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A reappraisal of the British and Irish dactylorchids, 1. The tetraploid marsh-orchids

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ABSTRACT

A detailed biometric study was performed on 15 tetraploid marsh-orchid populations to clarify the taxonomy of the British and Irish taxa. Multivariate analyses revealed continuous variation in most of the 51 characters examined and showed morphological overlap between all four formerly accepted species. They are therefore assigned to a single species, *Dactylorhiza majalis* (Reichenbach) P. F. Hunt & Summerhayes. The exceptional variation shown by *D. majalis* justifies the retention of the former species as subspecies which represent divisions of a broad morphological spectrum: subsp. *occidentalis* (Pugsley) P. D. Sell, subsp. *purpurella* (T. & T. A. Stephenson) D. Moresby Moore & Soó, subsp. *praetermissa* (Druce) D. Moresby Moore & Soó, and subsp. **traunsteinerioides** (Pugsley) Bateman & Denholm, **comb. nov.** Some other previously described British and Irish tetraploid marsh-orchid taxa are assigned varietal status. Principal coordinates provided the basis for revised diagnostic descriptions of *D. majalis* and its British and Irish subspecies.

INTRODUCTION

The extensive morphological variation shown by tetraploid marsh-orchids (genus *Dactylorhiza* Necker ex Nevski) has consistently confounded attempts to separate them into discrete taxa. Consequently, their nomenclature is unstable and they possess an unusually large number of confusing synonyms. It has generally been accepted over the past 30 years that four species occur in the British Isles (cf. Dandy 1958, Clapham 1962):

1. *D. majalis* (Reichenbach) P. F. Hunt & Summerhayes 'Broad-leaved Marsh-orchid'
2. *D. purpurella* (T. & T. A. Stephenson) Soó 'Northern Marsh-orchid'
3. *D. praetermissa* (Druce) Soó 'Southern Marsh-orchid'
4. *D. traunsteineri* (Sauter) Soó 'Narrow-leaved Marsh-orchid'

Many botanists will be aware that the characters used by standard Floras to separate these species are often inaccurate or too vague to be used with confidence in the field. Moreover, it is extremely difficult to assign all the individuals in a tetraploid marsh-orchid population[1] to one of the above species due to extensive intrapopulation variation. This has prompted some orchidologists to question the adequacy of the established classification.

When such complex levels of variation and intergradation are present, detailed biometric studies

[1]We regard populations and colonies as spatially isolated aggregates of dactylorchids. However, whereas a population consists of freely interbreeding individuals of a single species, a colony may comprise two or more coexisting populations (i.e. more than one species).

TABLE 1. DETAILS OF SAMPLE LOCALITIES AND STUDY POPULATIONS

Taxon[1]	Habitat and locality	Grid reference	Altitude (m O.D.)	Soil parent materials	Soil pH (in H_2O)	Approx. no. of plants	Peak flowering period[4]	Presence (and quantity) of other dactylorchids[5]
D. majalis								
subsp. *traunsteinerioides*	POLLARDSTOWN Fen, Newbridge, Co. Kildare, v.c. H19	22/775.166	185	Peat/Carb. limestone	7·9	3000	5/4–6/1	F(r), P(o), F×P(vr)
	Fen, CORS ERDDREINIOG, Anglesey, v.c. 52	23/476.823	75	Peat/till	7·5	1000	5/4	M×T(vr), I×T(vr), F(o), M(o), I(f), P(o).
	Marshy meadow, RHOS-Y-GAD, Anglesey, v.c. 52	23/510.788	35	Peat/till	6·8	200	5/4–6/1	F(o), M(o), I(f), P(o), F×P(vr), I×T(vr).
subsp. *occidentalis*	Damp meadow by R. Owenglin, CLIFDEN, W. Galway, v.c. H16	02/669.507	10	Peat & alluvium/ schist & gneiss	5·9	15	5/4	None
	Damp meadow by R. Caher, CAHERBANNAGH, Co. Clare, v.c. H9	12/167.076	105	Peat & alluvium/ Carb. limestone	7·6	20	5/4	F(vr)
	Boggy meadow nr BALLYCOTTEEN, Moher, Co. Clare, v.c. H9	11/045.930	180	Peat/Carb. shale	7·1	50	5/4	M(vr), M×O(vr)
var. *cambrensis*	Marshy meadow, MERIONETH, v.c. 48	23/5—.4—	5	Alluvium/Ordovician slate	6·6	20	6/1–2	F(vr), I(r)
subsp. *purpurella*	Tarn-side, HA MIRE WOOD, Craven, Mid-W. Yorks., v.c. 64	34/896.666	375	Peat/till	6·9	40	6/4–7/1	F(r), F×P(vr)
	MALHAM TARN Fen, Craven, Mid-W. Yorks., v.c. 64	34/883.671	375	Peat/till	6·8	250	6/3–4	F×P(vr)
	Umbra Dunes, MAGILLIGAN, Co. Londonderry, v.c. H40[2]	24/730.357	5	Blown sand	*c.*7·0	200	6/4–7/1	F(f), I(o), F×P(f)
subsp. *praetermissa*	Marshy meadow nr R. Rib, BRAUGHING, Herts., v.c. 20	52/389.247	75	Alluvium/chalk	7·7	45	6/1–2	None
	Marsh, OUGHTONHEAD Common, Hitchin, Herts., v.c. 20	52/169.303	60	Peat & alluvium/ chalk	7·7	40	6/3–4	None
	Damp grass/scrub nr Great Stew Pond, EPSOM COMMON, Surrey, v.c. 17[3]	51/185.607	60	London Clay	5·3	20	6/3	F×Pr(o)
	SAWBRIDGEWORTH Marsh, Herts., v.c. 20[3]	52/492.158	50	Peat & alluvium/ London Clay	7·7	300	6/4	None
	Marsh, TEWINBURY Meadow, Tewin, Herts., v.c. 20[3]	52/266.140	50	Alluvium/chalk	7·0	110	6/4	None

[1]See Classification for revised nomenclature.
[2]Data collected by D. H. Riley.
[3]Populations including a small proportion of *D. majalis* subsp. *praetermissa* var. *junialis* (plants with annular leaf markings).
[4]The number before the oblique indicates the month, the number(s) after the weeks of that month. Observations were made during 1981, a particularly early season.
[5]F=*D. fuchsii*, M=*D. maculata*, I=*D. incarnata*, O=*D. majalis* subsp. *occidentalis*, P=*D. majalis* subsp. *purpurella*, Pr=*D. majalis* subsp. *praetermissa*, T=*D. majalis* subsp. *traunsteinerioides*. f=frequent, o=occasional, r=rare, vr=very rare.

are necessary to quantify the similarities of populations and to search for morphological discontinuities that delimit species. Seven of the numerous papers relating to British and Irish tetraploid marsh-orchids have included biometric data (Heslop-Harrison 1953a, Lacey 1955, Lacey & Roberts 1958, Roberts & Gilbert 1963, Roberts 1961a, 1961b, 1966). Labellum, spur and leaf dimensions, plant height, leaf number, and the frequency of individuals possessing leaf markings were usually recorded, and the number of variates was often increased by calculating indices using two or more related characters. Data were presented as population means, often with standard errors or standard deviations. Heslop-Harrison (1953a) and Roberts (1961a) also constructed bivariate scatter-diagrams of some characters. However, recent studies have been performed by Continental botanists (e.g. Senghas & Sundermann 1968) who have ignored the biometric approach to marsh-orchid taxonomy.

This paper presents a detailed biometric survey designed to reappraise the status of the British and Irish representatives of this group and to investigate which characters, if any, best separate the taxa. The classification suggested by our study is presented in detail later. However, we use the following revised scientific and vernacular names throughout the text in order to avoid nomenclatural confusion (listed in the same order as above):

1. *D. majalis* subsp. *occidentalis* (Pugsley) P. D. Sell 'Western Marsh-orchid'
2. *D. majalis* subsp. *purpurella* (T. & T. A. Stephenson) D. Moresby Moore & Soó 'Northern Marsh-orchid'
3. *D. majalis* subsp. *praetermissa* (Druce) D. Moresby Moore & Soó 'Southern Marsh-orchid'
4. *D. majalis* subsp. *traunsteinerioides* (Pugsley) Bateman & Denholm 'Pugsley's Marsh-orchid'

MATERIALS AND METHODS

15 tetraploid marsh-orchid populations were sampled during 1981, including at least three populations of each of the four subspecies listed above. Details of these populations and the sample localities are presented in Table 1. Colonies containing spotted-orchids (*D. fuchsii* (Druce) Soó and *D. maculata* (L.) Soó) were avoided wherever possible to minimize the risk of sampling hybrids involving these species.

Morphological characters were recorded for each of ten randomly-chosen flowering plants per population. Vegetative characters were scored in the field. Floral and bract cell data were obtained within two days of sampling from a single flower, preferably excised when fully open from halfway along the inflorescence. Destructive studies of tuberoids and stem cavities were not attempted. 51 quantitative and qualitative (scaled) characters were recorded:

A. *Labellum* (14 characters).

All except character 7 were taken from flattened mounted labella. Labellum colour was measured immediately after mounting as it subsequently rapidly deepened. The base colour of the lower part of each labellum was matched to the nearest colour block of the Royal Horticultural Society Colour Chart (Anonymous 1966) and converted to three C.I.E. (Commission Internationale de l'Eclairage) coordinates. Two of these ('x' and 'y') define a position on a square grid superimposed on to a triangular array of colours which pale towards the centre of the triangle. The corners correspond to pure blue, pure green and pure red. Density of pigment is measured by a third coordinate (reflectivity, 'Y'), which decreases in value from the centre of the triangle outwards.

1. Length, from spur entrance to apex of central lobe.
2. Presence (1) or absence (0) of sinuses separating central and lateral lobes (i.e. three-lobed or entire labella).
3. Length, from base of spur entrance to base of sinus (if present).
4. Length, from base of spur entrance to apex of right lateral lobe (if sinuses present).
5. Maximum width.
6. Position of maximum width in relation to axis of maximum length, on a scale 1–3 (1=above middle; 2=±at middle; 3=below middle).

7. Amount of reflexion of lateral lobes, on a scale 1–6 (1=slightly deflexed, through to 6=completely reflexed).
8. Colour, x (arbitrary values ranging from 100 to 600).
9. Colour, y (arbitrary values ranging from 100 to 600).
10. Colour, percentage reflectivity (Y).
11. Type of markings, on a scale 0–5 (0=no markings; 1=spots; 2=spots and dashes; 3=dashes and loops; 4=loops; 5=±solid blotch).
12. Distribution of markings, on a scale 0–3 (0=no markings, through to 3=extensive coverage).
13. Contrast of markings with base colour, on a scale 0–3 (0=no markings; 1=pale; 2=well-defined; 3=bold).
14. Indentations on right lateral lobe, on a scale 0–2 (0=none; 1=one notch; 2=more than one notch).

B. *Spur* (4 characters).
All except character 18 were taken from flattened mounted spurs.
15. Length, from entrance to apex.
16. Width, at entrance.
17. Width, halfway along length.
18. Curvature, on a scale 1–5 (1=strongly recurved, through to 5=strongly decurved).

C. *Lateral outer perianth segments* (3 characters).
19. Position relative to the median outer perianth segment, on a scale 1–5 (1=*c.* 100°, through to 5=*c.* 10°).
20. Solid markings, on a scale 0–2 (0=none; 1=pale; 2=bold).
21. Annular markings, on a scale 0–2 (0=none; 1=pale; 2=bold).

D. *Bracts* (6 characters).
The size and shape of peripheral bract cells (characters 26 and 27) were examined at the suggestion of R. H. Roberts (pers. comm. 1980).
22. Length, basal bracts (base of inflorescence).
23. Length, floral bracts (halfway up inflorescence).
24. Anthocyanin pigmentation, on a scale 0–2 (0=none; 1=diffuse; 2=heavy).
25. Presence (1) or absence (0) of markings.
26. Mean length of five peripheral cells.
27. Mean shape of five peripheral cells, on a scale 1–3 (1=barrel-shaped; 2=subangular; 3=angular).

E. *Stem and inflorescence* (6 characters).
28. Plant height.
29. Inflorescence, length.
30. Inflorescence, maximum width.
31. Number of flowers.
32. Stem diameter, immediately above lowest sheathing leaf.
33. Stem anthocyanin immediately below inflorescence, on a scale 0–2 (0=none; 1=diffuse; 2=heavy).

F. *Leaves* (11 characters).
Three measurements were taken from each sheathing leaf: (i) length, (ii) maximum width, (iii) position of maximum width relative to length, on a scale 1–4 (1=0–10% of length; 2=10–25%; 3=25–50%; 4=>50%). These characters could not be compared directly as the number of sheathing leaves per plant varied. They were therefore summarized as characters 37–42.
34. Number of sheathing leaves (excluding basal leaf if present).
35. Number of non-sheathing leaves.
36. Presence (1) or absence (0) of a basal leaf. This is defined as ranging from a chlorophyllose sheath above ground level to a leaf up to half the length of the sheathing leaf immediately above.
37. Length of longest sheathing leaf.

38. Maximum width of widest sheathing leaf.
39. Relative positions of longest and widest sheathing leaves along stem, on a scale 1–3 (1=longest above widest; 2=longest is widest; 3=longest below widest).
40. Shape of uppermost sheathing leaf (for details of shape index see (iii) above).
41. Shape of longest sheathing leaf.
42. Shape of lowest sheathing leaf (excluding basal leaf).
43. Hooding of apex of longest sheathing leaf, on a scale 0–2 (0=none; 1=poorly-defined; 2=well-defined).
44. Colour of longest sheathing leaf, on a scale 1–3 (1=yellow-green; 2=bright green; 3=dark green).

G. *Leaf markings* (7 characters)
Characters 46–51 were taken from the longest sheathing leaf.
45. Presence (1) or absence (0) of markings on any leaf.
46. Area of upper surface covered.
47. Distribution on upper surface, on a scale 1–5 (1=slightly concentrated towards base, through to 5=extremely concentrated towards apex).
48. Mean shape, on a scale 1–5 (1=strongly longitudinally elongated, through to 5=strongly transversely elongated).
49. Mean diameter, on a scale 1–5 (1=*c.* 1 mm; 2=*c.* 1·5 mm; 3=*c.* 2·5 mm; 4=*c.* 4 mm; 5=*c.* 6 mm).
50. Proportion of annular markings (i.e. with green or very pale purple/brown centres), on a scale 0–2 (0=none; 1=<25% of total markings; 2=>25% of total markings).
51. Area of lower surface covered.

Some of the above characters were used to calculate the following indices, which summarize the shapes of certain structures. The characters are numbered according to the above list and preceded by the letter 'C':

a. Roundness of labellum. C1/(C1+C5).
b. Labellum shape index of Heslop-Harrison (1948) (if sinuses present). 2×C1/(C3+C4).
c. Prominence of central lobe (if sinuses present). C1−C4.
d. Tapering of spur. C17/(C17+C16).
e. Percentage of stem bearing flowers. 100×C29/C28.
f. Laxity of inflorescence (fls/cm). C31/C29.
g. Shape of longest leaf. C38/(C38+C37).

Data were analyzed by construction of bivariate scatter-diagrams and by multivariate analyses using the Rothamsted Genstat computer program (Alvey *et al.* 1977). Characters 3–4 (labellum dimensions) and 46–51 (details of leaf markings) were excluded from the multivariate analyses to avoid bias caused by series of zero values resulting from the absence of a single feature (i.e. labellum sinuses or leaf markings respectively). Character 10 (labellum colour coordinate Y) is the approximate equivalent of character 9 (labellum colour coordinate y) for the red-purples, purples and violet-purples of the tetraploid marsh-orchids, and was therefore also discarded from the multivariate analyses. Characters 6 and 12 could not be included as they were measured after the analyses had been performed.

The 40 remaining characters were used to compute two symmetrical matrices of indices that quantified the similarities of pairs of data sets using the formula

$$S_{ij} = 1 - \frac{\sum_{k=1}^{pl} |X_{ik} - X_{jk}|}{pl}$$

where S is the similarity between samples i and j in variate k, X_{ik} is the adjusted value for variate k in sample i, and pl is the total number of variates. The first matrix used population means which were linked according to diminishing maximum similarities to yield a dendrogram expressing their

TABLE 2. POPULATION MEANS (AND SAMPLE STANDARD DEVIATIONS IN PARENTHESES WHERE APPROPRIATE) OF RECORDED CHARACTERS

Character	Labellum													
Population	1 mm	2	(3)* mm	(4)* mm	5 mm	(6)	7	8 C.I.E.	9 units	(10) %	11	(12)	13	14
POLLARDSTOWN	8·78	1·0	7·14	7·79	10·81	2·8	3·5	324·5	204·1	16·5	2·4	2·2	1·1	0·2
	(0·71)		(0·71)	(0·84)	(1·10)			(6·5)	(24·2)	(5·7)				
CORS ERDDREINIOG	8·51	0·9	6·66	7·40	10·73	2·4	3·1	301·6	225·1	26·6	2·7	3·0	2·2	0·4
	(1·22)		(1·12)	(0·86)	(1·05)			(9·8)	(44·6)	(13·2)				
RHOS-Y-GAD	8·91	1·0	6·33	7·29	12·10	2·3	3·0	301·3	200·5	17·3	2·7	2·9	2·2	0·2
	(0·78)		(0·95)	(0·64)	(1·95)			(14·3)	(29·8)	(6·0)				
CLIFDEN	7·69	1·0	6·21	7·14	10·14	2·2	3·3	302·1	190·7	15·3	3·0	2·7	2·5	1·0
	(0·41)		(0·41)	(0·57)	(1·07)			(10·3)	(29·2)	(7·2)				
CAHERBANNAGH	7·71	1·0	5·89	6·91	10·69	2·2	3·2	316·9	195·1	12·6	3·1	2·2	1·9	1·0
	(0·50)		(0·52)	(0·61)	(1·38)			(9·8)	(30·6)	(2·7)				
BALLYCOTTEEN	7·89	1·0	6·25	7·05	10·60	2·1	3·5	310·7	186·3	12·9	3·1	2·3	2·1	0·7
	(0·97)		(1·13)	(1·29)	(1·60)			(11·2)	(11·6)	(2·0)				
MERIONETH	7·25	0·7	5·83	6·27	9·39	1·7	1·9	297·9	175·0	11·7	3·0	1·8	2·0	1·5
	(0·60)		(0·72)	(0·59)	(0·62)			(11·4)	(15·6)	(2·2)				
HA MIRE WOOD	6·32	0·5	5·28	5·40	7·71	2·2	1·2	309·5	179·5	15·3	3·6	2·4	2·1	0·5
	(0·69)		(0·61)	(0·51)	(0·82)			(1·6)	(10·0)	(6·9)				
MALHAM TARN	6·83	0·5	5·52	6·00	8·99	2·1	1·0	305·7	192·5	11·5	3·4	2·6	2·1	0·1
	(0·56)		(0·55)	(0·70)	(1·07)			(8·9)	(27·7)	(1·6)				
MAGILLIGAN	7·21	0·9	6·19	6·83	10·04	—	1·0	—	—	—	3·3	—	—	—
	(0·71)		(0·74)	(0·67)	(1·40)									
BRAUGHING	8·28	1·0	6·65	7·53	11·35	1·9	1·4	326·9	275·9	43·0	2·5	1·7	2·0	0
	(0·66)		(0·73)	(0·69)	(0·89)			(2·8)	(8·1)	(7·4)				
OUGHTONHEAD	8·60	1·0	7·00	7·78	11·96	1·9	1·8	326·2	206·0	16·2	1·9	1·7	1·5	0·4
	(0·82)		(0·80)	(0·80)	(1·05)			(2·5)	(10·5)	(1·7)				
EPSOM	7·44	1·0	6·20	6·99	11·64	2·1	1·8	294·0	210·0	22·4	2·0	1·4	1·6	0·1
	(0·47)		(0·71)	(0·67)	(1·68)			(6·2)	(38·4)	(11·6)				
SAWBRIDGEWORTH	7·97	0·7	6·53	7·11	10·88	1·9	2·0	300·0	220·7	23·9	2·8	1·6	1·8	0
	(0·48)		(0·43)	(0·33)	(0·61)			(8·7)	(33·4)	(9·5)				
TEWINBURY	8·04	0·9	6·62	7·06	10·86	2·1	1·8	299·1	224·9	28·0	2·2	1·6	1·8	0
	(0·63)		(0·53)	(0·67)	(1·02)			(9·7)	(39·3)	(14·5)				

TABLE 2 (*continued*)

Character	Spur				Lateral outer perianth segs			Bracts					
Population	15 mm	16 mm	17 mm	18	19	20	21	22 mm	23 mm	24	25	26 µm	27
POLLARDSTOWN	9·68 (1·15)	3·62 (0·34)	3·26 (0·72)	4·2	3·6	0·7	0	25·2 (4·4)	19·1 (3·1)	1·4	0	121·4 (15·3)	2·6
CORS ERDDREINIOG	9·02 (1·29)	3·86 (0·57)	3·59 (0·59)	3·3	4·6	1·2	0	20·7 (3·3)	15·1 (2·6)	1·1	0	95·2 (10·4)	2·9
RHOS-Y-GAD	9·02 (1·39)	4·00 (0·82)	3·81 (0·65)	3·1	3·8	1·3	0·3	24·2 (4·5)	16·4 (2·7)	1·6	0	89·9 (14·2)	2·7
CLIFDEN	7·75 (1·72)	3·14 (0·40)	2·64 (0·30)	4·0	2·5	1·4	0·3	22·6 (4·3)	14·8 (2·5)	1·1	0	95·8 (16·5)	3·0
CAHERBANNAGH	7·21 (0·71)	3·06 (0·46)	2·57 (0·39)	4·0	2·9	1·1	0·5	17·8 (4·0)	12·9 (2·0)	1·4	0·1	79·1 (14·7)	2·7
BALLYCOTTEEN	8·16 (1·38)	3·02 (0·56)	2·54 (0·69)	3·9	2·5	0·5	0·5	23·2 (4·3)	13·9 (2·0)	0·7	0	86·9 (7·9)	2·0
MERIONETH	7·09 (0·75)	3·85 (0·45)	3·10 (0·42)	3·9	2·6	1·1	0·4	22·6 (5·7)	14·1 (2·9)	0·5	0·7	74·4 (16·8)	2·2
HA MIRE WOOD	7·17 (0·58)	2·91 (0·46)	2·57 (0·35)	4·4	3·4	1·2	0·1	16·9 (3·5)	12·5 (2·7)	0·5	0	77·6 (13·1)	1·4
MALHAM TARN	7·79 (0·47)	2·97 (0·33)	2·51 (0·26)	4·2	4·1	1·5	0·3	25·3 (6·0)	15·4 (2·2)	0·6	0	76·4 (7·5)	2·2
MAGILLIGAN	8·27 (1·37)	3·76 (0·52)	2·90 (0·46)	3·7	3·9	1·4	0·2	20·5 (3·4)	14·7 (1·9)	—	—	—	—
BRAUGHING	7·44 (0·39)	2·97 (0·35)	2·45 (0·30)	3·5	3·3	0·4	0	27·3 (5·4)	16·2 (2·1)	1·2	0	75·9 (12·1)	2·6
OUGHTONHEAD	7·89 (0·44)	3·76 (0·40)	3·31 (0·37)	3·9	3·6	0·7	0	23·7 (5·0)	15·4 (2·4)	1·4	0	63·1 (7·7)	2·3
EPSOM	7·82 (1·00)	3·53 (0·30)	3·20 (0·29)	3·5	2·4	1·0	0	30·2 (7·2)	16·3 (2·2)	0·5	0	60·5 (9·8)	1·7
SAWBRIDGEWORTH	8·15 (0·47)	3·48 (0·27)	3·03 (0·34)	3·0	3·9	1·1	0	25·1 (5·3)	16·3 (1·6)	1·5	0	69·9 (8·3)	2·2
TEWINBURY	7·75 (0·86)	3·30 (0·42)	2·78 (0·46)	3·6	3·8	1·2	0	31·2 (7·8)	16·2 (2·6)	1·5	0	51·2 (5·4)	2·7

TABLE 2 (*continued*)

Character	Stem and inflorescence						Leaves										
Population	28 cm	29 mm	30 mm	31	32 mm	33	34	35	36	37 mm	38 mm	39	40	41	42	43	44
POLLARDSTOWN	25·1 (4·2)	41·2 (5·7)	32·5 (3·5)	14·0 (4·0)	4·18 (1·03)	1·9	2·7 (0·5)	1·0	1·0	97·6 (16·5)	12·8 (4·5)	2·0	1·9	2·5	2·8	1·0	2·1
CORS ERDDREINIOG	24·2 (4·3)	44·9 (13·5)	31·1 (3·7)	10·7 (2·5)	4·03 (0·67)	0·6	2·8 (0·6)	1·2	0·8	97·8 (17·6)	11·9 (1·4)	1·8	2·9	3·0	3·3	0·7	2·3
RHOS-Y-GAD	16·7 (5·2)	43·2 (12·4)	33·9 (3·0)	11·5 (5·0)	3·94 (1·19)	1·4	2·6 (0·5)	1·0	0·8	85·4 (17·0)	13·6 (4·9)	1·6	2·5	2·9	3·1	1·1	1·9
CLIFDEN	16·3 (2·8)	40·8 (1·2)	32·4 (4·1)	29·4 (19·3)	5·07 (1·38)	0·7	4·2 (0·4)	2·3	0·8	89·6 (13·5)	21·0 (5·4)	1·4	2·0	2·8	3·0	0·7	2·2
CAHERBANNAGH	12·3 (3·1)	30·4 (4·8)	27·2 (3·3)	12·1 (2·9)	4·10 (0·80)	1·5	3·8 (0·4)	1·3	0·9	76·4 (19·9)	17·0 (5·1)	1·4	1·8	2·9	3·1	1·0	2·0
BALLYCOTTEEN	22·9 (3·4)	54·3 (16·4)	34·9 (4·7)	33·1 (14·6)	6·08 (1·52)	1·1	4·2 (0·6)	2·2	0·8	101·4 (20·9)	25·7 (6·8)	1·1	1·8	2·8	3·2	0·6	2·7
MERIONETH	22·2 (4·0)	39·5 (11·4)	32·9 (3·8)	23·2 (10·3)	5·31 (1·18)	0·6	4·5 (0·7)	1·5	1·0	106·4 (18·0)	19·9 (3·9)	2·0	1·9	2·8	3·1	0·4	2·6
HA MIRE WOOD	15·4 (3·2)	27·1 (6·1)	28·0 (2·3)	9·9 (3·3)	4·08 (0·52)	0·7	3·7 (0·5)	1·0	1·0	85·0 (18·5)	13·2 (2·1)	1·4	2·0	2·8	3·1	0·7	2·0
MALHAM TARN	24·1 (8·5)	41·7 (15·6)	30·4 (3·2)	14·0 (4·1)	5·37 (0·83)	0·5	3·9 (0·3)	1·0	1·0	131·2 (26·5)	20·0 (4·1)	1·9	2·1	3·1	3·2	0·6	2·2
MAGILLIGAN	20·1 (5·2)	52·5 (13·1)	32·7 (4·5)	26·0 (8·1)	6·56 (1·05)	—	—	—	1·0	102·3 (12·9)	26·1 (6·6)	1·4	1·4	3·4	3·5	0·7	2·0
BRAUGHING	28·5 (7·2)	47·8 (11·8)	32·8 (2·4)	28·7 (10·6)	6·13 (1·12)	0·7	4·4 (0·8)	2·2	1·0	123·5 (27·7)	24·0 (4·1)	1·2	2·0	2·6	3·0	0·4	2·2
OUGHTONHEAD	30·6 (9·7)	46·0 (7·0)	33·0 (5·2)	18·9 (4·9)	6·38 (1·26)	1·1	4·1 (0·7)	1·7	0·8	152·2 (26·5)	25·2 (5·4)	1·4	2·4	3·1	3·1	0·7	2·0
EPSOM	44·3 (9·9)	59·9 (23·6)	36·4 (5·6)	44·1 (26·2)	8·93 (2·06)	0	4·5 (0·9)	2·5	0·9	162·1 (51·0)	39·6 (12·4)	1·1	2·6	3·1	3·5	0·1	1·9
SAWBRIDGEWORTH	42·9 (6·8)	77·0 (23·4)	32·2 (1·1)	28·8 (11·0)	5·77 (1·08)	0·6	4·0 (0·7)	2·4	1·0	130·5 (10·4)	24·9 (2·7)	1·1	2·1	2·9	3·5	0	2·1
TEWINBURY	49·0 (11·5)	88·4 (31·0)	32·9 (4·9)	40·2 (17·2)	6·89 (1·28)	0·4	4·5 (0·5)	2·0	1·0	166·3 (53·8)	25·8 (6·6)	1·3	1·9	2·9	3·2	0·4	2·1

TABLE 2 (*continued*)

Character	Leaf markings							Indices						
Population	45	(46)* %	(47)*	(48)*	(49)*	(50)*	(51)* %	(a)	(b)*	(c)* mm	(d)	(e) %	(f) fls/cm	(g)
POLLARDSTOWN	0·9	4·5	4·8	3·3	1·9	0	0	0·448	1·18	1·0	0·47	14·0	2·5	0·106
CORS ERDDREINIOG	0·1	5·0	5·0	3·0	2·0	0	0	0·442	1·25	1·1	0·48	15·7	1·9	0·109
RHOS-Y-GAD	0·2	10·0	5·0	4·0	1·5	0	0	0·424	1·33	1·7	0·49	20·5	2·1	0·132
CLIFDEN	0·6	14·0	4·4	3·4	2·6	0·8	0	0·431	1·17	0·6	0·45	20·1	4·2	0·167
CAHERBANNAGH	0·9	9·9	3·4	3·2	2·2	0·7	0	0·418	1·22	0·8	0·46	19·6	2·8	0·173
BALLYCOTTEEN	1·0	12·1	3·6	3·6	2·9	0·3	0	0·426	1·20	0·8	0·45	19·1	3·8	0·192
MERIONETH	0·9	19·3	2·8	2·9	2·6	0·3	0	0·436	1·22	1·0	0·45	15·3	3·7	0·151
HA MIRE WOOD	0·2	2·0	2·0	3·0	1·0	0	0	0·450	1·19	0·9	0·47	14·9	2·7	0·138
MALHAM TARN	0	0	0	0	0	0	0	0·432	1·16	0·8	0·46	14·8	2·5	0·131
MAGILLIGAN	0·1	2·0	1·0	4·0	1·0	0	0	0·418	1·11	0·4	0·44	26·1	5·0	0·182
BRAUGHING	0	0	0	0	0	0	0	0·422	1·17	0·8	0·45	14·4	3·8	0·147
OUGHTONHEAD	0	0	0	0	0	0	0	0·418	1·17	0·8	0·47	13·1	2·9	0·133
EPSOM	0·1	0	0	0	0	0	0	0·390	1·12	0·5	0·47	11·9	4·3	0·188
SAWBRIDGEWORTH	0·2	45·0	3·5	3·5	4·0	2·0	0	0·423	1·16	0·8	0·47	15·2	2·7	0·146
TEWINBURY	0·1	30·0	4·0	4·0	4·0	2·0	0	0·425	1·17	1·0	0·46	15·2	3·1	0·124

The Magilligan population and characters in parentheses for all populations were not used in multivariate analyses.
* Characters that depend on the presence of either a labellum sinus or leaf markings. They may therefore be based on only a proportion of the sample.

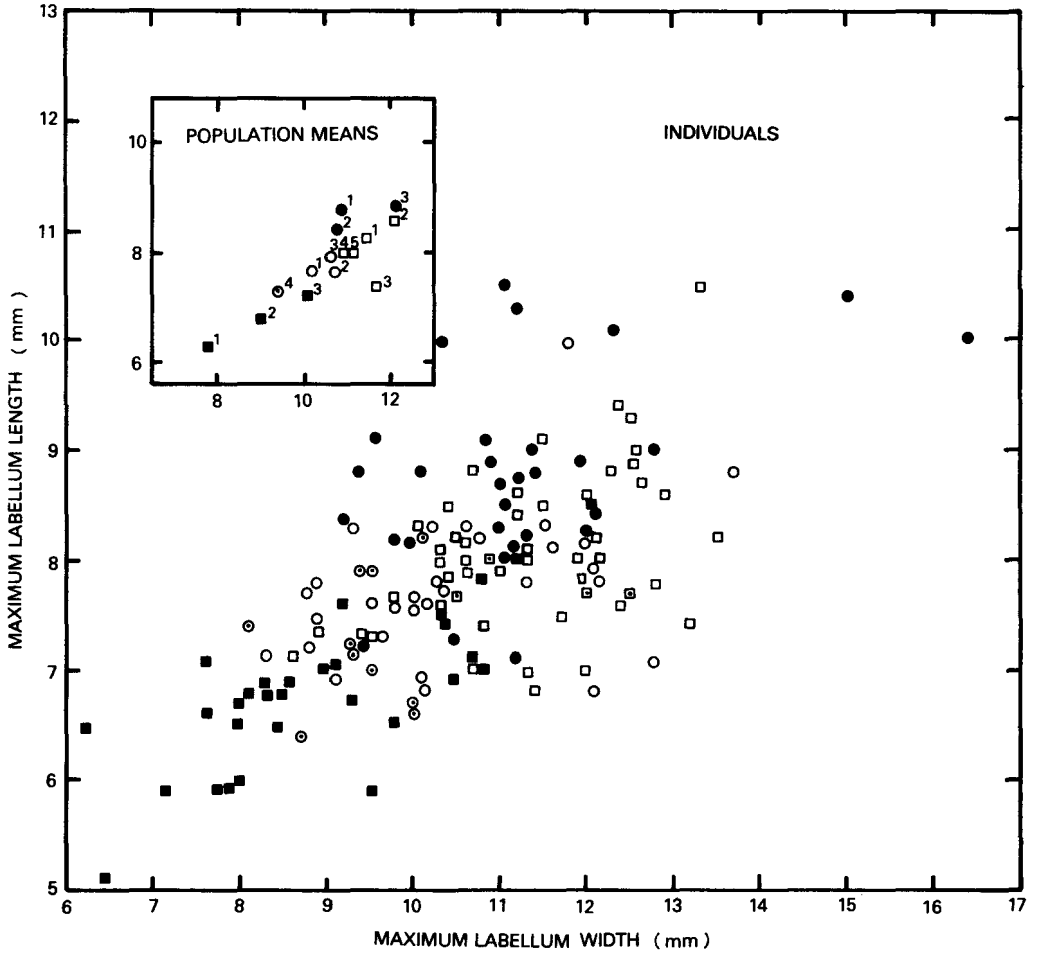

FIGURE 1. Bivariate scatter-diagram of labellum dimensions for individual plants (main graph) and population means (inset).
The following symbols are used throughout the figures:
○ subsp. *occidentalis* (⊙ var. *cambrensis*)
■ subsp. *purpurella*
□ subsp. *praetermissa* (⊡ var. *junialis*)
● subsp. *traunsteinerioides*
Superscripts denote populations (listed in Fig. 5, with the addition of Magilligan as the third population of subsp. *purpurella*).

phenetic relationships (Gower & Ross 1969). The second similarity matrix was produced from data for individual plants and was used to calculate principal coordinates (Gower 1966, Blackith & Reyment 1971, Sneath & Sokal 1973), compound vectors that incorporate positively or negatively correlated characters which are most variable and therefore of potential diagnostic value. The first three principal coordinates (PC1, PC2, PC3) were plotted in pairwise combinations to assess the degree of morphological separation of taxa in these three dimensions.

Data for the Magilligan population are included in the bivariate scatter-diagrams but were received after the multivariate analyses had been completed.

VARIATION IN SINGLE CHARACTERS

Population means for all recorded characters are listed in Table 2, with sample standard deviations where applicable. There are very few all-or-none characters (i.e. those scored as 0 or 1) that would enable cladistic classification of marsh-orchids, or aid the construction of workable dichotomous keys (this has been attempted using characters that we measured, e.g. Summerhayes 1951, Hunt & Summerhayes (1967), Soó (1980)). Leaf markings are the most distinctive all-or-none character but they occur in all of the subspecies, albeit at different frequencies, and are more useful for delimiting varieties.

Many other characters are less diagnostic than has previously been suggested. For example, flower colour, a visually striking character, is invariably used to describe marsh-orchid taxa. However, our results show that C.I.E. coordinate x (character 8, a measure of the type of red-purple anthocyanin pigment present) is remarkably constant. Each of the subspecies also includes plants with flowers containing high densities of red-purple anthocyanin (reflectivity $<15\%$, $y<200$) but they are most frequent in populations of *D. majalis* subsp. *purpurella* and subsp. *occidentalis*. The frequencies of anthocyanin in flowers, bracts, stems and leaves of individual plants are poorly correlated; this evidence does not support the existence of the anthocyanin-high and anthocyanin-low modes postulated by Heslop-Harrison (1953a, 1954).

Variation in labellum size was examined by constructing a scatter-diagram of maximum length against maximum width (Fig. 1). The distribution of population means (inset) suggests that the subspecies can be separated using this criterion. However the plot of individual plants reveals considerable overlap of subspecies and extensive variation within them; this obscures the small differences in population means and considerably reduces their diagnostic value. The characteristic deltoid labellum shape of *D. majalis* subsp. *traunsteinerioides* is accentuated in the field by greater reflexion of the upper part of the lateral lobes than of the lower part. It is less evident when labella are mounted.

Maximum leaf length is plotted against maximum leaf width in Fig. 2. These characters largely separate *D. majalis* subsp. *traunsteinerioides* (small leaves) from subsp. *praetermissa* (large leaves). However, leaves of *D. majalis* subsp. *occidentalis* (formerly called the 'Broad-leaved Marsh-orchid') are rarely very broad in relation to length, and those of subsp. *traunsteinerioides* (formerly called the 'Narrow-leaved Marsh-Orchid') are rarely very narrow.

MULTIVARIATE ANALYSES AND TAXONOMIC STATUS

31 of the 40 characters used for multivariate analyses contributed appreciably to the first three principal coordinates (Table 3), which together accounted for only 38·3% of the total variance present. This low figure reflected the dispersion of individuals in many dimensions due to poor correlation of characters. The first principal coordinate (PC1 on Figs. 3 & 4) separated *D. majalis* subsp. *occidentalis* from subsp. *praetermissa*. PC2 partially separated *D. majalis* subsp. *traunsteinerioides* from the other subspecies, and PC3 partially separated *D. majalis* subsp. *purpurella* from the remainder. All four subspecies overlapped on these plots; morphological discontinuities were absent.

Additional principal coordinates analyses were performed using pairs of subspecies in order to polarise the variation and reduce its dimensionality. The resulting vectors accounted for a larger proportion of the total variance, but limited overlap was still evident between each pair of subspecies except *D. majalis* subsp. *traunsteinerioides* and subsp. *purpurella*. Furthermore, the variation demonstrated by Roberts (1961a) for *D. majalis* subsp. *purpurella* and described by Hall (1937) and Roberts (1961b) for subsp. *occidentalis* shows that this study did not encompass all the variation that exists within the subspecies; morphological overlap is undoubtedly greater than our data suggest.

As the morphological discontinuities that would be expected to delimit species are absent, we cannot justify the continued recognition of four species of British and Irish tetraploid marsh-orchids. We believe that they comprise a single very variable species, for which the appropriate name is *Dactylorhiza majalis* (see under Classification). The four taxa previously regarded as species form equally cohesive groups on the principal coordinates plots, and provide a means of partitioning the extensive variation encompassed by *D. majalis*. We therefore favour their retention as subspecies of

TABLE 3. VARIATES CONTRIBUTING TO THE FIRST THREE PRINCIPAL COORDINATES, LISTED IN ORDER OF DECREASING IMPORTANCE

Principal coordinate	PC1	PC2	PC3
Percentage of variance accounted for	16·7%	11·2%	10·4%
Taxonomic significance of coordinate	Separates *D. majalis* subsp. *praetermissa* and subsp. *occidentalis*	Partially separates *D. majalis* subsp. *traunsteinerioides* from the remainder	Partially separates *D. majalis* subsp. *purpurella* from the remainder
Variate number, variate name, and direction of increase in value of variate in relation to increase in value of vector (e.g. individuals with leaf markings tend to occur towards the right side of PC1 on Fig. 3, whereas tall plants tend to occur towards the left side).	45 Leaf markings, presence +	24 Bracts, anthocyanin +	5 Labellum, width −
	28 Plant height −	34 Leaves, number of sheathing −	2 Labellum, presence of sinuses +
	37 Leaves, length of longest −	38 Leaves, width of widest −	30 Inflorescence, width −
	32 Stem, diameter −	31 Inflorescence, number of flowers −	1 Labellum, length to central lobe −
	33 Stem, anthocyanin +	19 L.o.p.s.*, position +	31 Inflorescence, number of flowers −
	29 Inflorescence, length −	33 Stem, anthocyanin +	29 Inflorescence, length −
	14 Labellum, lateral lobe indentations +	32 Stem, diameter −	22 Bracts, length of basal −
	22 Bracts, length of basal −	1 Labellum, length to central lobe +	35 Leaves, number of non-sheathing −
	38 Leaves, width of widest −	27 Bracts, shape of peripheral cells +	32 Stem, diameter −
	26 Bracts, length of peripheral cells +	35 Leaves, number of non-sheathing −	38 Leaves, width of widest −
	7 Labellum, lateral lobe reflexion +	43 Leaves, hooding of tips +	7 Labellum, lateral lobe reflexion −
	9 Labellum, colour coordinate 'y' −	45 Leaf markings, presence −	23 Bracts, length of floral −
	11 Labellum, type of markings +	14 Labellum, lateral lobe indentations −	20 Lo.p.s., solid markings +
	31 Inflorescence, number of flowers −	25 Bracts, presence of markings −	28 Plant height −
	43 Leaves, hooding of tips +		45 Leaf markings, presence −
	18 Spur, curvature +		11 Labellum, type of markings +
	21 L.o.p.s.*, annular markings +		19 L.o.p.s.*, position −
	35 Leaves, number of non-sheathing −		15 Spur, length −
			16 Spur, width at entrance +

*L.o.p.s.=lateral outer perianth segments.

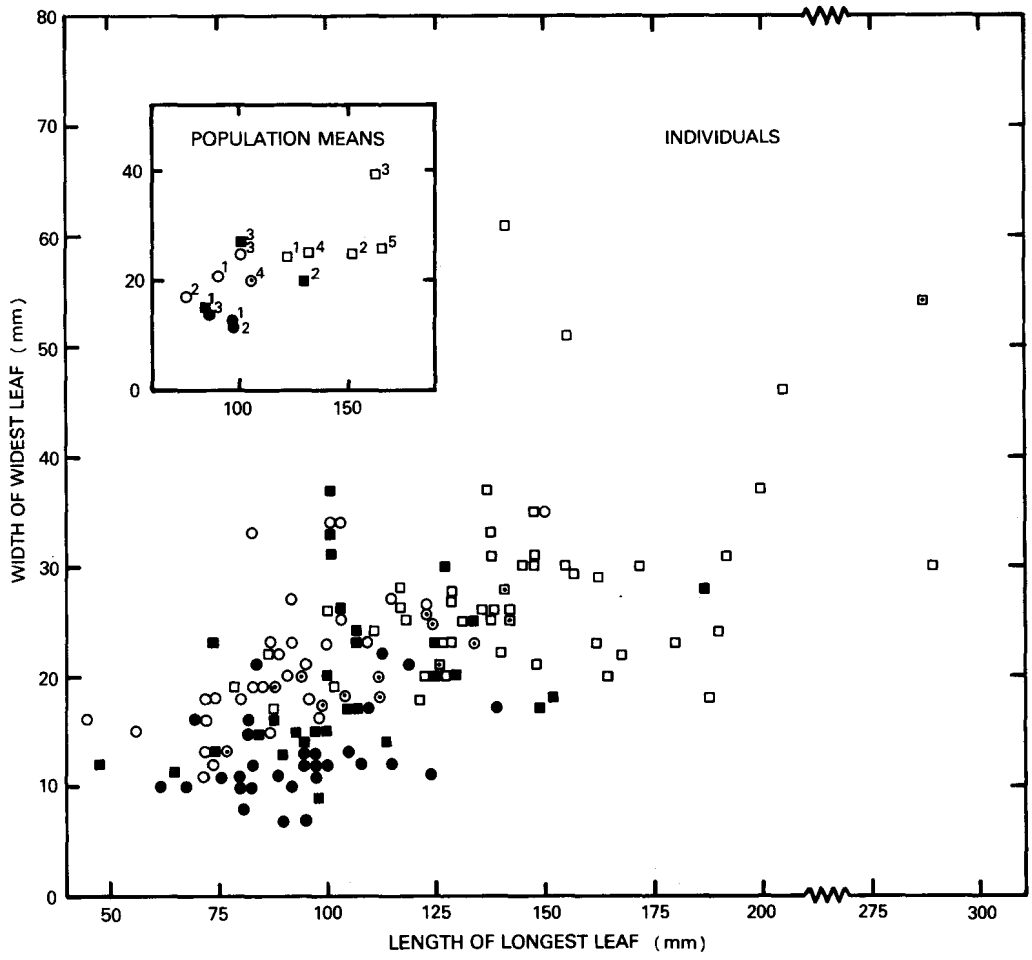

FIGURE 2. Bivariate scatter-diagram of leaf dimensions for individual plants (main graph) and population means (inset).
See Fig. 1 for explanation of symbols.

D. majalis, even though they appear to comprise a morphological continuum. They may therefore be no more than nominal subspecies as defined by Lewin (1981), providing convenient subdivisions of a broad morphological spectrum but of little biological significance.

Our interpretation of the status of these taxa is based solely on morphological criteria. Mayr (1965, 1970) and other advocates of the 'biological species concept' argue that in some cases phenetic relationships may be unreliable indicators of true taxonomic status, which should ideally be determined by the extent of hybridization and reproductive isolation (this is discussed further in a later section). However, such information is lacking for most organisms, and the phenetic species is probably the best approximation to the biological species that can be realistically achieved (Sokal & Crovello 1970). This is true at present for the tetraploid marsh-orchids.

Our treatment of the taxa is also supported by the dendrogram of population means (Fig. 5); all the subspecies branch off over a fairly narrow range of maximum similarities (84·6–87·4%). However, the Merioneth population of *D. majalis* subsp. *occidentalis* and the Pollardstown population of subsp. *traunsteinerioides* also branch off over this range, and four of the five populations of subsp. *praetermissa* separate below 91% maximum similarity. Variation between populations of the same subspecies of *D. majalis* can thus be as great as variation between

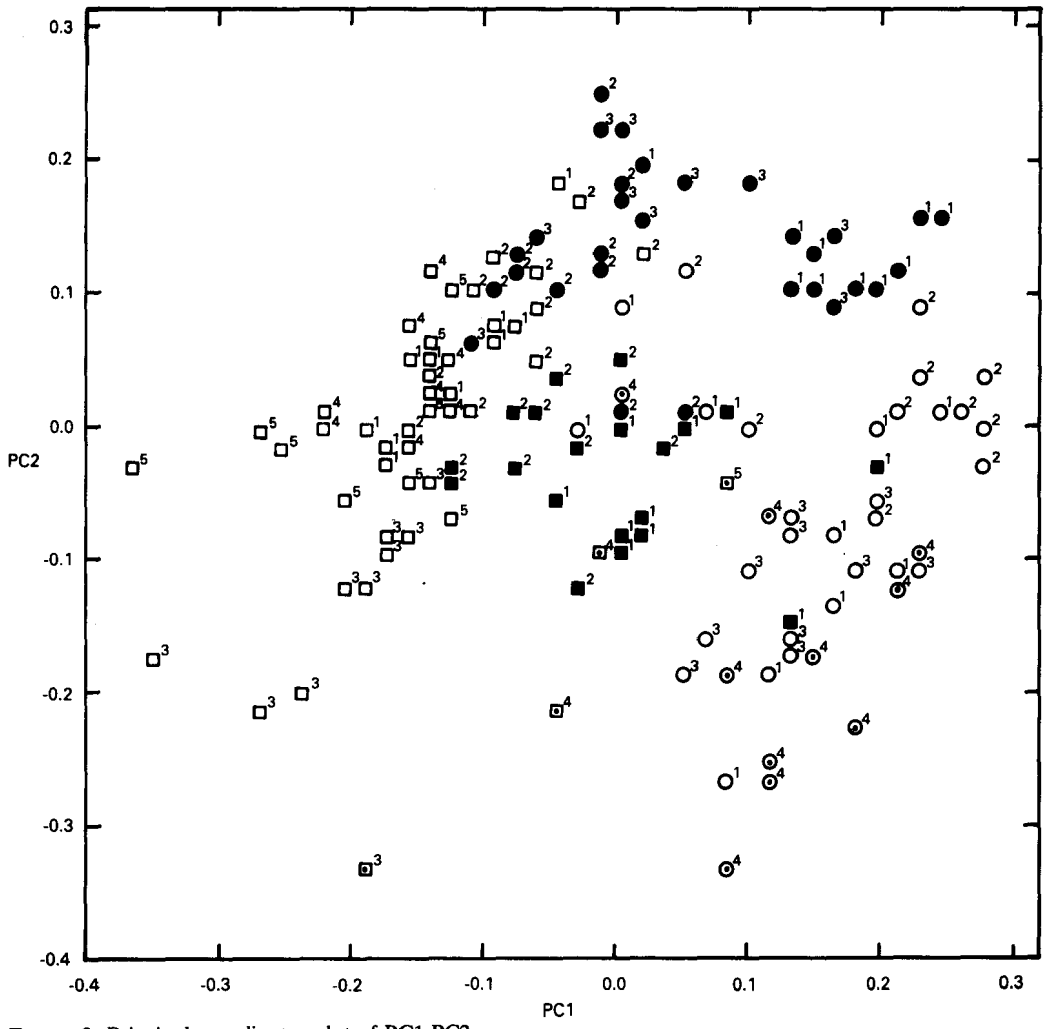

FIGURE 3. Principal coordinates plot of PC1:PC2.
See Fig. 1 for explanation of symbols.

populations of different subspecies. An alternative phenetic classification, derived solely from population means, would require the creation of a taxon for each of most of the populations that we examined.

Most original diagnoses describe holotypes that were probably atypical of the populations from which they were taken. Previous workers have either ignored morphological intermediates or given them subspecific or varietal status. Named intermediates are most frequent between *D. majalis* subsp. *occidentalis* and subsp. *purpurella* (Fig. 6). They can be divided into three arbitrary sequences: I, labellum sinuses present, leaf markings usually absent; II, labellum sinuses often absent, leaf markings usually present; III, all structures smaller. Two (possibly four) of these varieties are near-identical and can be regarded as synonymous. Similar sequences of largely unnamed intermediates exist between each pair of subspecies but rarely form 'pure' populations. Some varieties have occasionally been transferred from one subspecies to another (e.g. *D. majalis* subsp. *purpurella* var. *pulchella* (Druce) Soó, subsp. *praetermissa* var. *junialis* (Vermeulen) Senghas); this illustrates their intermediate nature and also partly explains their confused nomenclature.

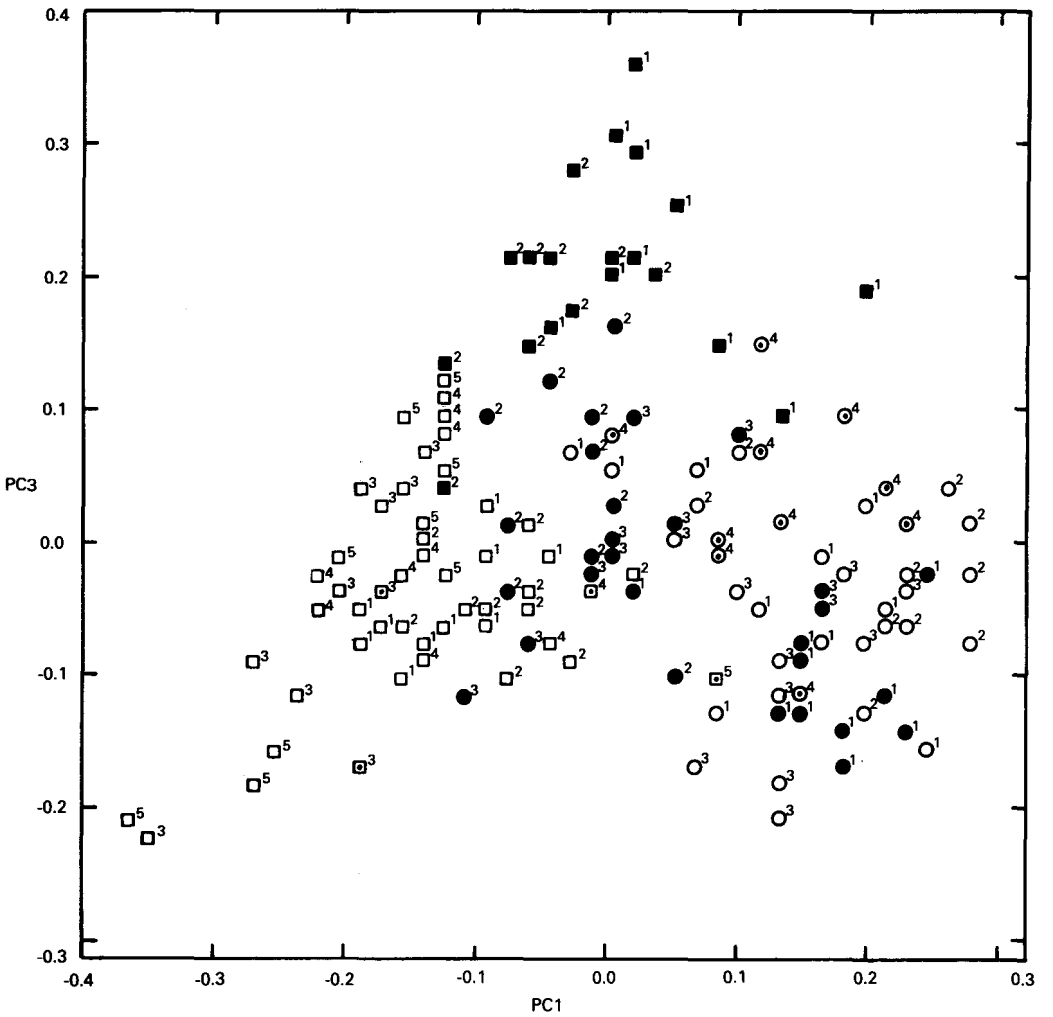

FIGURE 4. Principal coordinates plot of PC1:PC3.
See Fig. 1 for explanation of symbols.

Previous emphasis on morphological extremes has also resulted in the publication of diagnoses that give a misleading impression of the degree of dissimilarity and ease of identification of taxa. *D. majalis* subsp. *occidentalis*, subsp. *purpurella* and subsp. *praetermissa* are correctly treated as subspecies of *D. majalis* in *Flora Europaea* (Soó 1980) but many of the diagnostic characters presented in the *Flora* are difficult to interpret objectively. The botanist is expected to be able to differentiate between the "deep violet-purple" flowers of *D. majalis* subsp. *occidentalis*, the "bright or deep reddish-purple" flowers of subsp. *purpurella*, and the "pale or dull reddish-purple" flowers of subsp. *praetermissa*. Furthermore, although broad ranges are given for the few quantitative characters described, many are inaccurate. The single range of labellum dimensions presented for *D. majalis* subsp. *praetermissa* (10–14 mm) only encompasses the maximum length of 2% of the plants that we examined. Consequently, these diagnoses are useless in the field.

The principal coordinates plots show that some individuals in most populations of a subspecies resemble more closely the median characteristics of another subspecies. Heslop-Harrison (1954) and Nelson (1976) were therefore correct in their assertion that extensive intra-population variation prevents the confident assignment of many individual plants (particularly herbarium specimens, which cannot be measured accurately) to a subspecies. Since the subspecies of *D. majalis* can only be

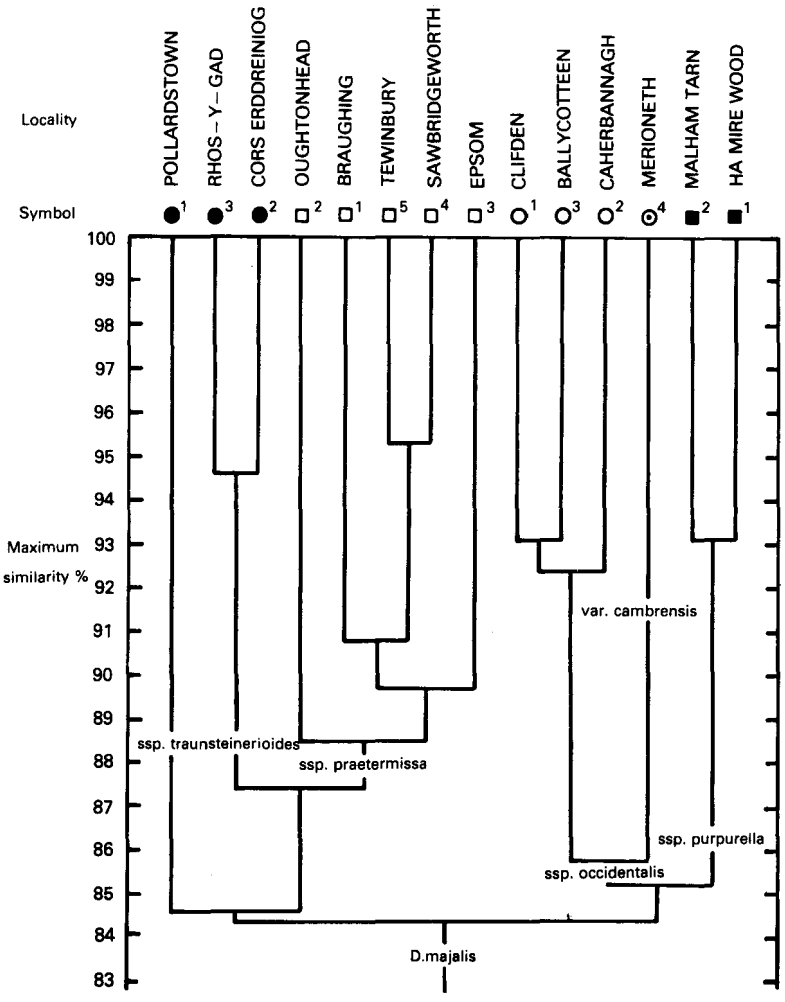

FIGURE 5. Dendrogram expressing the maximum similarities of populations. Derived from population means for 40 characters.

separated by differences in the frequency of characters, the most diagnostic characters (see Classification) must be studied for a representative sample of a population before identification is attempted.

In addition to the four subspecies, there is a residuum of several named variants. Each is attributed to one subspecies in our classification, but differs from the type variety of that subspecies in few characters that are usually at one extreme of their range of variation within the subspecies. These variants are therefore best treated as varieties. Some appear to be peripheral to the range of morphological variation of *D. majalis*, e.g. *D. majalis* subsp. *traunsteinerioides* var. *francis-drucei* (Wilmott) Bateman & Denholm, but the majority are intermediate between the type varieties of two or more subspecies; both *D. majalis* subsp. *praetermissa* var. *junialis* and subsp. *occidentalis* var. *cambrensis* (R. H. Roberts) Bateman & Denholm occupy intermediate positions on the principal coordinates plots (Figs. 3 & 4).

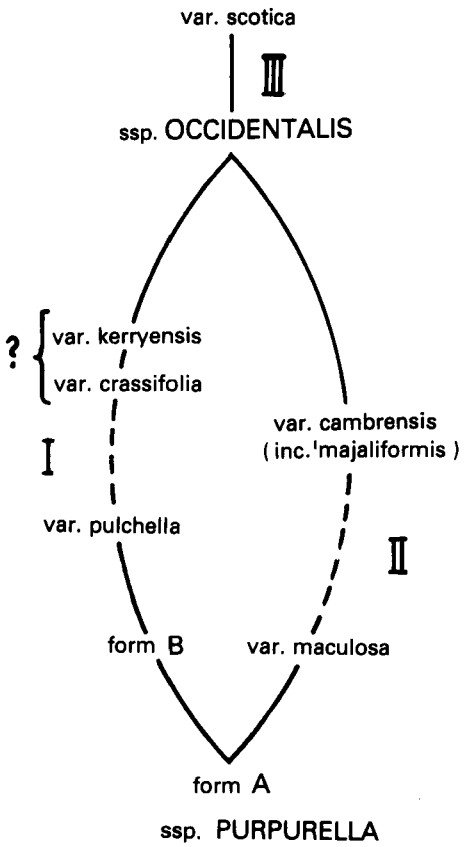

FIGURE 6. Morphological relationships of varieties of *D. majalis* subsp. *occidentalis* and subsp. *purpurella* (schematic).
Sequence I: Labellum sinuses present, leaf markings usually absent
Sequence II: Labellum sinuses often absent, leaf markings usually present
Sequence III: All structures smaller.

CAUSES OF MORPHOLOGICAL VARIATION

Godfery (1933) described a two- to three-fold increase in the plant height, inflorescence length and leaf size of a specimen of *D. majalis* subsp. *traunsteinerioides* var. *eborensis* (Godfery) Bateman & Denholm after it had been transplanted from the field to a greenhouse, demonstrating that the dwarfing of these characters is environmentally induced. However, Roberts (pers. comm. 1982) observed little morphological change in single specimens of *D. majalis* subsp. *purpurella* and subsp. *praetermissa* and three specimens of subsp. *traunsteinerioides* in cultivation. Large-scale transplantation experiments under controlled conditions are necessary to determine how much of the phenotypic variation exhibited by marsh-orchids is a consequence of environmental modification rather than adaptive genetic differentiation.

Ontogeny also affects the morphology of individuals (Cook 1968); many structures of young plants are smaller and less numerous than those of mature individuals. Some of the characters which distinguish *D. majalis* subsp. *praetermissa* (e.g. tall, broad stem; large leaves (Fig. 2) and inflorescence) show that it is the most vigorous subspecies and therefore has the greatest potential for ontogenetic variation. Only smaller (presumably younger) individuals of *D. majalis* subsp. *praetermissa* overlap with subsp. *traunsteinerioides* on the principal coordinates plots (Figs. 3 & 4). However, Fig. 2 shows that the labella of *D. majalis* subsp. *praetermissa* are only moderately large despite its general vegetative superiority. Vegetative characters are evidently more susceptible to

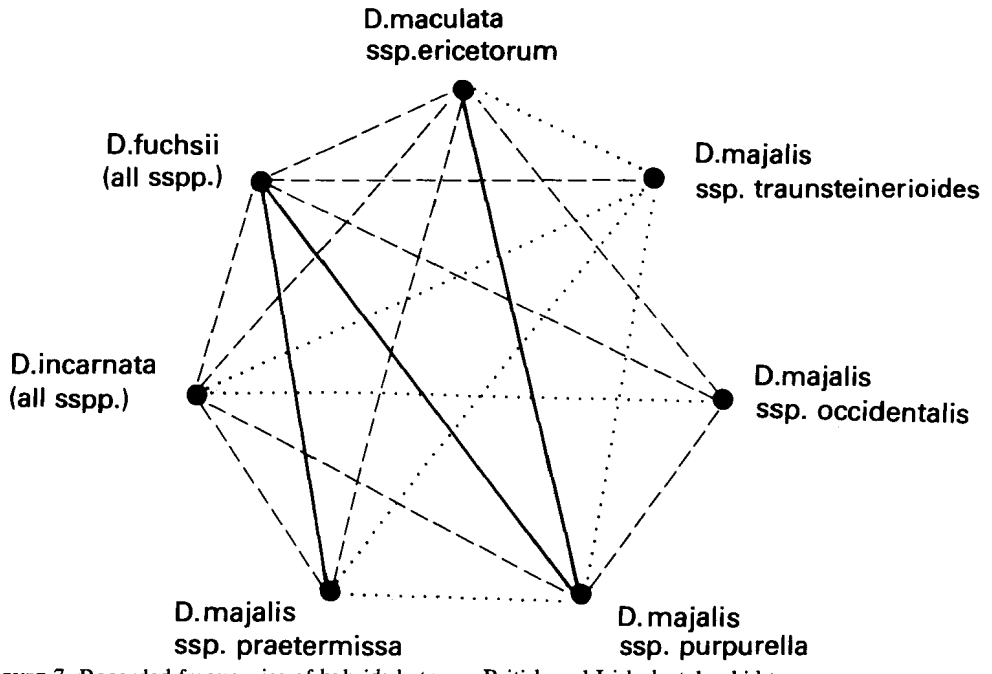

FIGURE 7. Recorded frequencies of hybrids between British and Irish dactylorchid taxa. Information largely from Roberts (1975) but modified according to the authors' observations.
Solid line: widespread and locally frequent
Dashed line: widespread and rare, or very locally frequent
Dotted line: very rare.

both environmental modification and ontogenetic variation than floral characters (Clausen *et al.* 1940, Heslop-Harrison 1953b, Heywood 1967, Jones & Luchsinger 1979), which show the smallest range of variation in *D. majalis* (generally about two-fold; see Classification). Multivariate analyses were therefore repeated using first only floral characters (nos 1–2, 5, 7–9, 11, 13–21) and then only vegetative characters (nos 22–45), but each provided considerably less separation of the taxa than the combination of floral and vegetative characters initially used.

ISOLATION AND HYBRIDIZATION

The biological species is usually defined as an assemblage of interbreeding populations that is reproductively isolated from other such groups (Mayr 1970). Frequencies of hybridization reflect the combined efficiency of isolating mechanisms and provide a complementary method of assessing the status and affinities of taxa. Since morphological similarity is generally proportional to the interfertility of related taxa and the fertility of F_1 hybrids (Stace 1975), hybridization between subspecies of *D. majalis* should be commonplace. Surprisingly, records of such hybrids are rare (Fig. 7); only *D. majalis* subsp. *occidentalis* × subsp. *purpurella* is locally frequent and two of the possible combinations are unrecorded. Hybrids between marsh-orchids and spotted-orchids are more frequently recorded.

There are several isolating mechanisms that could restrict hybridization between tetraploid marsh-orchids. Temporal isolation may limit gene flow between *D. majalis* subsp. *occidentalis* and subsp. *traunsteinerioides* which generally flower in late May-early June, and subsp. *purpurella* and subsp. *praetermissa* which flower in June-early July. However, many populations of *D. majalis* subsp. *praetermissa* (including Braughing, Table 1) are in full flower in the first week of June, and subsp. *occidentalis* var. *cambrensis* and var. *scotica* (Nelson) Bateman & Denholm can still be in flower in July. The flowering periods of individuals and populations of all dactylorchids are prolonged and permit locally frequent hybridization between *D. incarnata* (L.) Soó (early June) and

D. maculata or *D. fuchsii* (late June-early July). It is doubtful whether temporal isolation of subspecies of *D. majalis* is ever completely effective.

The distribution of *D. majalis* subsp. *traunsteinerioides* overlaps those of all other subspecies, providing opportunities for hybridization, but there is partial geographical separation of the predominantly north-western *D. majalis* subsp. *purpurella* (and subsp. *occidentalis*) and the south-eastern subsp. *praetermissa*. However, their distributions overlap along a broad zone from Pembrokeshire through Caernarvonshire and Lancashire to Yorkshire and Durham (Perring & Walters 1962). There may be less geographical separation than is generally supposed; the discovery of *D. majalis* subsp. *purpurella* near Southampton (Summerhayes 1968) revealed the fallacy of the popular circular argument that subsp. *purpurella* does not grow in south-eastern England and therefore subsp. *purpurella*-like populations occurring in that region must be aberrant subsp. *praetermissa*. More emphasis should be placed on the morphology of populations than on their geographical locations. Differences in ecological requirements may result in local spatial separation, but the coexistence of tetraploid marsh-orchid subspecies in North Wales (Roberts 1966), East Anglia (Heslop-Harrison 1968), Ireland (Hall 1937) and elsewhere demonstrates the inefficiency of any ecological barriers that may exist.

There are no significant differences between subspecies in characters such as spur size and position of viscidia that determine the ability of insects to effect cross-pollination, and various bee species are thought to be the main pollinators of all British and Irish dactylorchids (Summerhayes 1951). Roberts (pers. comm. 1982) observed bumble bees visiting cultivated plants of *D. majalis* subsp. *traunsteinerioides*, subsp. *purpurella* and subsp. *praetermissa* in succession. Cross-pollination should therefore occur between subspecies where they coexist (Roberts 1966). Furthermore, Lord & Richards (1977) demonstrated that introgression between the diploid *D. fuchsii* and tetraploid *D. majalis* subsp. *purpurella* has resulted in triploid F_1 hybrids and several aneuploid karyotypes. Since these species are probably more dissimilar than any pair of subspecies of *D. majalis*, this also casts doubt upon the existence of the intrinsic sterility barriers invoked by Roberts (1966) to account for the apparent coexistence of *D. majalis* subsp. *purpurella* with both subsp. *occidentalis* var. *cambrensis* and subsp. *traunsteinerioides* in North Wales. He examined the distribution of some floral and vegetative characters in mixed populations and concluded that little or no hybridization had occurred. However, these distributions were based on the subjective visual and phenological segregation of individuals into two groups that were analysed separately; distributions of all characters except sheathing leaf number are normal if the two data sets are summated. Furthermore, F_1 progeny of dactylorchids may exhibit hybrid vigour and need not be morphologically intermediate between their parents. Any morphologically intermediate tetraploid hybrids would lie within the range of overlap of their parents and would be impossible to identify by their morphology or karyotypes. It is therefore not surprising that such hybrids are rarely recorded. We believe that gene flow between subspecies is at most only partially restricted, although an objective search for morphological discontinuities in mixed colonies is evidently required to test this hypothesis.

THE CONSPECIFICITY OF THE TETRAPLOID MARSH-ORCHIDS

Most botanists treat the British and Irish tetraploid marsh-orchids as four distinct species, whereas our results have shown that their specific status is not justified. Some previous workers also advocated their conspecificity. Pugsley (1935, 1936) originally described *D. majalis* subsp. *occidentalis* and subsp. *traunsteinerioides* as a variety and a subspecies respectively of *Orchis majalis* Reichenbach. Following a visit to Ireland, Hall (1937) concluded that *D. majalis* subsp. *occidentalis* var. *occidentalis* (Pugsley) Bateman & Denholm, subsp. *occidentalis* var. *kerryensis* (Wilmott) Bateman & Denholm and subsp. *traunsteinerioides* were conspecific. He also suggested that *D. majalis* subsp. *purpurella*, and subsp. *traunsteinerioides* var. *francis-drucei* and var. *eborensis* were probably subordinate taxa of *D. majalis*. Heslop-Harrison (1954) recognized four species (*D. majalis*, *D. purpurella*, *D. praetermissa* and *D. traunsteineri*) but commented that there was equal justification for reducing their status to subspecies of *D. majalis*. Sundermann (1975, 1980) regarded *D. majalis* subsp. *occidentalis* (which he included in subsp. *majalis*), subsp. *traunsteinerioides* (which he included in subsp. *traunsteineri*) and subsp. *purpurella* as subspecies of *D. majalis*, but placed subsp. *praetermissa* under *D. incarnata*. Amaral Franco & Moore (1978) and Soó (1980) relegated *D. majalis* subsp.

occidentalis, subsp. *purpurella* and subsp. *praetermissa* to subspecies of *D. majalis*, but treated *D. traunsteineri* (including *D. majalis* subsp. *traunsteinerioides*) as a separate species.

This nomenclatural instability and the subjective nature of many previous classifications may have prompted Dressler (1981) to state that some European orchid genera are too finely divided. Objective biometric studies should therefore be performed on several European dactylorchid 'species', e.g. *D. cordigera* (Fries) Soó, *D. baltica* (Klinge) Orlova, *D. russowii* (Klinge) Holub, *D. elata* (Poiret) Soó, *D. traunsteineri* (Sauter) Soó, and *D. sphagnicola* (Hopper) Soó. We doubt that many of these taxa are separated from other taxa by morphological discontinuities and believe that some may be subspecies or varieties of *D. majalis*.

CLASSIFICATION

The classification and diagnostic descriptions that follow are based on the principal coordinates (Figs. 3 & 4; Table 3), dendrogram (Fig. 5), and population means (Table 2). Data published by Heslop-Harrison (1953a), Lacey & Roberts (1958), Roberts (1961a, 1961b), and Roberts & Gilbert (1963), and unpublished data of N. R. Campbell (pers. comm. 1981) have also been considered. Three characters (22, basal bract length; 24, bract anthocyanin; 33, stem anthocyanin) made important contributions to principal coordinates but are as variable within subspecies as between subspecies and therefore are not diagnostic. The frequencies of character states in the taxa are given using the following terminology: rarely, <20%; occasionally, 20–50%; often, 51–80%; usually, >80%. Frequencies of the best diagnostic characters (italicized) show most discontinuity between subspecies.

Several varieties of *D. majalis* are of little value and are included in the classification for completeness only. The characters that distinguish *D. majalis* subsp. *occidentalis* var. *scotica* and subsp. *traunsteinerioides* var. *eborensis* and var. *francis-drucei* are probably the result of environmental rather than genetic influences. Other varieties are extremely rare; since their original discoveries in single localities, there have been no subsequent records of *D. majalis* subsp. *purpurella* var. *maculosa* (T. Stephenson) Bateman & Denholm, subsp. *praetermissa* var. *macrantha* (Sipkes) Bateman & Denholm, or subsp. *traunsteinerioides* var. *francis-drucei*. Further work may show that *D. majalis* subsp. *purpurella* var. *crassifolia* (T. Stephenson) Landwehr is identical with subsp. *occidentalis* var. *kerryensis*, and therefore superfluous. The inclusion of these varieties has necessitated the naming of a type variety for each subspecies that encompasses the residuum of variation within the subspecies as a whole. Varieties that have been defined using biometric data are indicated by asterisks. Brief descriptions of the remaining varieties are based on their original diagnoses.

Known synonyms are listed for all taxa.

Genus *Dactylorhiza* Necker ex Nevski, Acta Inst. bot. Acad. sci. URSS, **4**: 332 (1937)
Sect. *Maculatae* (Parlatore) Vermeulen, Stud. Dactyl. 65 (1947)

The four subspecies that follow have previously been assigned (as species) to three subsections: subsect. *Majales* (Pugsley) Vermeulen (*D. majalis* subsp. *occidentalis*, subsp. *purpurella*), subsect. *Subsesquipedales* (Pugsley) Vermeulen (*D. majalis* subsp. *praetermissa*), and subsect. *Angustifoliae* Vermeulen (*D. majalis* subsp. *traunsteinerioides*). Clearly, the subsections of *Dactylorhiza* require revision.

Dactylorhiza majalis (Reichenbach) P. F. Hunt & Summerhayes, Watsonia, **6**: 130 (1965)
Basionym: *Orchis majalis* Reichenbach, Pl. Crit., **6**: 7 (1828)
Synonym: *Dactylorchis majalis* (Reichenbach) Vermeulen, Stud. Dactyl. 67 (1947)

Stem 10–60 cm, 3–11 mm in diameter. Basal lf or sheath 1, broadest ± at middle; sheathing lvs 2–6, either ± evenly distributed up stem or somewhat crowded towards the base, upright or recurved, broadest below middle, largest 5–25×1–6 cm, ratio of width/length decreasing up stem, bright green

to dark greyish-green, hooding of tips usually absent or poorly-developed; non-sheathing lvs 1–3, narrow, broadest at base; lvs unmarked or with solid or annular spots on upper surface often concentrated towards tips. Inflorescence usually 2–12×2·5–4 cm, 10–35% of total stem length, usually with 6–60 fls, lax to dense (2–9 fls/cm). Basal bracts exceeding fls; floral bracts ± equalling fls, rarely spotted; bracts and/or upper part of stem often suffused with anthocyanin; peripheral bract cells 45–140μm long, barrel-shaped to triangular. Labellum usually broader than long, 6–10×7–14 mm, usually broadest ± at middle but occasionally above (obtriangular) or below (deltoid); base colour varying densities (reflectivity=9–50%, y=160–285, C.I.E. coordinates) of red-purple, purple, and violet-purple (x=290–330); markings pale to bold dots, dashes or loops, occasionally concentrated in the centre; sinuses poorly- to well-developed (labellum three-lobed), occasionally absent (labellum entire); central lobe equalling or exceeding lateral lobes; lateral lobes often indented, ± flat to strongly reflexed; lateral outer perianth segments slightly above horizontal to near vertical, often with solid or annular markings; upper outer perianth segment and inner perianth segments connivent; spur straight to slightly decurved, 6·5–10·5×2·5–5 mm at entrance, 2–4·5 mm halfway along (when flattened), usually slightly tapering, rarely cylindrical or sac-like. 2n=80. Flowering late May to early July. Locally frequent throughout the British Isles.

D. majalis is preferred to *D. latifolia* (L.) Soó, which has also been used as a synonym for *D. incarnata* (L.) Soó and *D. sambucina* (L.) Soó (Pugsley 1935; Vermeulen 1947, 1976) and is a *nomen rejiciendum* (Anon. 1975) endorsed by the 1975 Leningrad Conference. The type specimen of *Orchis latifolia* L. is not *D. majalis* and may be a hybrid of *D. incarnata* (Vermeulen 1976). *D. majalis* subsp. *majalis* does not occur in the British Isles.

a. Subsp. *occidentalis* (Pugsley) P. D. Sell, in Sell & Walters, Acta Fac. Rerum nat. Univ. comen., Bratisl., **14**: 19 (1968)
'Western Marsh-orchid'

Basionym: *Orchis majalis* Reichenbach var. *occidentalis* Pugsley, Bot. J. Linn. Soc., **49**: 586 (1935)

Synonyms: *O. majalis* Reichenbach subsp. *occidentalis* (Pugsley) Pugsley, Proc. Linn. Soc. Lond., **148**: 124 (1936)
O. occidentalis (Pugsley) Wilmott, in Campbell, Rep. botl Soc. Exch. Club Br. Isl., **11**: 551 (1937)
Dactylorchis occidentalis (Pugsley) Vermeulen, Stud. Dactyl. 67 (1947)
D. majalis (Reichenbach) Vermeulen subsp. *occidentalis* (Pugsley) Heslop-Harrison f., Ber. geobot. Forsch. Inst. Rübel, **1953**: 55 (1954)
Dactylorhiza latifolia (L.) Soó subsp. *occidentalis* (Pugsley) Soó, Nom. nov. gen. *Dactylorhiza* 5 (1962)

Stem rarely exceeding 30 cm, occasionally exceeding 5 mm in diameter. Sheathing lvs usually 4 or more, *often distinctly more crowded towards the base of the stem* (less evident in var. *cambrensis*), longest lf rarely over 12 cm long, widest lf usually more than 1·5 cm wide; non-sheathing lvs often 2; *lf markings usually present* (except var. *kerryensis*), occasionally annular (rarely predominant), often more than 2 mm in diameter, round or slightly transversely elongated, often concentrated towards lf tips. Inflorescence rarely over 7 cm long, often more than 20% of stem length, rarely lax (fewer than 3·5 fls/cm), often with more than 18 fls. Peripheral bract cells often over 80μm long. Labellum often more than 7·5×9·5 mm, usually broadest ± at middle; *base colour usually dark* (*reflectivity less than 15%*, except var. *kerryensis*); markings usually dashes and/or loops (except var. *kerryensis*), usually covering most of labellum; sinuses present (occasionally absent in var. *cambrensis*), poorly- to well-developed; central lobe occasionally exceeding lateral lobes by more than 1 mm; lateral lobes often indented, *usually reflexed*; lateral outer perianth segments often nearer horizontal than vertical, annular markings occasionally present; spur often less than 8·5 mm long, tapering. *Flowering late May to early June.* Locally frequent in central and western Ireland, rare in north-western Wales and western Scotland, possibly also Yorkshire.

D. majalis subsp. *occidentalis* has been given two vernacular names, 'Broad-leaved Marsh-orchid' (Dony *et al.* 1974) and 'Irish Marsh-orchid'. We propose that these are replaced by 'Western Marsh-orchid' as *D. majalis* subsp. *occidentalis* is neither especially broad-leaved nor exclusively Irish. *D. majalis* subsp. *majalis* is said to be more robust than subsp. *occidentalis* and to lack markings

in the centre of the labellum, but a detailed biometric study of subsp. *majalis* is desirable to determine their similarity. The generally-accepted link between the British and Irish *D. majalis* subsp. *occidentalis* and the Continental subsp. *majalis* remains unproven.

i. *Var. **occidentalis** (Pugsley) Bateman & Denholm, **comb. nov.**
Basionym: *Orchis majalis* Reichenbach var. *occidentalis* Pugsley, Bot. J. Linn. Soc., **49**: 586 (1935)

Stem usually exceeding 10 cm. Sheathing lvs usually 4 or more, often distinctly more crowded towards the base of the stem, widest lf usually over 1·5 cm wide; non-sheathing lvs often 2; lf markings usually present. Inflorescence often more than 20% of stem length. Bracts rarely spotted. Labellum often more than 7·5×9·5 mm; base colour usually dark (reflectivity less than 15%); markings usually dashes and/or loops; sinuses present; lateral lobes rarely ± flat; spur rarely exceeding 3·5 mm wide at entrance. Flowering late May to early June. Locally frequent in central and western Ireland.

ii. Var. **kerryensis** (Wilmott) Bateman & Denholm, **comb. nov.**
Basionym: *Orchis kerryensis* Wilmott, Proc. Linn. Soc. Lond., **148**: 126 (1936)
Synonyms: *O. occidentalis* (Pugsley) Wilmott subsp. *kerryensis* (Wilmott) Clapham, in Clapham *et al.*, Fl. Br. Isl. 1321 (1952)
Dactylorchis kerryensis (Wilmott) Vermeulen, Stud. Dactyl. 67 (1947)
Dactylorhiza latifolia (L.) Soó subsp. *occidentalis* (Pugsley) Soó var. *kerryensis* (Wilmott) Soó, Nom. nov. gen. *Dactylorhiza* 4 (1962)
D. kerryensis (Wilmott) P. F. Hunt & Summerhayes, Watsonia, **6**: 131 (1965)
D. majalis (Reichenbach) P. F. Hunt & Summerhayes subsp. *kerryensis* (Wilmott) Senghas, Jber. naturw. Ver. Wuppertal, **21–22**: 53 (1968)

Stem usually exceeding 10 cm. Sheathing lvs usually 4 or more, often distinctly more crowded towards the base of the stem, widest lf usually over 1·5 cm wide; non-sheathing lvs often 2; *lf markings absent.* Inflorescence often more than 20% of stem length. Bracts unspotted. Labellum often more than 7·5×9·5 mm; base colour only occasionally dark (reflectivity less than 15%); *markings dots and/or dashes*; sinuses present; *lateral lobes often ± flat*; spur rarely exceeding 3·5 mm wide at entrance. Flowering late May to June. Locally frequent in south-western and western Ireland.

iii. *Var. **cambrensis** (R. H. Roberts) Bateman & Denholm, **comb. et stat. nov.**
Basionym: *Dactylorchis majalis* (Reichenbach) Vermeulen subsp. *cambrensis* R. H. Roberts, Watsonia, **5**: 41 (1961)
Synonyms: *Dactylorhiza latifolia* (L.) Soó subsp. *cambrensis* (R. H. Roberts) Soó, Nom. nov. gen. *Dactylorhiza* 5 (1962)
D. majalis (Reichenbach) P. F. Hunt & Summerhayes subsp. *cambrensis* (R. H. Roberts) R. H. Roberts, Watsonia, **7**: 104 (1969)
D. purpurella (T & T. A. Stephenson) Soó subsp. *majaliformis* Nelson, Taxon, **28**: 593 (1979)

Stem usually exceeding 10 cm. Sheathing lvs usually 4 or more, *usually only slightly crowded towards the base of the stem*, widest lf usually over 1·5 cm wide; non-sheathing lvs often 2; lf markings usually present (often abundant). Inflorescence occasionally more than 20% of stem length. *Bracts often spotted.* Labellum occasionally more than 7·5×9·5 mm; base colour usually dark (reflectivity less than 15%); markings usually dashes and/or loops; sinuses occasionally absent; lateral lobes occasionally ± flat; *spur often more than 3·5 mm wide at entrance.* Flowering June. Local in north-western Wales, possibly also north-western Scotland and Yorkshire.

iv. Var. **scotica** (Nelson) Bateman & Denholm, **comb. et stat. nov.**
Basionym: *Dactylorhiza majalis* (Reichenbach) P. F. Hunt & Summerhayes subsp. *scotica* Nelson, Taxon, **28**: 593 (1979)

Stem only occasionally exceeding 10 cm. Sheathing lvs usually 2–3, often distinctly more crowded towards the base of the stem, *widest lf rarely more than 1·5 cm wide; non-sheathing lvs usually 1*; lf markings usually present (often abundant). Inflorescence often more than 20% of stem length. Bracts often spotted. *Labellum rarely more than 7·5×9·5 mm*; base colour usually dark (reflectivity less than 15%); markings usually dashes and/or loops; sinuses present; lateral lobes usually reflexed; spur rarely more than 3·5 mm wide at entrance. Flowering late May to June. Local in north-western (possibly also northern) Scotland.

The high frequency of individuals with leaf markings is one of the most distinctive features of *D. majalis* subsp. *occidentalis*. However, most populations contain a proportion of plants which lack leaf markings. These are often indiscriminately referred to var. *kerryensis*, despite the additional requirements for paler labella lacking loop markings in the original diagnosis of *Orchis kerryensis* (Wilmott 1936). *D. majalis* subsp. *occidentalis* var. *kerryensis* has occasionally been used incorrectly as a synonym for *D. majalis* subsp. *occidentalis* var. *occidentalis*, e.g. by Hunt & Summerhayes (1965, 1967) and Senghas (1968). It resembles *D. majalis* subsp. *purpurella* var. *crassifolia*, which may be sufficiently similar to be considered a synonym. Unfortunately we did not obtain measurements of either variety and therefore cannot prove their similarity. *D. majalis* subsp. *occidentalis* is also linked to *D. majalis* subsp. *purpurella* (especially 'form A') by *D. majalis* subsp. *occidentalis* var. *cambrensis*, which appears to be identical with *D. purpurella* subsp. *majaliformis* Nelson, described in detail by Nelson (1976). They show the unusual character of leaf markings that extend to the bracts (these are not mentioned in Nelson's original description of *D. purpurella* subsp. *majaliformis* but are shown in one of the figures in his Iconograph and in the line-drawing of Lojtnant (1979)), and we regard *D. purpurella* subsp. *majaliformis* as a synonym of *D. majalis* subsp. *occidentalis* var. *cambrensis*. The population of the latter that we examined had almost equal similarities to subsp. *occidentalis* var. *occidentalis* and subsp. *purpurella* (Fig. 5), but other populations in Anglesey and Cardigan more closely resemble subsp. *occidentalis* var. *occidentalis* (Roberts 1961b, 1962). Roberts (1961b) separated *D. majalis* subsp. *occidentalis* var. *cambrensis* from var. *occidentalis* primarily by the broader leaves and narrower spurs of the only population of var. *occidentalis* measured by Heslop-Harrison (1953a) in Co. Clare, Ireland. Unfortunately, this population was atypical of var. *occidentalis* in these characters. *D. majalis* subsp. *occidentalis* has also been reported from the Hebrides (Campbell 1937, Hall 1937, Harrison 1944), Orkney and Shetland (Pugsley 1935), Sutherland (Pugsley 1935, Hall 1937), and Caithness (Hall 1937). Nelson (1976) referred these Scottish populations to *D. majalis* subsp. *scotica* Nelson, a smaller plant with fewer leaves. We consider it to be a variety of *D. majalis* subsp. *occidentalis*.

b. Subsp. *purpurella* (T. & T. A. Stephenson) D. Moresby Moore & Soó, in Amaral Franco & Moore, Bot. J. Linn. Soc., **76**: 367 (1978)
'Northern Marsh-orchid'
Basionym: *Orchis purpurella* T. & T. A. Stephenson, J. Bot., Lond., **58**: 164 (1920)
Synonyms: *Dactylorchis purpurella* (T. & T. A. Stephenson) Vermeulen, Stud. Dactyl. 67 (1947)
Dactylorhiza purpurella (T. & T. A. Stephenson) Soó, Nom. nov. gen. *Dactylorhiza* 5 (1962)
D. majalis (Reichenbach) P. F. Hunt & Summerhayes prosp. *purpurella* (T. & T. A. Stephenson) Sundermann, Europ. mediterr. Orchideen 45 (1975)

Stem rarely exceeding 30 cm, often exceeding 5 mm in diameter. Sheathing lvs usually 4 or more, often slightly more crowded towards the base of the stem (especially var. *crassifolia*); longest lf occasionally more than 12 cm long, widest lf often more than 1·5 cm wide; non-sheathing lvs usually 1–2; lf markings occasionally present, not annular, usually *c.* 1 mm in diameter, usually round, often concentrated towards lf tips. Inflorescence rarely more than 7 cm, occasionally more than 20% of stem length, occasionally lax (fewer than 3·5 fls/cm), occasionally with over 18 fls. Peripheral bract cells often over 80μm long. Labellum occasionally more than 7·5×9·5 mm (except var. *crassifolia*), usually broadest at or above middle, *base colour usually dark (reflectivity less than 15%*, except var. *maculosa*); markings dashes and/or loops (except var. *pulchella*), covering most of labellum; sinuses absent or poorly-developed; central lobe occasionally exceeding side lobes by more than 1 mm;

lateral lobes occasionally indented, *usually* ± *flat*; lateral outer perianth segments often nearer vertical than horizontal, annular markings rarely present; spur often less than 8·5 mm long, tapering. *Flowering June to early July*. Locally frequent in Scotland, Ireland, northern and western Wales and northern England (also two adjacent localities in Hampshire).

i. *Var. **purpurella** (T. & T. A. Stephenson) Bateman & Denholm, **comb. nov.**
Basionym: *Orchis purpurella* T. & T. A. Stephenson, J. Bot., Lond., **58**: 164 (1920)

Sheathing lvs 4(−5), often slightly more crowded towards the base of the stem, widest lf rarely more than 3 cm wide; non-sheathing lvs 1–2; lf markings occasionally present, small, few. Labellum occasionally more than 7·5×9·5 mm; base colour usually dark (reflectivity less than 15%); markings dashes and/or loops; poorly-developed sinuses often present; lateral lobes occasionally indented. Occurs throughout the range of the subspecies.

ii. Var. *pulchella* (Druce) Soó, Nom. nov. gen. *Dactylorhiza* 5 (1962)
Basionym: *Orchis praetermissa* Druce var. *pulchella* Druce, Rep. botl Soc. Exch. Club Br. Isl., **5**: 577 (1920)
Synonym: *O. purpurella* T. & T. A. Stephenson var. *pulchella* (Druce) Pugsley, Bot. J. Linn. Soc., **49**: 583 (1935)

Sheathing lvs 4(−5), often slightly more crowded towards the base of the stem, widest lf rarely more than 3 cm wide; non-sheathing lvs 1–2; lf markings absent. Labellum occasionally more than 7·5×9·5 mm; base colour usually dark (reflectivity less than 15%); *markings often spots and/or dashes*; poorly-developed sinuses present; lateral lobes often indented. Scotland, possibly also northern Ireland.

iii. Var. **maculosa** (T. Stephenson) Bateman & Denholm, **comb. nov.**
Basionym: *Orchis purpurella* T. & T. A. Stephenson var. *maculosa* T. Stephenson, Rep. botl Soc. Exch. Club Br. Isl., **11**: 355 (1937)

Sheathing lvs 4(−5), often slightly more crowded towards the base of the stem, widest lf rarely more than 3 cm wide; non-sheathing lvs 1–2; *lf markings present*, small, *abundant*. Labellum occasionally more than 7·5×9·5 mm; *base colour only occasionally dark* (reflectivity less than 15%); markings dashes and/or loops; poorly-developed sinuses often present; lateral lobes occasionally indented. Rare, only reliably reported from south-eastern Scotland.

iv. Var. *crassifolia* (T. Stephenson) Landwehr, Orchideeën, **37**: 80 (1975)
Basionym: *Orchis purpurella* T. & T. A. Stephenson var. *crassifolia* T. Stephenson, Rep. botl Soc. Exch. Club Br. Isl., **11**: 356 (1937)

Sheathing lvs 5–6, often distinctly more crowded towards the base of the stem, widest lf often more than 3 cm wide; non-sheathing lvs 2–3; lf markings absent. *Labellum usually more than 7·5×9·5 mm*; base colour usually dark (reflectivity less than 15%); markings dashes and/or loops; poorly-developed sinuses often present; lateral lobes occasionally indented. Distribution includes Scotland, N. Wales and Ireland (not fully known).

Several 'subspecies' and varieties have been described that are morphological intermediates between *D. majalis* subsp. *purpurella* and subsp. *occidentalis* (Fig. 6). Stephenson & Stephenson (1920) recognized two 'forms': 'form A' (sinuses absent, labellum dark) and 'form B' (poorly-developed sinuses present, labellum often paler). *D. majalis* subsp. *purpurella* var. *pulchella* is more vigorous than subsp. *purpurella* 'form B' and has more broken labellum markings. *D. majalis* subsp. *purpurella* 'form B' and subsp. *purpurella* var. *pulchella* have affinities with both subsp. *occidentalis* and subsp. *praetermissa*. *D. majalis* subsp. *purpurella* 'form B' is linked by subsp. *purpurella* var. *crassifolia* to subsp. *occidentalis* var. *kerryensis*. Unfortunately the original description of var. *crassifolia* (Stephenson 1937) lacks detail, but does suggest that it is very similar to subsp. *occidentalis* var. *kerryensis*; indeed, it may more closely resemble subsp. *occidentalis* than

subsp. *purpurella*. *D. majalis* subsp. *purpurella* 'form A' is linked to subsp. *occidentalis* var. *cambrensis* by subsp. *purpurella* var. *maculosa*, which has leaves that are more heavily marked than those of var. *purpurella* (although leaf markings were included in the original diagnosis of *Orchis purpurella* (Stephenson & Stephenson 1920)). The affinities of *D. majalis* subsp. *majaliformis* are discussed under *D. majalis* subsp. *occidentalis*.

The Irish (Magilligan) population of *D. majalis* subsp. *purpurella* is similar to subsp. *occidentalis*, particularly var. *cambrensis*, in many characters (Table 2). Magilligan plants have fairly large labella with poorly- to well-developed sinuses, and leaves that are on average broader relative to their length than are those of any other of the populations of *D. majalis* subsp. *purpurella* that we measured. They differ from subsp. *occidentalis* only in their lower frequency of leaf markings, more-or-less flat labella, and later flowering period. We have seen very similar plants on Anglesey.

c. Subsp. *praetermissa* (Druce) D. Moresby Moore & Soó, in Amaral Franco & Moore, Bot. J. Linn. Soc., **76**: 367 (1978)
'Southern Marsh-orchid'
Basionym: *Orchis praetermissa* Druce, Rep. botl Exch. Club Br. Isl., **3**: 340 (1914)
Synonyms: *Dactylorchis praetermissa* (Druce) Vermeulen, Stud. Dactyl. 67 (1947)
Dactylorhiza praetermissa (Druce) Soó, Nom. nov. gen. *Dactlyorhiza* 5 (1962)
D. incarnata (L.) Soó prosp. *praetermissa* Sundermann, Europ. mediterr. Orchideen 45 (1975)

Stem often exceeding 30 cm, *usually exceeding 5 mm in diameter*. Sheathing lvs usually 4 or more, often slightly more crowded towards base of stem, *longest lf usually over 12 cm long, widest lf usually over 2 cm wide*; non-sheathing lvs often 2; leaf markings absent (except var. *junialis*). Inflorescence occasionally more than 7 cm long, occasionally more than 20% of stem length, rarely lax (fewer than 3·5 fls/cm), often with more than 18 fls. *Peripheral bract cells rarely more than 80μm long*. Labellum usually more than 7·5×9·5 mm, usually broadest ± at middle; *base colour only occasionally dark* (reflectivity less than 15%); markings often spots and/or dashes (except var. *junialis*), *often concentrated in central part of labellum*; sinuses usually present, poorly– to well-developed; central lobe occasionally exceeding lateral lobes by more than 1 mm (especially var. *macrantha*); lateral lobes rarely indented, *usually ± flat*; lateral outer perianth segments usually nearer vertical than horizontal, annular markings absent; spur usually less than 8·5 mm long, tapering. *Flowering June* (rarely early July). Locally frequent in southern and central England and in Wales.

Sundermann (1975, 1980) assigned *D. majalis* subsp. *praetermissa* to *D. incarnata*, apparently in the mistaken belief that they both have entire or shallowly three-lobed labella.

i. *Var. **praetermissa** (Druce) Bateman & Denholm, **comb. nov.**
Basionym: *Orchis praetermissa* Druce, Rep. botl Exch. Club Br. Isl., **3**: 340 (1914)

Lf markings absent. Inflorescence rarely lax (fewer than 3·5 fls/cm). Labellum usually more than 7·5×9·5 mm; markings often spots and/or dashes; central lobe occasionally exceeding lateral lobes by more than 1 mm. Occurs throughout the range of the subspecies.

ii. *Var. *junialis* (Vermeulen) Senghas, Jber. naturw. Ver. Wuppertal, **21–22**: 126 (1968)
Basionym: *Orchis latifolia* L. var. *junialis* Vermeulen, Ned. Kruidk. Archf., **43**: 404 (1933)
Synonyms: *O. pardalina* Pugsley, Bot. J. Linn. Soc., **49**: 581 (1935)
Dactylorchis praetermissa (Druce) Vermeulen var. *junialis* (Vermeulen) Vermeulen, Stud. Dactyl. 67 (1947)
Dactylorhiza praetermissa (Druce) Soó subsp. *junialis* (Vermeulen) Soó, Nom. nov. gen. *Dactylorhiza* 5 (1962)
D. majalis (Reichenbach) P. F. Hunt & Summerhayes subsp. *pardalina* (Pugsley) Nelson, Mon. Ikon. Orchidac. Gatt. *Dactylorhiza* 88 (1976)

Lf markings present (often abundant), usually large (more than 2 mm in diameter), transversely

elongated and predominantly annular. Inflorescence rarely lax (fewer than 3·5 fls/cm). Labellum usually more than 7·5×9·5 mm; *markings usually broad solid loops*; central lobe occasionally exceeding lateral lobes by more than 1 mm. Local in southern England, rare elsewhere.

iii. Var. **macrantha** (Sipkes) Bateman & Denholm, **comb. nov.**
Basionym: *Orchis praetermissa* Druce var. *macrantha* Sipkes, Levende Nat., **26**: 52 (1921)
Synonym: *Dactylorchis praetermissa* (Druce) Vermeulen var. *macrantha* (Sipkes) Vermeulen, Ned. kruidk. Archf., **56**: 229 (1949)

Lf markings absent. *Inflorescence often lax* (fewer than 3·5 fls/cm). *Labellum usually much more than 7·5×9·5 mm*; markings often spots and/or dashes; *central lobe exceeding lateral lobes by much more than 1 mm*. Rare (distribution unknown).

D. majalis subsp. *praetermissa* var. *junialis* resembles var. *praetermissa* in dimensions and habit but has distinctive annular leaf markings and bolder labellum markings. It was first described by Vermeulen (1933) as a Dutch variety of '*Orchis latifolia*', but was later elevated to a subspecies of *Dactylorhiza praetermissa* (Soó 1960, 1962). However, some Continental botanists continued to believe that *junialis* was a variety of *O. majalis* when that name superseded *O. latifolia*. The same morphological type was named *O. pardalina* in Britain (Pugsley 1935), a name that was subsequently adopted by many botanists (e.g. Summerhayes 1951) in preference to *junialis*, which has precedence at subspecific and varietal level. This nomenclatural confusion was further compounded by Ettlinger (1976) who incorrectly differentiated between 'f. *pardalina*', with annular leaf markings, and 'f *junialis*', with solid leaf markings (the latter are usually hybrids with the spotted-orchids). Soó (1980) made a similar error, correctly referring *junialis* to *D. majalis* subsp. *praetermissa* but attributing *pardalina* to only *D. majalis sensu lato* in the index of *Flora Europaea*. Finally, Sussex specimens of *D. majalis* subsp. *praetermissa* with leaf markings were inexplicably referred to subsp. *occidentalis* by Hall (1980), who misquoted *O. pardalina* as a synonym and *Flora Europaea* as a guideline.

Vermeulen (1949) claimed that *D. majalis* subsp. *praetermissa* var. *macrantha* occurs in Britain but did not specify its localities. There are no subsequent records.

d. Subsp. **traunsteinerioides** (Pugsley) Bateman & Denholm, **comb. nov.**
'Pugsley's Marsh-orchid'
Basionym: *Orchis majalis* Reichenbach subsp. *Traunsteinerioides* Pugsley, Proc. Linn. Soc. Lond., **148**: 124 (1936)
Synonyms: *O. Traunsteinerioides* (Pugsley) Pugsley, J. Bot., Lond., **78**: 179 (1940)
Dactylorchis traunsteinerioides (Pugsley) Vermeulen, Stud. Dactyl. 66 (1947)
Dactylorhiza traunsteineri (Sauter) Soó subsp. *traunsteinerioides* (Pugsley) Soó, Nom. nov. gen. *Dactylorhiza* 6 (1962)
D. traunsteinerioides (Pugsley) Landwehr, Orchideeën, **37**: 80 (1975)
D. traunsteineri (Sauter) Soó subsp. *hibernica* Landwehr, Orchideeën, **37**: 79 (1975)

Stem only occasionally exceeding 30 cm, *rarely exceeding 5 mm in diameter. Sheathing lvs usually fewer than 4, often ± evenly distributed along stem*, largest lf rarely more than 12 cm long, widest lf occasionally more than 1·5 cm wide; non-sheathing lvs usually 1; lf markings occasionally present (except var. *francis-drucei*), not annular (except var. *eborensis*), usually less than 2 mm in diameter, round or slightly transversely elongated, usually concentrated towards lf tips. Inflorescence rarely more than 7 cm long, occasionally more than 20% of stem length, *usually lax* (fewer than 3·5 fls/cm), rarely with more than 18 fls. Peripheral bract cells usually more than 80μm long. Labellum usually more than 7·5×9·5 mm (except var. *eborensis* and var. *francis-drucei*), *often broadest below middle; base colour only occasionally dark* (reflectivity less than 15%), markings often dashes and/or loops, usually covering most of labellum; sinuses usually present, poorly- to well-developed; central lobe often exceeding lateral lobes by more than 1 mm (especially var. *francis-drucei*); lateral lobes occasionally indented, *usually reflexed*; lateral outer perianth segments usually nearer vertical than horizontal, annular markings rarely present; spur occasionally less than 8·5 mm long (especially var. *eborensis*), often tapering, occasionally cylindrical, rarely sac-like (wider halfway along than at

entrance). *Flowering late May to early June.* Local in Ireland, N. Wales and northern and eastern England; rare elsewhere in the British Isles.

Heslop-Harrison (1953a) critically examined this taxon and tentatively assigned British and Irish plants to the Continental *Orchis traunsteineri* Sauter (now *Dactylorhiza traunsteineri* (Sauter) Soó), but accepted that biometric investigation of Alpine plants was desirable. Comparison of data on British and Irish populations collected by Heslop-Harrison (1953a), Lacey & Roberts (1958), Roberts & Gilbert (1963), Roberts (1966) and ourselves with the descriptions of Alpine plants of Vermeulen (1949) and Nelson (1976) reveals several discrepancies. True Alpine *D. traunsteineri* is reported to have narrower leaves (less than 1 cm wide), longer, more lax inflorescences, smaller labella with poorly-developed sinuses, shorter central lobes, and smaller spurs. They also flower later. The supposed British and Irish *D. traunsteineri* show morphological overlap with *D. majalis* subsp. *praetermissa* and subsp. *occidentalis*; they are clearly allied to *D. majalis*. We therefore support the original subspecific status accorded to *D. majalis* subsp. *traunsteinerioides* by Pugsley (1936), and suggest 'Pugsley's Marsh-orchid' as its vernacular name. We also recommend that biometric measurements should be taken from Alpine populations of *D. traunsteineri* to quantify their differences from *D. majalis* subsp. *traunsteinerioides*.

i. *Var. **traunsteinerioides** (Pugsley) Bateman & Denholm, **comb. nov.**
Basionym: *Orchis majalis* subsp. *Traunsteinerioides* Pugsley, Proc. Linn. Soc. Lond., **148**: 124 (1936)

Stem usually exceeding 15 cm. Longest sheathing lf usually more than 7 cm long; markings occasionally present, solid. Inflorescence often with more than 8 fls. Labellum usually more than 7·5×9·5 mm, broader than long; base colour only occasionally dark (reflectivity less than 15%); central lobe often exceeding lateral lobes by more than 1 mm; spur occasionally less than 8·5 mm long. Occurs throughout the range of the subspecies.

ii. Var. **eborensis** (Godfery) Bateman & Denholm, **comb. nov.**
Basionym: *Orchis latifolia* L. var. *eborensis* Godfery, Mon. Icon. Br. nat. Orchidaceae 219 (1933)
Synonym: *O. majalis* Reichenbach subsp. *traunsteinerioides* Pugsley var. *eborensis* (Godfery) Pugsley, J. Bot., Lond., **77**: 54 (1939)

Stem rarely exceeding 15 cm. Longest sheathing lf usually more than 7 cm long; *markings present, often annular.* Inflorescence often with more than 8 fls. *Labellum rarely more than 7·5×9·5 mm, usually ± as broad as long*; base colour only occasionally dark (reflectivity less than 15%); central lobe occasionally exceeding lateral lobes by more than 1 mm; *spur usually less than 8·5 mm long.* Rare, only recorded from Yorkshire.

iii. Var. **francis-drucei** (Wilmott) Bateman & Denholm, **comb. et stat. nov.**
Basionym: *Orchis Francis-Drucei* Wilmott, Proc. Linn. Soc. Lond., **148**: 129 (1936)
Synonym: *Dactylorhiza traunsteineri* (Sauter) Soó subsp. *francis-drucei* (Wilmott) Soó, Nom. nov. gen. *Dactylorhiza* 6 (1962)

Stem rarely exceeding 15 cm. Longest sheathing lf rarely more than 7 cm long; unmarked. Inflorescence rarely with more than 8 fls. Labellum rarely more than 7·5×9·5 mm, often longer than broad; base colour relatively pale (reflectivity more than 15%); *central lobe exceeding lateral lobes by much more than 1 mm; spur less than 8·5 mm long.* Only recorded from near Loch Maree, W. Ross, v.c. 105; possibly extinct.

D. majalis subsp. *traunsteinerioides* var. *eborensis* is essentially a very local dwarf variant of var. *traunsteinerioides*, smaller in all its parts, although it is unusual in frequently having annular leaf markings. It was described from Helmsley, Yorkshire, by Godfery (1933). Roberts & Gilbert (1963) and Tennant (1979) have shown that other Yorkshire populations are morphologically variable but generally closer to Pugsley's type variety. *D. majalis* subsp. *traunsteinerioides* var. *francis-drucei* is also a dwarf variant of var. *traunsteinerioides*, with less anthocyanin in the labellum and reduced lateral lobes. It has not been recorded since its discovery near Loch Maree, W. Ross, by A. J. Wilmott in 1935 (Wilmott 1936).

Landwehr (1975) described *D. traunsteineri* subsp. *hibernica* Landwehr from Scraw Bog, Co. Westmeath. His diagnosis is generalized and applicable to some individuals in most populations of *D. majalis* subsp. *traunsteinerioides*; *D. traunsteineri* subsp. *hibernica* is therefore a worthless taxon. However, the Irish (Pollardstown) population appears to be sufficiently dissimilar from the Anglesey populations studied to warrant subspecific status (Fig. 5). Pollardstown plants are distinguished from other populations of subsp. *traunsteinerioides* by the following characters (Table 2):

Leaves occasionally crowded towards base of stem and recurved; leaf markings more frequent. Base colour of labellum redder (x more than 315); labellum markings less distinct, usually concentrated in centre of labellum; labellum more often broader below middle; lateral lobes occasionally very reflexed; spur decurved. Upper part of stem usually heavily suffused with anthocyanin.

Evidence of the constancy of the above characters in other Irish populations is required before they can be designated as additonal subspecies of *D. majalis*. Our field observations, together with data presented by Heslop-Harrison (1953a), suggest that the majority of Irish populations of *D. majalis* subsp. *traunsteinerioides* are morphologically closer than Pollardstown plants to Welsh populations.

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