon peculiar to, or present on, Rhum.

The infraspecific taxonomy of the spotted-orchids has also been strongly influenced in the past by speculative interpretations of their population biology. Heslop-Harrison (1952, 1954, 1968) justified subspecific status for *hebridensis* and *okellyi* by arguing that in their "extreme" forms both approach ecologically and morphologically well-defined races, probably of monophyletic origin, that are largely reproductively isolated from the type due to their disjunct geographical ranges. However, he also noted that vars. *hebridensis* and *okellyi* intergrade extensively with var. *fuchsii*, both by extensive geographical clines and by 'hybridization' at sites where two taxa occur (Heslop-Harrison 1948, 1949, 1951, 1952, 1954; Allen 1971; Wiefelspütz 1976). Our observations suggest that populations of *D. fuchsii* are not as differentiated as the above argument implies, and we do not believe that taxonomic decisions should be based solely on geographical and morphological extremes. It seems more appropriate to regard *D. fuchsii* as a variable species whose populations differ locally in 'mean morphology' in response to prevailing edaphic and climatic factors, both through adaptive shifts in gene frequencies and environmental modification of phenotypes. We believe that morphological continuity in both species probably reflects potentially unrestricted gene flow within and between the poorly-differentiated groups of populations; if so, terms such as 'intergradation' and 'hybridization' are inapplicable in this context. However, neither hypothesis can be substantiated without non-morphological data and new insights into the control and adaptive significance of particular morphological traits.

#### POSSIBLE CONSPECIFICITY OF THE SPOTTED-ORCHIDS

Most British workers have regarded *D. fuchsii* and *D. maculata* as separate species, distinguished by consistent differences in morphology (principally labellum shape) and chromosome number. The supposed cytological discontinuity dates from a few chromosome counts by Hagerup (1938) of  $2n=40$  (diploid) for *D. fuchsii* and  $2n=80$  (tetraploid) for *D. maculata* subsp. *maculata* and subsp. *elodes*. Much emphasis has been placed on this apparent discontinuity by subsequent authors, including ourselves. However, in the same year, Heusser (1938) demonstrated the presence in Switzerland of diploid and tetraploid populations that were both assignable to *D. fuchsii* on morphological criteria, and the potential taxonomic significance of this observation was quickly realized by Pugsley (1939). Hagerup (1944) then described *D. fuchsii* embryos with  $2n=20$  and  $2n=60$ , and a few *D. maculata* embryos with  $2n=40$ . Heslop-Harrison (1948) reported  $2n=40$  for *D.*

*maculata* subsp. *rhoumensis* from Rhum. Populations of *D. fuchsii* in Austria may be  $2n=40$ , 60 or 80 without showing significant morphological differences (Groll 1965, 1968; Voth 1978; Voth & Greilhuber 1980), and Averyanov (1977) reported *D. maculata* near Leningrad with  $2n=60$ . Thus, both spotted-orchid species appear to be capable of maintaining cytologically stable populations that are diploid, triploid or tetraploid, and previous assumptions of chromosome number based on extrapolation from morphology may have been rash.

When Druce (1915) first separated *D. fuchsii* from *D. maculata* he speculated that the morphological differences between the two species may simply reflect differences in the soils that they inhabit. Stephenson & Stephenson (1921) and Godfery (1921) questioned this hypothesis, noting that the two species remained morphologically distinct in mixed colonies. Heslop-Harrison (1948) compared soil pH from several populations of *D. fuchsii* and *D. maculata* in the Hebrides, and concluded that the former occupied soils of pH less than 5.5 and the latter soils of pH greater than 5.0. He subsequently repeated these figures as generally characteristic of the habitats of the two species (Heslop-Harrison 1951, 1954). However, 11 of our 23 study populations of *D. maculata* occupied soils of pH greater than 5.5 (Table 2), and four populations grew in neutral soils (pH >6). *D. fuchsii* is almost confined to neutral or alkaline soils, though our study population of *D. fuchsii* that most closely resembled *D. maculata* (Harpenden) occupied a slightly acidic soil (pH 5.8; Table 1). Its labella had relatively shallow sinuses and central lobes that equalled or only slightly exceeded the laterals, resulting in a small labellum shape index (1.23) similar to that of the Harris population of *D. maculata* (1.24). Furthermore, the Harpenden *D. fuchsii* had unusually broken labellum markings and a small value for mean leaf shape index (0.11) more typical of *D. maculata*. Four populations of *D. maculata* had appreciably larger mean values for the labellum shape index than the remainder; two were from isolated southern populations in only mildly acidic soils (Bricketwood and Stanmore) and two were environmentally-stunted (Harris and White Nook). Plants from Bricketwood and Harris also had central labellum lobes that considerably exceeded the laterals, approaching *D. fuchsii* in this respect (e.g. Stephenson & Stephenson 1921). Thus, spotted-orchid populations showing intermediate characteristics tend to occupy intermediate habitats, and an edaphic influence on their morphology is possible.

Biometric studies on spotted-orchid populations from mainland Europe (Heslop-Harrison 1951; Groll 1965, 1968; Voth 1978; Voth & Greilhuber 1980; Reinhard 1985) indicate that *D. fuchsii* and *D. maculata* are less distinct on the Continent than in the British Isles (see also Summerhayes 1951, p. 273). Thus, Continental workers (e.g. Vermeulen 1949; Landwehr 1977; Soó 1980) have attempted to partition a more restricted range of variation, and have consequently created a large number of poorly-defined and often overlapping infraspecific spotted-orchid taxa. This observation also explains why *D. fuchsii* was first described as a species by a British worker (Druce) as late as 1915; during the previous 80 years, Continental workers, including several who were content to treat apparently much more trivial entities as species, had recognized *D. fuchsii* under several different names at varietal and formal rank (see 'Classification'). If *D. fuchsii* and *D. maculata* prove to be both morphologically and cytologically indistinct on the Continent, there is a strong argument for following Nelson (1976) and Sundermann (1980), and relegating *D. fuchsii* to *D. maculata* (L.) Soó subsp. *fuchsii* (Druce) Hylander.

#### CLASSIFICATION

The classification and diagnostic descriptions that follow are based on our principal coordinates (Figs. 1–5, Tables 3–7), minimum spanning trees, analyses of population means, and ranges for individual characters. Published data on British plants (Heslop-Harrison 1948, 1951, 1954) and on Continental plants (Heslop-Harrison 1951; Groll 1965, 1968; Voth 1978; Voth & Greilhuber 1980; Reinhard 1985) have also been considered.

The following terms are used to describe the frequencies of character states in taxa: rarely, less than 20% of individuals; occasionally, 20–50%; often, 51–80%; usually, greater than 80%. Frequencies of the best diagnostic characters (italicized) show most discontinuity between varieties. Some terms used in the descriptions are qualitative but are derived from quantitative measurements:

Density of inflorescence: dense, index 'f' value greater than 7. Depth of labellum sinuses: very deep,

index 'b' value greater than 1.5 (the term 'labellum shape index' refers exclusively to index 'b'). Roundness of labellum: broad, index 'a' value less than 0.4. Position of lateral outer perianth segments:  $\pm$  horizontal, categories 1 and 2 on our scale.  
Soil pH: acid, <6; neutral, 6–7; alkaline, >7.

Genus *Dactylorhiza* Necker ex Nevski, *Acta hort. bot. Acad. sci. URSS* 4: 332 (1937).

Sect. *Maculatae* (Parlatore) Vermeulen, *Stud. Dactyl.* 65 (1947).

Subsect. *Eumaculatae* Vermeulen, *Stud. Dactyl.* 68 (1947).

1. *Dactylorhiza fuchsii* (Druce) Soó, *Nom. nov. gen. Dactylorhiza* 8 (1962).

*Orchis fuchsii* Druce in *Rep. botl Soc. Exch. Club Br. Isl.* 4: 105 (1915).

*O. maculata* L. var. *trilobata* Brébisson, *Fl. Normandie* 313 (1835).

*O. maculata* L. var. *meyeri* Reichenbach f., *Icon. Fl. Germ.* 67 (1851).

*O. maculata* L. subsp. *meyeri* (Reichenbach f.) Camus, *Mon. Orch. Eur.* 193 (1908).

*O. maculata* L. var. *obscura* Neuman in *Bot. Notiser* 1909: 153 (1909).

*O. fuchsii* Druce subvar. *albiflora* Druce in *Rep. botl Soc. Exch. Club Br. Isl.* 5: 167 (1918).

*Dactylorchis fuchsii* (Druce) Vermeulen, *Stud. Dactyl.* 147 (1947).

*D. fuchsii* (Druce) Vermeulen var. *meyeri* (Reichenbach f.) Vermeulen, *Stud. Dactyl.* 146 (1947).

*Dactylorhiza fuchsii* (Druce) Soó var. *meyeri* (Reichenbach f.) Soó, *Nom. nov. gen. Dactylorhiza* 8 (1962).

Stem 7–50(–70) cm, 1.5–7.5(–11) mm in diameter, often lacking anthocyanins. Basal lf or sheath 0–1, broadest at or above middle; sheathing lvs (2–)3–6(–7), usually strongly crowded towards base of stem, usually recurved, narrowly to broadly lanceolate, usually broadest well above base, longest lf usually above widest, 4.5–16.5 cm long, widest lf 0.5–4(–5.5) cm wide, width/length ratio of lvs decreasing up stem, usually bright to dark green, tips rarely distinctly hooded; non-sheathing lvs (1–)2–6(–9), narrow, broadest at base; lvs usually sparsely to densely marked on upper surface only, markings usually solid (very rarely annular), usually  $\pm$  evenly distributed and transversely elongated, usually 1.5–6 mm in mean diameter. Inflorescence 1.5–10(–22) cm, 8–30% of stem length, fls 8–60(–95), fairly lax to dense (3.5–10(–13) fls/cm). Basal bracts 7.5–23(–38) mm, 1.5–2.5 times the length of the ovaries, floral bracts 5–12 mm, approximately equalling the ovaries, often suffused with anthocyanins; peripheral bract cells (40–)55–135(–170)  $\mu$ m long, barrel-shaped to triangular. Labellum width exceeding length (usually considerably), 4.5–8.5(–9.5)  $\times$  7–12(–13.5) mm, widest  $\pm$  at middle or above (obtriangular), base colour varying densities (reflectivity 10–89%) of purple or less frequently white; markings pale to bold dashes and/or loops, occasionally dots and dashes, rarely absent or a solid blotch, often covering about two-thirds of the labellum, occasionally more or less; sinuses present (labellum three-lobed), usually deep, central lobe often exceeding lateral lobes by >1 mm, labellum shape index usually >1.25; lateral lobes usually indented, slightly deflexed to moderately reflexed; lateral outer perianth segments usually nearer horizontal than vertical, often with solid (rarely annular) markings; median outer perianth segment and inner perianth segments connivent; spur straight to moderately decurved, 3.5–8  $\times$  1–2.5 mm at entrance, 0.8–2.3 mm halfway along (2–3.7 mm at entrance, 1.6–3.2 mm halfway along in var. *cornubiensis*), usually slightly tapering, half as long to as long as the ovary.  $2n=?$ 40. Flowering mid-June to late July. Frequent and locally common throughout most of the British Isles, local in northeast Scotland and the southwest. Neutral to alkaline (rarely slightly acid) soils.

Most early classifications recognized only a single species of spotted-orchid, *Orchis maculata* (Linnaeus 1753). However, towards the end of the 19th Century, some workers began to realize that two distinct taxa occurred in the British Isles. One had oval, planar lower leaves, deeply and subequally three-lobed labella with the central lobe projecting beyond the laterals, and fairly narrow, tapering spurs (*D. fuchsii*). It inhabited calcareous and neutral soils. The second had lanceolate, keeled lower leaves, shallowly three-lobed labella with the lateral lobes equalling the central lobe in length and considerably exceeding it in area, and very narrow, parallel-sided spurs (*D. maculata*). It inhabited acid soils. Early attempts to recognize this taxonomic distinction were made at infraspecific levels within *D. maculata*. *D. fuchsii* was regarded as *O. maculata sensu stricto* and therefore treated as the type, and what we now call *D. maculata* was the segregate. Webster's

(1886) *O. maculata* var. *praecox* was a restricted and unusual taxon, but Linton (1900) provided a much more generally applicable description of British *D. maculata* as *O. maculata* subsp. *ericetorum* Linton, a name that is still in general use in Britain (Table 9; see also discussion of *D. maculata*).

Few short papers can have initiated more taxonomic and nomenclatural controversy than that of Druce (1915), which segregated the calcicolous spotted-orchids as a new species, *Orchis fuchsii*, and treated the calcifuge as Linnaeus' *O. maculata*. He was repeatedly obliged to justify this decision (Druce 1915, 1918, 1924a, b, 1925) in barbed exchanges with Godfery (1921, 1923, 1924, 1933), who believed that *O. maculata* was the calcicolous species. The debate was eventually settled in Druce's favour by Vermeulen (1947, 1968) and Heslop-Harrison (1951), who demonstrated that Linnaeus' type specimen of *O. maculata* was the calcifuge taxon.

The evolution of spotted-orchid nomenclature on the Continent resembles that in Britain. Early workers included a broad morphological range in *O. maculata*, but this was progressively subdivided at subspecific or, more often, varietal level. *D. fuchsii* was repeatedly segregated from *D. maculata*, most notably as *O. maculata* var. *trilobata* Brébisson (1836), var. *meyeri* Reichenbach f. (1851) and var. *obscura* Neuman (1909) (Heslop-Harrison 1951). Most Continental workers now include these taxa in *D. fuchsii*, but few are willing to treat *D. fuchsii* as a full species.

One notable exception is Holub (1983), who argued that *D. fuchsii* is a junior synonym of *D. longibracteata* (F. W. Schmid) Holub, based on *Orchis longibracteata* F. W. Schmid (1791). However, Jagietto (1986) convincingly demonstrated that the original description of *longibracteata*, although ambiguous, is clearly discordant with *D. fuchsii*.

#### *Extremes of pigmentation*

About 20% of the *D. fuchsii* individuals at Oddy Hill occurred as an anthocyanin-rich form with labellum markings more-or-less fused into a solid blotch and the upper surface of the sheathing leaves with at least 50% areal coverage of large (mean diameter >6 mm) markings or entirely covered with diffuse anthocyanins. Such plants also frequently possess spotted bracts and dashes on their stems and ovaries, resembling some plants of var. *hebridensis*. This variant has also been recorded in other chalk grassland populations at Beacon Hill, N. Hants. (D. M. T. Ettlinger pers. comm. 1985; A. R. G. Mundell pers. comm. 1987), Mickleham, Surrey and Barton-le-Clay, Beds. (R. M. Bateman), and "near Winchester" (Godfery 1933, p. 206 and Plate 50/22, 25), from limestone grassland near Buxton, Derbyshire (D. M. T. Ettlinger pers. comm. 1987) and from mildly acid coastal grassland at Armadale, Skye (R. M. Bateman). Nelson (1976, p. 100 and Plate 70c, d) illustrated similar plants from Scandinavia. Analogous variants occur in *D. maculata* (q.v.), *D. majalis* subsp. *purpurella* (T. & T. A. Stephenson) D. Moresby Moore & Soó (near Hartlepool) and *D. ?incarnata* (L.) Soó (near Southampton) (D. M. T. Ettlinger pers. comm. 1986).

Anthocyanin-less individuals have white or very pale cream-coloured flowers and have been called subvar. *albiflora* Druce (1918). They form a small proportion of many populations of var. *fuchsii* (e.g. Pitstone) and a much larger proportion of populations of var. *okellyi*.

#### a. var. *fuchsii* (Druce) Bateman & Denholm, **comb. nov.**

*Orchis fuchsii* Druce in *Rep. botl Soc. Exch. Club Br. Isl.* 4: 105 (1915).

*Dactylorchis fuchsii* (Druce) Vermeulen subsp. *typica* Vermeulen, *Stud. Dactyl.* 148 (1947).

*Dactylorhiza fuchsii* (Druce) Soó subsp. *fuchsii* (Druce) Soó, *Nom. nov. gen. Dactylorhiza* 8 (1962).

*Stem usually >20 cm*, often >3.5 mm in diameter, occasionally suffused with anthocyanins (rarely densely). Sheathing 1vs usually 4 or more, longest 1f often >9 cm long, widest 1f often >2 cm wide; non-sheathing 1vs often 4 or more; markings usually present, often covering >10% of the upper surface. Inflorescence often >4 cm, occasionally >20% of stem length, occasionally dense, fls often more than 25. *Floral bracts often >8 mm, occasionally suffused with anthocyanins* (rarely densely); peripheral bract cells occasionally angular. Labellum often >6.7 mm long to apex of central lobe, often >5.5 mm to apex of lateral lobe, occasionally >4 mm to base of sinus, often >9.5 mm wide, occasionally broad, sinuses occasionally very deep; *reflectivity of base colour often >40%* (rarely >80%); markings usually present; lateral outer perianth segments often  $\pm$  horizontal, markings often present (rarely annular); spur occasionally >2 mm wide at entrance, >1.8 mm halfway along. Flowering June/early July. Throughout the range of the species.

Var. *fuchsii* is a very heterogeneous taxon, encompassing considerable variation in vigour and pigmentation (see 'Major trends in morphological variation').

b. var. **hebridensis** (Wilmott) Bateman & Denholm, **comb. nov.**

*Orchis hebridensis* Wilmott in *J. Bot., Lond.* 77: 192 (1939).

*O. fuchsii* Druce var. *hebridensis* (Wilmott) Heslop-Harrison p. in *Vasculum* 25: 111 (1940).

*O. fuchsii* Druce subsp. *hebridensis* (Wilmott) Clapham, *Fl. Br. Isl.* 1317 (1952).

*Dactylorchis maculata* (L.) Vermeulen subsp. *hebridensis* (Wilmott) Vermeulen, *Stud. Dactyl.* 141 (1947).

*D. fuchsii* (Druce) Vermeulen subsp. *hebridensis* (Wilmott) Heslop-Harrison f. in *Ber. geobot. Forsch. Inst. Rübel* 1953: 55 (1954).

*Dactylorhiza fuchsii* (Druce) Soó subsp. *hebridensis* (Wilmott) Nelson, *Mon. Ikon. Orchid. Gatt. Dactylorhiza* 102 (1976).

*D. maculata* (L.) Soó subsp. *hebridensis* (Wilmott) Nelson, *Mon. Ikon. Orchid. Gatt. Dactylorhiza* 102 (1976).

*D. hebridensis* (Wilmott) Averyanov in *Bot. Zhurn.* 71: 92 (1986).

Stem rarely >20 cm, occasionally >3.5 mm in diameter, usually suffused with anthocyanins (often densely). Sheathing lvs often 4 or more, longest lf rarely >9 cm long, widest lf occasionally >2 cm wide; non-sheathing lvs rarely 4 or more; markings usually present, usually covering >10% of the upper surface. Inflorescence rarely >4 cm, rarely >20% of stem length, usually dense, fls occasionally more than 25. Floral bracts rarely >8 mm, usually suffused with anthocyanins (often densely); peripheral bract cells usually angular. Labellum usually >6.7 mm long to apex of central lobe, usually >5.5 mm to apex of lateral lobe, occasionally >4 mm to base of sinus, usually >9.5 mm wide, usually broad, sinuses occasionally very deep; reflectivity of base colour rarely >40%; markings usually present; lateral outer perianth segments usually  $\pm$  horizontal, markings often present (occasionally annular); spur occasionally >2 mm wide at entrance, >1.8 mm halfway along. Flowering late June/July. Hebrides and western Ireland.

Many authors (Summerhayes 1951; Clapham 1952; Akeroyd & Curtis 1980; Lang 1980; Davies *et al.* 1983; Webb & Scannell 1983) have argued that var. *hebridensis* is merely an environmentally dwarfed ecotype of *D. fuchsii* with unusually dark flowers. However, Wilmott's (1939) original description of *Orchis hebridensis* stipulates unusually broad labella, and its large labellum and spur were demonstrated biometrically by Heslop-Harrison (1954); see also Clapham (1962) and Ettliger (1976). Our data indicate strong bimodality in flower size that distinguishes dark-flowered populations along the coasts of Cornwall, western Ireland and the Outer Hebrides from those further east with similarly coloured but much smaller flowers (usually <6.7  $\times$  9.5 mm; Fig. 6). The larger-flowered populations also tend to have less prominent central labellum lobes (and therefore smaller values (<1.5) for the labellum shape index), broader spurs (often >2.0 mm at the mouth), and greater proportions of plants with annular lateral outer perianth segment markings (though there are exceptions to all these criteria). We have therefore segregated the smaller-flowered plants as var. *alpina* (q.v.), which includes some populations along the west coast of the Inner Hebrides and Scottish mainland that have traditionally been regarded as var. *hebridensis* (e.g. Oldshore).

Populations of *D. fuchsii* with dark flowers and large labella occur in three areas (Heslop-Harrison 1954; Perring & Sell 1968): the Outer Hebrides (Wilmott 1939; Heslop-Harrison 1948, 1951), western Ireland (Brenan & Simpson 1949; Heslop-Harrison 1949, 1950, 1951, 1952; Akeroyd & Curtis 1980; Webb & Scannell 1983) and Cornwall (Pugsley 1940; Heslop-Harrison 1951, 1954; Margetts & David 1981). Most of the populations occupy coastal machair (or machair-like) habitats. The Cornish populations have been separated as var. *cornubiensis* Pugsley (q.v.).

Other characters that reputedly distinguish var. *hebridensis* from var. *fuchsii* are as follows: shorter (c. 10 cm) stems (Lang 1980; Davies *et al.* 1983) bearing fewer, narrower leaves (Summerhayes 1951; Lang 1980; Davies *et al.* 1983) that are less heavily spotted (Lang 1980; Davies *et al.* 1983) or more heavily spotted (Summerhayes 1951), a denser inflorescence (Akeroyd & Curtis 1980; Davies *et al.* 1983), labella with more broken markings (Wiefelspütz 1976; Lang 1980) and a more prominent central lobe (Ettliger 1976), and spurs more than 7 mm long (Heslop-Harrison 1954, p. 71) but narrow (Wiefelspütz 1976), c. 1 mm wide (Clapham 1952). However, the Baleshare

and Robach populations resembled many populations of var. *fuchsii* in all these respects. Vermeulen's (1947) suggestions that var. *hebridensis* is later flowering than var. *fuchsii* and tetraploid are incorrect (Heslop-Harrison 1952). A population of var. *hebridensis* in Co. Galway had taller stems and longer spurs than any of our study populations (Heslop-Harrison 1954), and white-flowered plants may occur rarely in the Outer Hebrides (Wiefelspütz 1976). Heslop-Harrison (1948, 1954) thoroughly described var. *hebridensis*, but exaggerated its distinctness from var. *fuchsii* as his data on the latter encompassed an unrealistically narrow range of morphological variation.

c. var. **cornubiensis** (Pugsley) Soó, *Nom. nov. gen. Dactylorhiza* 8 (1962).

*Orchis maculata* var. *cornubiensis* Pugsley in *J. Bot., Lond.* 78: 180 (1940).

*O. fuchsii* Druce var. *cornubiensis* (Pugsley) Clapham, *Fl. Br. Isl.* 1317 (1952).

Stem rarely >20 cm, rarely >3.5 mm in diameter, often suffused with anthocyanins (occasionally densely). Sheathing lvs often 4 or more, longest lf occasionally >9 cm long, widest lf rarely >2 cm wide; non-sheathing lvs occasionally 4 or more; markings usually present, usually covering >10% of the upper surface. Inflorescence occasionally >4 cm, often >20% of stem length, rarely dense, fls rarely more than 25. *Floral bracts often >8 mm*, usually suffused with anthocyanins (occasionally densely); peripheral bract cells rarely angular. Labellum usually >6.7 mm long to apex of central lobe, often >5.5 mm to apex of lateral lobe, *usually >4 mm to base of sinus*, usually >9.5 mm wide, *rarely broad*, sinuses rarely very deep; reflectivity of base colour rarely >40%; markings usually present; *lateral outer perianth segments rarely ± horizontal*, markings often present (occasionally annular); *spur usually >2 mm wide at entrance, >1.8 mm halfway along*. Flowering June. Cornwall.

The Cornish populations were first described by Pugsley (1940) as *Orchis maculata* var. *cornubiensis*, and incorporated into *Dactylorhiza fuchsii* subsp. *hebridensis* by Heslop-Harrison (1954). The long obscure type locality, "a cliff-top near St Ives", may have been refound recently (M. Jenkinson pers. comm. 1987). Otherwise, the only known populations of var. *cornubiensis* are those we studied on a cliff-top at Tintagel and stabilized dunes at Lelant (Perring & Sell 1968; Margetts & David 1981). However, Pugsley's (1940) description of the St Ives plants is consistent with these other Cornish populations, which tend to have wider spurs (median width >2 mm), more lax inflorescences (<6 fls/cm) and longer leaves (longest lf >8 cm) than those in the Hebrides. Wiefelspütz (1976) over-simplified when describing var. *cornubiensis* as intermediate to var. *hebridensis* and var. *fuchsii*.

Many populations of var. *hebridensis* and var. *cornubiensis* have acquired unusual characteristics, perhaps as a consequence of geographical isolation. The large mean labellum width of the Baleshare population (12.3 mm) exceeds those of all populations of *D. majalis* described by Bateman & Denholm (1983). Similarly, the spur widths of the Lelant population (mean value for median width 2.5 mm) match those of the smaller-flowered populations of *D. majalis* (Bateman & Denholm 1983), *D. incarnata* (Bateman & Denholm 1985) and *D. saccifera* (e.g. Nelson 1976), and the stems of the Tintagel plants are as broad (mean diameter 4.6 mm) as those of marsh-orchid populations of similar stature, suggesting that they may be hollow. As in the type population of var. *hebridensis* on Barra (Wilmott 1939), a small proportion of the Robach plants have spots on the undersides of the leaves and bracts, and dashes on the stems and ovaries, features otherwise confined in British orchids to the most anthocyanin-rich individuals of *D. incarnata* subsp. *cruenta* (O. F. Müller) P. D. Sell and *Neotinea maculata* (Desfontaines) Stearn. In contrast, many of the plants in a population of var. *hebridensis* from Co. Donegal lacked leaf markings (Heslop-Harrison 1949).

d. var. **alpina** (Landwehr) Bateman & Denholm, **comb. et stat. nov.**

*Dactylorhiza fuchsii* (Druce) Soó f. *alpina* Landwehr in *Orchideeën* 37: 78 (1975).

Stem occasionally >20 cm, rarely >3.5 mm in diameter, usually suffused with anthocyanins (occasionally densely). Sheathing lvs occasionally 4 or more, longest lf rarely >9 cm long, widest lf rarely >2 cm wide; non-sheathing lvs occasionally 4 or more; markings usually present, often covering >10% of the upper surface. Inflorescence rarely >4 cm, occasionally >20% of stem length, rarely dense, fls rarely more than 25. Floral bracts rarely >8 mm, usually suffused with anthocyanins (often densely); peripheral bract cells rarely angular. Labellum occasionally >6.7 mm

long to apex of central lobe, rarely  $>5.5$  mm to apex of lateral lobe, rarely  $>4$  mm to base of sinus, rarely  $>9.5$  mm wide, occasionally broad, sinuses often very deep; reflectivity of base colour rarely  $>40\%$ ; markings usually present; lateral outer perianth segments occasionally  $\pm$  horizontal, markings often present (rarely annular); spur rarely  $>2$  mm wide at entrance,  $>1.8$  mm halfway along. Flowering late June/July. Scotland and northern England, possibly also Wales and Ireland.

Landwehr (1977) described and illustrated slender plants with small, dark flowers from the Austrian Alps as *D. fuchsii* f. *alpina*. His original diagnosis fits well the populations of small, dark-flowered plants that we have measured, though the maximum stem height of 25 cm would have to be increased to allow the inclusion of the taller plants from Keltneyburn and Ashes Gill. Figure 40.8 of Landwehr (1977) shows unusually large leaf markings on a plant of f. *alpina* taken into cultivation, but they are not mentioned in his diagnosis. We have therefore adopted this name for fairly homogeneous British populations of *D. fuchsii* with small, dark flowers. As these populations are as distinct from var. *fuchsii* as are vars. *hebridensis* and *cornubiensis*, we have raised *alpina* to varietal status. The populations from inland meadows at Keltneyburn and Ashes Gill attain a stature (mean height 23 and 30 cm respectively typical of var. *fuchsii* in such habitats, but the Oldshore and Polin populations (mean height c. 10 cm) are from exposed coastal habitats and consequently environmentally-dwarfed. This taxon was recognized (though not named) by Clapham (1952, p. 1317): "northern forms [of *D. fuchsii*] are commonly smaller with narrower basal lvs, stem purplish above, and smaller fls, often pale reddish-violet in colour".

When first describing *D. fuchsii*, Druce (1915) cited the French taxon *O. maculata* var. *trilobata* Brébisson (1836, p. 313) as its earliest possible synonym, but regarded the brief original description as ambiguous: "épi grêle; fl. petites; labelle à trois lobes profonds presque égaux" (inflorescence lax; flowers small; labellum with three deep, subequal lobes). He later described var. *trilobata* as "very close to [the white-flowered] *o'kellyi*, but it has spotted leaves and tinted flowers", a statement followed by several British records for this taxon (Druce 1918, p. 167). Since flower colour is not mentioned in the original diagnosis of *trilobata*, Druce's logic eludes us, but it is a recurring theme in subsequent treatments of *trilobata*. Godfery (1933, p. 206) applied the name to typical populations of *D. fuchsii* occupying limestone grassland, which he regarded as having paler labella with shorter central lobes than woodland populations. A similar morphological distinction between these "habitat races" was described by Summerhayes (1951), but it is not supported by our data.

A second school regards *trilobata* as a small, dark-flowered form that is probably our *D. fuchsii* var. *alpina*; indeed, records of *trilobata* from "Kenmore, Mid-Perth" (Druce 1916) and "near Aberfeldy, Perthshire" (Wiefelspütz 1976) may both refer to our study population of var. *alpina* at Keltneyburn. Similarly dark-flowered plants, with exceptionally reduced lateral labellum lobes, were illustrated as *D. fuchsii* f. *trilobata* (Brébisson) Landwehr (a combination that does not appear to have been validly published) by Landwehr (1977, Plate 43.5, 6). As flower colour was omitted from the original diagnosis of var. *trilobata*, and the stipulation for small flowers was probably intended to distinguish var. *trilobata* from *D. maculata* rather than other infraspecific taxa of *D. fuchsii*, we reject use of this epithet for both pale-flowered calcicolous populations and dark-flowered populations occupying neutral or slightly acid soils.

e. var. **okellyi** (Druce) Bateman & Denholm, **comb. nov.**

*Orchis maculata* L. var. *okellyi* Druce in *Irish Nat.* 9: 211 (1909).

*O. okellyi* (Druce) Druce in *Rep. botl Soc. Exch. Club Br. Isl.* 4: 108 (1915).

*O. maculata* L. subsp. *okellyi* (Druce) Druce, in Hayward, *Bot. Pocket-book*, 15th ed. 277 (1917).

*Dactylorhiza fuchsii* (Druce) Vermeulen subsp. *okellyi* (Druce) Vermeulen, *Stud. Dactyl.* 149 (1947).

*Dactylorhiza fuchsii* (Druce) Soó subsp. *okellyi* (Druce) Soó, *Nom. nov. gen. Dactylorhiza* 8 (1962).

Stem rarely  $>20$  cm, rarely  $>3.5$  mm in diameter, occasionally suffused with anthocyanins (rarely densely). Sheathing lvs often 4 or more, longest lf rarely  $>9$  cm long, widest lf rarely  $>2$  cm wide; non-sheathing lvs occasionally 4 or more; markings often present, occasionally covering  $>10\%$  of the upper surface. Inflorescence rarely  $>4$  cm, occasionally  $>20\%$  of stem length, occasionally dense, fls occasionally more than 25. Floral bracts rarely  $>8$  mm, occasionally suffused with



*anthocyanins* (rarely densely); peripheral bract cells occasionally angular. Labellum rarely >6.7 mm long to apex of central lobe, rarely >5.5 mm to apex of lateral lobe, rarely >4 mm to base of sinus, occasionally >9.5 mm wide, often broad, sinuses occasionally very deep; *reflectivity of base colour usually* >40% (occasionally >80%); markings often present; lateral outer perianth segments occasionally  $\pm$  horizontal, markings occasionally present (rarely annular); spur rarely >2 mm wide at entrance, >1.8 mm halfway along. Flowering June/early July. Western Ireland, western Scotland, Isle of Man.

Although discussion of var. *okellyi* usually centres on its type locality in the Burren, it was probably first reported from Sutherland by E. S. Marshall in 1908 (as *Orchis scotica*). Several other populations have since been located in western Scotland (Druce 1915, 1918; Heslop-Harrison 1954; Perring & Sell 1968; Summerhayes 1968; Lang 1980) and the Isle of Man (Perring & Sell 1968; Allen 1963, 1971, 1986), leading to its description as an "Irish-Hebridean race" (Allen 1971) with "a wide distribution exhibiting . . . a neat Atlantic pattern" (D. E. Allen pers. comm. 1987).

The origin of the epithet is confused. Druce was shown non-flowering plants of *Orchis immaculata* in the Burren by P. B. O'Kelly, who subsequently supplied the type material (also in a non-flowering state according to Praeger (1934)) described by Druce (1909). It proved to be a white-flowered variant of *D. fuchsii*, though Praeger (1934) claimed that the plants were selected by O'Kelly in error for the white-flowered form of *D. maculata*, which is also unusually frequent in the Burren. Wiefelspütz's (1976) statement that *okellyi* was originally described as a variant of *Orchis mascula* L. is undoubtedly incorrect.

Previous authors have disagreed over the range of pigmentation encompassed by var. *okellyi*. The most stringent do not allow any floral or vegetative anthocyanins (McKechnie 1918; Stephenson & Stephenson 1920, 1924; Godfery *et al.* 1924; Camus & Camus 1929; Godfery 1933; Clapham 1952; Keane 1980), others permit labellum markings only (Druce 1909, 1915, 1918; Stelfox 1924; Vermeulen 1947; Ettliger 1976; Webb & Scannell 1983), and the most liberal accept a minority of individuals with both labellum and leaf markings (Summerhayes 1951; Heslop-Harrison 1954; Clapham 1962; Allen 1971; Wiefelspütz 1976; Landwehr 1977; Lang 1980; Davies *et al.* 1983). Druce caused much of the confusion by (1) precluding all pigmentation from *O. fuchsii* var. *okellyi* in his original diagnosis (Druce 1909) and in its redescription as a full species, *O. okellyi* (Druce 1915), but adding in the latter paper that some plants have labellum markings, and (2) including a misprint in the original diagnosis, which should have read "leaves . . . unspotted" rather than "leaves . . . spotted". Summerhayes (1951) provided the most accurate description: "Flowers are very frequently almost white . . . with very faint pink or lilac markings on the lip, but in some populations there may be quite a high proportion of plants with more heavily and brightly marked lips". In fact, pigmented plants predominated in all the populations that we measured. Taxonomic recognition of *okellyi* at the population level therefore requires diagnostic characters other than those dependent on pigmentation.

*D. fuchsii* var. *okellyi* supposedly has smaller flowers (Druce 1909, 1915, 1918; Camus & Camus 1929; Summerhayes 1951; Allen 1971; Wiefelspütz 1976; Lang 1980; Davies *et al.* 1983) whose labella have "more rounded" lateral lobes (Allen 1971; Ettliger 1976) with crenate margins (Stelfox 1924), and less prominent central lobes (Druce 1909; Allen 1971; Wiefelspütz 1976; Lang 1980), resulting in a smaller labellum shape index (Heslop-Harrison 1954). Thus, the labella and spurs should be intermediate in shape between those of *D. fuchsii* var. *fuchsii* and *D. maculata* subsp. *ericetorum*. Our data (which are consistent with the single data set for Burren *okellyi* published by Heslop-Harrison (1954)) reveal considerable variation between populations of var. *okellyi* in flower size and shape. Black Head plants have similar labellum dimensions (means 6.7  $\times$  9.5 mm) to var. *fuchsii* (Fig. 6). Khyber Pass differs from all other populations in having wide but short labella, resulting in very small mean values for labellum roundness (0.37), labellum shape index (1.32) and central lobe prominence (0.6 mm). Corrofin and Gelain have small labella (mean values c. 5.7  $\times$  8.8 mm) of similar size to *D. fuchsii* var. *alpina*. Only one population (Gelain) had unusually short (<5 mm), narrow (median width <1.5 mm) spurs.

Var. *okellyi* is also supposed to have short (Allen 1971), slender (Druce 1915, 1918; Godfery *et al.* 1924; Summerhayes 1951; Allen 1971) stems with few (Ettliger 1976; Wiefelspütz 1976), slender leaves (Druce 1909; Camus & Camus 1929; Godfery 1933; Summerhayes 1951; Allen 1971; Ettliger 1976; Wiefelspütz 1976; Lang 1980) and a narrow (Vermeulen 1947), dense (Druce 1909),

cylindrical/flat-topped inflorescence (Druce 1909, 1915; Camus & Camus 1929; Godfrey 1933; Lang 1980; Davies *et al.* 1983). However, our data show that its stem height and diameter are not unusually small, nor are its leaves unusually short. Its leaves are fairly narrow (means 13–17 mm) but are matched by populations of *D. fuchsii* var. *hebridensis*, var. *cornubiensis* and var. *alpina*. Inflorescence shape is not a useful taxonomic character; it reflects the length of the inflorescence and the proportion of flowers open, and therefore changes during anthesis. We have also been unable to detect the strong changes during anthesis. We have also been unable to detect the strong fragrance attributed to *okellyi* by Stelfox (1924), Godfrey (1933), Clapham (1962), Landwehr (1977), Lang (1980) and Davies *et al.* (1983), and there is little evidence to support the claim by Wiefelspütz (1976) that it can flower as early as April. Thus, populations of *D. fuchsii* var. *okellyi* are much less distinct from var. *fuchsii* than has been suggested.

It is therefore tempting to regard var. *okellyi* as anthocyanin-less individuals rather than populations, but it is equally difficult to distinguish Burren anthocyanin-less individuals from those elsewhere in the British Isles. Druce (1915, 1918), subsequently supported by McKechnie (1918, p. 185), Stelfox (1924), Summerhayes (1951, p. 271) and Lang (1980), argued that this was possible, but at the same time he described white-flowered plants from several sites in Yorkshire as var. *okellyi* (Druce 1916). Similarly, Godfrey (1933) listed numerous records for var. *okellyi* from throughout the British Isles. Stelfox's (1924) argument that var. *okellyi* always has yellow pollinia while other white-flowered individuals of *D. fuchsii* have pink pollinia is void, as both pollinia colour morphs occur throughout the range of *D. fuchsii*. Heslop-Harrison (1949, p. 293) stated that plants of *D. fuchsii* in Co. Donegal with white flowers and unmarked leaves "are simply aberrant forms of the natural population; the white [*D. fuchsii*] races of north Clare [i.e. var. *okellyi* on the Burren] are more worthy of critical examination". However, three years later he wrote more cautiously "In *O. fuchsii* populations elsewhere [i.e. outside the Burren] albino individuals occur which agree with the type diagnosis of ssp. *okellyi*, but this does not remove the necessity for recognising as a distinct taxonomic entity the race which occurs in Clare and Sutherlandshire" (Heslop-Harrison 1952, p. 105). We agree; anthocyanin-less individuals of *D. fuchsii* from the Burren cannot be reliably distinguished from those elsewhere in the British Isles, and the name *okellyi* is best retained at varietal level to describe heterogeneous, anthocyanin-low populations of *D. fuchsii* along the western coasts of the British Isles.

D. E. Allen (pers. comm. 1986) argued that anthocyanin-low populations of *D. fuchsii* on the Isle of Man that have been attributed to var. *okellyi* (Allen 1963, 1971, 1986; Perring & Sell 1968) are more distinct from var. *fuchsii* than those in the Burren, having very small labella with three subequal lobes and showing different geographical and ecological distributions from the type. If these observations can be supported by biometric data, the Manx populations lie outside the range of variation encompassed by var. *okellyi* and represent a new infraspecific taxon.

We cannot detect any characters in descriptions of the diploid Hungarian 'endemic' *D. fuchsii* subsp. *sooiana* (Borsos) Borsos (Borsos 1959, 1961; Landwehr 1977; Soó 1980) that justify its separation from plants of var. *okellyi* with pigmented but unmarked labella.

## 2. *Dactylorhiza maculata* (L.) Soó, *Nom. nov. gen.* *Dactylorhiza* 7 (1962).

*Orchis maculata* L., *Sp. Pl.* 942 (1753).

*Dactylorhiza maculata* (L.) Vermeulen, *Stud. Dactyl.* 130 (1947).

*Orchis candidissima* Krockner, *Fl. Silesiaca* 3: 16 & tab. 2 (1814).

*O. elodes* Grisebach, *Über. Bild. Torfs Emsm.* 25 (1846).

*O. maculata* L. var. *helodes* (Grisebach) Reichenbach f., *Icon Fl. Germ. Helv.* 67 (1851).

*O. maculata* L. var. *praecox* Webster, *Brit. Orchid.* 54 (1886).

*O. maculata* L. f. *candidissima* (Krockner) Schulze, *Orchid. Deutsch., Deutsch. Schweiz* (1894).

*O. maculata* L. subsp. *ericetorum* Linton, *Fl. Bournemouth* 208 (1900).

*O. maculata* L. subsp. *elodes* (Grisebach) Camus, *Mon. Orch. Eur.* 192 (1908).

*O. ericetorum* (Linton) Marshall in *Rep. botl Soc. Exch. Club Br. Isl.* 3: 127 (1912).

*O. maculata* subvar. *leucantha* Druce in *Rep. botl Soc. Exch. Club Br. Isl.* 8: 213 (1916).

*O. maculata* L. f. *ericetorum* (Linton) Hagerup in *Dansk. Bot. Ark.* 11: 3 (1944).

*Dactylorhiza maculata* (L.) Vermeulen subsp. *ericetorum* (Linton) Vermeulen, *Stud. Dactyl.* 69 (1947).

- D. maculata* (L.) Vermeulen subsp. *typica* Vermeulen, *Stud. Dactyl.* 131 (1947).  
*D. elodes* (Grisebach) Vermeulen, *Stud. Dactyl.* 137 (1947).  
*Orchis fuchsii* Druce subsp. *rhoulensis* Heslop-Harrison f. in *Trans. Proc. bot. Soc. Edinb.* **35**: 53 (1948).  
*Dactylorhiza maculata* (L.) Vermeulen subsp. *elodes* (Grisebach) Vermeulen in *Ned. Kruidk. Archf.* **56**: 235 (1949).  
*D. maculata* (L.) Vermeulen var. *candidissima* (Krocker) Vermeulen in *Ned. Kruidk. Archf.* **56**: 235 (1949).  
*D. maculata* (L.) Vermeulen subsp. *rhoulensis* (Heslop-Harrison f.) Heslop-Harrison f. in *Watsonia* **4**: 48 (1957).  
*D. maculata* (L.) Vermeulen var. *ericetorum* (Linton) Vermeulen, in *Fl. Neerlandica* (1958).  
*D. fuchsii* (Druce) Vermeulen subsp. *rhoulensis* (Heslop-Harrison f.) Clapham, *Fl. Br. Isl.*, 2nd ed. 1046 (1962).  
*Dactylorhiza maculata* (L.) Soó subsp. *rhoulensis* (Heslop-Harrison f.) Soó, *Nom. nov. gen. Dactylorhiza* **7** (1962).  
*D. maculata* (L.) Soó subsp. *elodes* (Grisebach) Soó, *Nom. nov. gen. Dactylorhiza* **7** (1962).  
*D. maculata* (L.) Soó var. *praecox* (Webster) Soó, *Nom. nov. gen. Dactylorhiza* **7** (1962).  
*D. maculata* (L.) Soó subsp. *ericetorum* (Linton) P. F. Hunt & Summerhayes in *Watsonia* **6**: 132 (1965).  
*D. maculata* (L.) Soó f. *candidissima* (Krocker) Landwehr in *Orchideeën* **37**: 79 (1975).

Stem 4–40(–50) cm, 1.3–5.5(–8.5) mm in diameter, often lacking anthocyanins. Basal lf or sheath 0–1, broadest at or above middle; sheathing lvs (1–)2–4(–5), usually strongly crowded towards base of stem, usually recurved, narrowly lanceolate, usually broadest well above base, longest lf often also widest, 4–16(–19) cm long, widest lf 0.5–2(–2.5) cm wide, width/length ratio of lvs decreasing up stem, usually bright to dark green, tips occasionally distinctly hooded; non-sheathing lvs (1–)2–5(–7), narrow, broadest at base; lvs usually sparsely to densely marked on upper surface only, markings usually solid (very rarely annular),  $\pm$  evenly distributed or concentrated towards tips,  $\pm$  round to transversely elongated, usually 1–3 mm in mean diameter. Inflorescence 1–8(–10) cm, 8–35% of stem length, fls 5–50(–60), lax to dense (2–10(–12) fls/cm). Basal bracts 6–20(–25) mm, 1.5–2 times the length of the ovaries, floral bracts 4–12(–15) mm, approximately equalling the ovaries, often suffused with anthocyanins; peripheral bract cells 55–120(–150)  $\mu$ m long, barrel-shaped to triangular. Labellum width usually exceeding length (often considerably), (4–)5–9.5(–11)  $\times$  (5.5–)6.5–13(–15) mm, widest  $\pm$  at middle or less frequently above (obtriangular), base colour varying densities (reflectivity (10–)25–89%) of purple, less frequently red-purple or white; markings pale to bold, ranging from dots to dashes and loops (rarely absent or only loops), often covering about two-thirds of the labellum, occasionally more or less; sinuses present (labellum three-lobed), usually shallow, central lobe rarely exceeding lateral lobes by >1 mm, labellum shape index rarely >1.25; lateral lobes often indented, slightly deflexed to moderately reflexed; lateral outer perianth segments usually nearer horizontal than vertical, usually with solid (rarely annular) markings; median outer perianth segment and inner perianth segments connivent; spur straight to moderately decurved, (2.5–)3.5–8(–9.5)  $\times$  0.6–2.2 mm at entrance, 0.5–2 mm halfway along, cylindrical or slightly tapering, half as long to as long as the ovary.  $2n=780$ . Flowering mid-June to late July (rarely August in the west). Frequent and locally common in the north and west, local in central and eastern England and Ireland. Neutral to moderately acid soils.

Five noteworthy intraspecific taxa of *D. maculata* have been recognized in the British Isles (Table 9). Subsp. *rhoulensis*, a relatively recent segregate confined to Rhum, is discussed later. No author has chosen to recognize *Orchis maculata* var. *praecox* since its original description (Webster 1886; Druce 1912), but there is considerable disagreement concerning which of the other three subspecies encompass(es) British and Irish populations of *D. maculata*. Most British authors (e.g. Bennett 1921; Summerhayes 1951; Heslop-Harrison 1951, 1954; Ettliger 1976; Lang 1980) have only recognized one subspecies, subsp. *ericetorum*, and have regarded Grisebach's (1846) *Orchis elodes* as a synonym of *ericetorum* and subsp. *maculata* as exclusively Continental. Godfery (1921, 1923, 1933) dissented on a nomenclatural point, arguing that subsp. *elodes* is synonymous with, and has priority over, subsp. *ericetorum*. In contrast, most Continental workers believe that subsp. *maculata*

occurs in Britain, together with a second subspecies. This may be subsp. *ericetorum*, with *elodes* treated as a separate, exclusively Continental subspecies (Soó 1960; Wiefelspütz 1976; Delforge & Tyteca 1984), or it may be subsp. *elodes*, with *ericetorum* treated as a synonym of *elodes* (Camus & Camus 1929; Senghas 1968) or of subsp. *maculata* (Soó 1980). Alternatively, all three subspecies may occur in the British Isles (Vermeulen 1947; Landwehr 1977). The complex reasons for this lack of consensus are a microcosm of taxonomic problems in general, and will be discussed in detail elsewhere.

#### *D. MACULATA* SUBSP. *RHOUMENSIS*

*D. maculata* subsp. *rhoumensis* was originally described as a subspecies of *D. fuchsii* endemic to Rhum by Heslop-Harrison (1948). He initially attributed it to *D. fuchsii* due to its apparently diploid karyotype, but later transferred it to *D. maculata*, which it more closely resembled in morphology (Heslop-Harrison 1957). Clapham (1952, 1962) and Perring & Sell (1968) considered it morphologically indistinguishable from *D. maculata* subsp. *ericetorum*, though Ettlinger (1976) and Davies *et al.* (1983) stated that it has unusually bold, looped labellum markings. The exceptionally late flowering period (August) attributed to *rhoumensis* by Heslop-Harrison has been overlooked by most subsequent authors, whilst most Continental workers have overlooked this taxon completely (Table 9b).

Our three study populations from Rhum spanned a wide flowering period from early July (Kinloch) to early August (Harris). Each population deviated considerably from the original diagnosis of *rhoumensis*. Kinloch was the closest in overall morphology, but it flowered much too early and had leaf markings that were much too dense (mean areal coverage 25%). Kilmory also flowered too early, and had pale flowers (mean reflectivity 72.6%) with broken labellum markings of only low to moderate contrast. Harris flowered at the prescribed time for subsp. *rhoumensis* and had the stipulated dark flower colour (mean reflectivity 40%), but the plants were too short (mean height 6.9 cm), had a large mean labellum shape index (1.24) intermediate to typical values for *D. fuchsii* and *D. maculata*, and was tetraploid ( $2n = c. 80$ ; A. Karp pers. comm. 1985). Furthermore, Heslop-Harrison (1948, p. 53) specifically excluded from subsp. *rhoumensis* the populations of *D. maculata* occupying the Harris machair.

Thus, none of our three study populations fulfilled the morphological criteria in the original diagnosis of subsp. *rhoumensis*. Since Rhum populations of *D. maculata* are very variable, and overlap almost completely populations elsewhere in the British Isles, we conclude that *rhoumensis* is not a convincing taxon.

#### OTHER INFRASPECIFIC TAXA

Nonetheless, the August-flowering population from Harris provided an interesting comparison with Porlock, an August-flowering population from Exmoor (Table 1). These two populations were much the darkest-flowered of those studied (mean reflectivities <40%) and had narrow (c. 2 mm) stems bearing few (c. 3), narrow (c. 7 mm) sheathing leaves. However, they differed from each other considerably in several other characters. The shorter stem, shorter, more basally concentrated leaves and proportionately longer inflorescences of the Harris plants may merely reflect environmental dwarfing, but this is unlikely to explain their more sparse leaf markings, much shorter (c. 4 mm) spurs and more prominent (c. 1 mm) central labellum lobes. It would therefore be unwise to unite these populations as an infraspecific taxon.

None of the plants measured approached the 18 mm labellum width of Druce's (1920, p. 579) *D. maculata* var. *macroGLOSSA*, which was probably a hybrid, but several exceeded the 12.5 mm labellum width required for *D. maculata* f. *grandiflora* (Vermeulen) Soó (Landwehr 1977). However, we see no merit in perpetuating a taxon diagnosed by a single size character.

The tall, relatively slender Llandegfan plants resembled *D. maculata* var. *traunsteinerifolia* (Harz) Soó (see Landwehr (1977, p. 37)). Other morphologically distinct populations were Stanmore, with an unusually large number of non-sheathing leaves, and Thursley, with unusually reflexed lateral labellum lobes more characteristic of *D. incarnata* (Bateman & Denholm 1985). Some British and Irish populations of *D. maculata*, particularly those growing in exposed habitats, resemble Scandinavian endemics described by Landwehr (1975, 1977): *D. maculata* subsp. *deflexa* Landwehr, *montellii* (Vermeulen) Landwehr and *elodes* var. *darnalensis* Landwehr. The latter

closely resembles the late-flowering Porlock population. Comparative studies of British and Scandinavian populations are desirable to investigate these relationships.

#### EXTREMES OF PIGMENTATION

Stephenson & Stephenson (1921, p. 123) described a plant of *D. maculata* subsp. *ericetorum* with "the whole centre of the lip taken up by a patch of bright magenta". This anthocyanin-rich form of *D. maculata*, analogous to that already described for *D. fuchsii*, has also been reported from the Continent. It was named *Dactylorhiza maculata* var. *concolor* Vermeulen (1949, p. 232), later demoted to *Dactylorhiza maculata* f. *concolor* (Vermeulen) Landwehr (1975, p. 79).

The well-known anthocyanin-low mode of *D. fuchsii* in the Burren (var. *okellyi*) occurs with a similar but less distinct mode of *D. maculata* which includes a few anthocyanin-less individuals (Druce 1915, 1918) that may have been confused with albino *D. fuchsii* (Praeger 1934; Heslop-Harrison 1952, 1954). Burren *D. maculata* also have labella that are on average unusually broad relative to their length (index 'a' means 0.40–0.42) and wide spurs (means 1.4–1.7 mm for median width) resembling those of *D. fuchsii*, though we could not detect the fragrance attributed to them by Clapham (1952, 1962). Anthocyanin-low populations of *D. maculata* occur in other limestone districts (Heslop-Harrison 1954); all four anthocyanin-less plants that we measured were found at Ashes Gill and White Nook, populations from the Carboniferous limestone of Yorkshire. However, even here the frequency of albinos has been exaggerated due to lack of close scrutiny; Marshall (1912) described white-flowered *D. maculata* as "not uncommon" in Yorkshire, but qualified this by stating that they were "seldom quite pure white"!

Interestingly, the epithet *candidissima* (currently *D. maculata* f. *candidissima* (Krocker) Landwehr (1975, p. 79)) is usually applied solely to albinos (e.g. Heslop-Harrison 1954). The original description of *Orchis candidissima* (Krocker 1814, p. 16 & Plate 2) is sufficiently detailed to show that it is indeed a variant of *D. maculata* (Druce 1925; Vermeulen 1947) but also that it is not a suitable basionym for a taxon composed of anthocyanin-less individuals; Krocker specified lightly spotted leaves, a pigmented spur and purple pollinia for *candidissima*. As Druce was aware of this (Druce 1925, p. 139), it is surprising that he suggested synonymy of *candidissima* with his *Orchis maculata* subvar. *leucantha* Druce (1916) (see also Godfery (1933)).

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